

EPIPHYTE–GRAZER INTERACTIONS ON *ZOSTERA MARINA* (ANTHOPHYTA: MONOCOTYLEDONES): EFFECTS OF DENSITY ON COMMUNITY FUNCTION¹

Timothy A. Nelson²

Department of Botany, University of Washington, Seattle, Washington 98195

ABSTRACT

Interactions between algal epiphytes and their grazers can have a significant impact on the structure and function of eelgrass (*Zostera marina* L.) meadows. In Puget Sound, the herbivorous gastropod *Lacuna variegata* Carpenter and its congeners appear to remove large quantities of the epiphytic community from eelgrass blades. When snails at typical field densities were used in microcosms, *Lacuna* significantly reduced epiphytic biomass and areal productivity. Biomass-specific productivity of the epiphytic community showed an increasing trend with increasing snail density. Epiphytic productivity increased nonlinearly with increasing epiphytic biomass. The commonly used logistic population growth formula adequately described this relationship. Grazing rate also increased nonlinearly with increasing epiphytic biomass. The Holling equation adequately described the relationship between grazing rate and epiphytic biomass. The proportion of the epiphytic biomass found on the oldest blade of an eelgrass shoot was related linearly to epiphytic biomass, suggesting that a constant fraction of the epiphytic community is lost regardless of epiphytic density. *Lacuna* clearly removed large quantities of epiphytic material from eelgrass blades, significantly altering community function. Modified Lotka–Volterra equations, incorporating the logistic growth form and Holling grazing equation, should prove useful in modeling the epiphyte–grazer interaction.

Key index words: biomass; diatoms; grazing; *Lacuna*; models; productivity

Seagrass communities are of vital importance as both habitat and food for numerous economically important and rare or endangered species (McRoy and Helfferich 1977, Phillips and McRoy 1980). The epiphytic community on eelgrass (*Zostera marina* L.) and other seagrasses is diverse and highly productive (Borum and Wiium-Andersen 1980). The interactions between algal epiphytes and their grazers are critical components of the seagrass ecosystem. Whereas the contribution of epiphytic production to total system productivity can be large, epiphytes are capable of overgrowing their host. Grazers may prevent epiphytic overgrowth, thus increasing host fitness by increasing light or nutrients (including HCO_3^-) available to the host (Orth and van Montfrans 1984, van Montfrans et al. 1984, Hootsmans and Vermaat 1985, Howard and Short 1986, Dudley 1992, Neckles et al. 1993, Jernakoff et al. 1996). In

subtidal seagrass meadows of the Pacific Northwest coast of the United States, the herbivorous gastropod *Lacuna variegata* Carpenter and its congeners appear to be important grazers of epiphytic algae (Nelson 1995).

This study considers whether the interaction between algal epiphytes and *Lacuna* can be modeled with a variation of the Lotka–Volterra predator–prey equations. To demonstrate that *Lacuna* has a significant impact on epiphytes, the effect of three densities of *Lacuna* on epiphyte biomass and productivity was measured. This study then tests several common functional forms for grazing and epiphytic productivity terms of the model with respect to changes in the density of epiphytes and grazers. The fit of the various forms is evaluated by examining the coefficient of determination (r^2) and residual analyses of regression models. Predicted values for maximum grazing rate, maximum epiphytic productivity, and epiphytic carrying capacity under the alternative forms are evaluated for consistency with biologically meaningful values. If one of the alternative forms of the modeling terms fails to fit the data well or produces biologically unrealistic parameter values, the form is rejected.

The following modified Lotka–Volterra equations are proposed to describe the interaction between algal epiphytes and grazers in seagrass meadows:

$$\begin{aligned} \delta E / \delta t = & r_e E (1 - E / K_e) \\ & - \tau EG / (E + \alpha) - d_e E \end{aligned} \quad (1a)$$

and

$$\delta G / \delta t = -r_g G + \tau \Phi EG / (E + \alpha) \quad (1b)$$

where E is the biomass of epiphytes, G is the biomass of grazers, t is time, r_e is epiphytic productivity per unit biomass, K_e is the carrying capacity for epiphytes, τ is the maximum feeding rate per unit grazer biomass, α is the biomass of epiphytes at which the feeding rate is $1/2$ the maximum, d_e is the proportion of epiphytic biomass lost due to leaf sloughing, r_g is the rate at which biomass is lost in the absence of food, and Φ is grazer assimilation efficiency.

Biomass, rather than the number of individuals, is used to quantify both state variables (E and G). Individual snails and epiphytes can appear in a range of sizes and, at least for epiphytes, shapes. The model assumes that biomass represents a “typical” combination of shapes and sizes. Although this may be unrealistic, it seems more realistic than equating individuals of vastly different sizes and shapes. Wootton and Power (1993:1386) point out that measur-

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² Present address: Department of Biology, Seattle Pacific University, Seattle, Washington 98119.

ing biomass is advantageous because it puts "the dynamics of all trophic levels on similar scales" and "account[s] for changes due to storage and growth as well as demographic processes." Settlement of algae on eelgrass and of the planktonic larval stage of the grazer is ignored by this model. However, the contribution of such settlement to biomass or productivity is probably minimal (Borum 1987). This model treats all epiphytic algae as being equivalent. This simplification is necessary to facilitate model evaluation, but may not be realistic. For example, the grazer may prefer one species over another, although the grazer of interest in this study will eat all available epiphytic algal species. Some authors have demonstrated food preferences among grazers of epiphytes (Jernakoff et al. 1996), but other analyses indicate that algal composition does not significantly affect grazing rates (Cattaneo and Mousseau 1995).

The functional form of each of the model's terms will be evaluated. The first term in equation (1a) is the commonly used Verhulst-Pearl logistic equation (reviewed in Pielou 1969, May 1973) used to describe productivity. Alternative forms are listed in Table 1A and are considered. The second terms in both equations (1a) and (1b) describe grazing and are equivalent if assimilation efficiency is constant regardless of the density of epiphytes or snails. The functional form of the grazing term (the second term in equations [1a] and [1b]) is from Holling (1959, 1966). Alternative forms are listed in Table 1B and are also tested. The third term in (1a) implies that the rate of epiphytic loss due to leaf sloughing is a fixed portion of the epiphytic biomass, regardless of the density of epiphytes or grazers. If the rate at which leaves are sloughed is constant, then the rate of epiphytic loss is simply the sloughing rate multiplied by the fraction of the community found on the oldest (and thus next to be sloughed) leaf in a shoot. There is no *a priori* reason to expect that this fraction is constant over a variety of epiphytic and snail biomasses, as the modeling equations assume, so the effect of the density of epiphytes and grazers on the portion of the epiphytic community on the oldest leaf is evaluated. There may be times when the rate of leaf sloughing is not constant (e.g. very low irradiance conditions [Backman and Barilotti 1976] or at the time of a shift in production from "winter leaves" to "summer leaves" and *vice versa* [Phillips 1972]). Therefore, the general scope of this model will be limited to conditions under which the rate of loss of eelgrass leaves is more or less constant.

MATERIALS AND METHODS

Effects of Lacuna density on epiphytic community function. The effect of three snail densities (0, 5, and 10 snails $[10 \text{ cm eelgrass}]^{-1}$) on epiphytic community function was tested in microcosms containing the snails and one 10-cm length of eelgrass leaf. The maximum density tested (1 snail $[\text{cm eelgrass}]^{-1}$) is the highest natural density observed in the field and is found only on the distal,

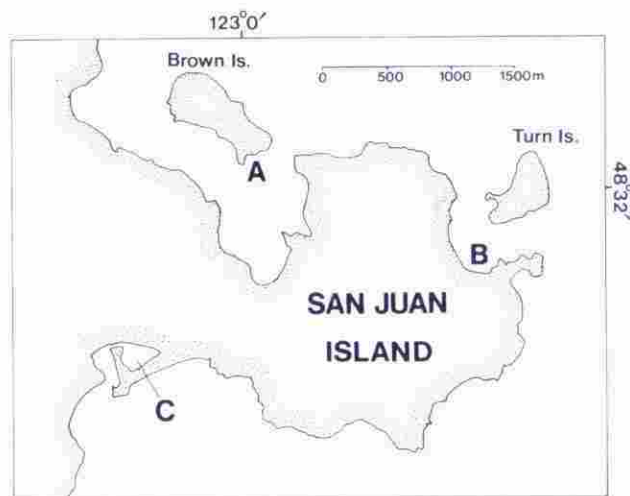


FIG. 1. Site maps. A and B mark the location of the subtidal eelgrass meadows at Brown Island and Turn Cove, respectively. The meadow at Argyle Lagoon (C) is cut off from open water by a tidal stream; thus, it is perpetually under 0.5–1 m water.

most heavily epiphytized portion of the blade. Microcosms were used in this study because *Lacuna* is too small to be included or excluded by caging. Any cage with a mesh size small enough to contain *Lacuna* will greatly reduce water flow and light around the host eelgrass plant and the epiphytic community.

Specimens were collected from the vicinity of Friday Harbor Laboratories, San Juan Island, Washington, U.S.A. Heavily epiphytized eelgrass shoots (selected for high apparent epiphytic biomass) were collected from a subtidal (ca. -1.5 m MLLW) meadow in Turn Cove (Fig. 1, $48^{\circ}32' \text{ N}$, $122^{\circ}58' \text{ W}$) on 5 August 1988. The epiphytic community consisted almost entirely of diatoms. One 10-cm segment was cut from the distal region of the oldest leaf on each shoot. Only segments with no brown or necrotic spots were selected. Specimens of *Lacuna variegata* were collected from a dense population found along a transect line through a subtidal eelgrass meadow near Brown Island in Friday Harbor (Fig. 1, $48^{\circ}32' \text{ N}$, $122^{\circ}59' \text{ W}$). Every snail seen along the line was collected. Snails and epiphytes were collected from different sites because there were virtually no epiphytes at the Brown Island site and an insufficient number of snails at the Turn Cove site.

Blade segments and snails were incubated for 10–12 days in 20 replicate 500-mL Erlenmeyer flasks per snail density (60 total microcosms). The flasks were capped with Nyltex screen and set up as flow-through systems. Unfiltered seawater was pumped into each flask, via Tygon tubing penetrating the screen cap, and flowed out through the screen. The volume of the flask was turned over ~ 150 times per hour. The flasks were submerged in a clear plexiglass sea table and left outdoors. The photoperiod was approximately 14:10 h LD. The sea table was exposed to unfiltered sunlight at $1800\text{--}2200 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at noon each day (based on the observations of T.A.N. for the same site and season during other years). Water temperature was maintained at 12° C by the flowing seawater.

Following the incubation period and productivity measurements (described below), epiphytic biomass on the blades was measured as dry mass and chlorophyll *a*. One side of each eelgrass segment was cleaned with a glass microscope slide onto preweighed filter paper (9 cm Whatman #1). Filter paper and epiphytes were dried to constant weight. One-half of the other side was cleaned with a small piece of filter paper. Chlorophyll *a* was extracted from this filter paper in 10 mL of 90% acetone, and the Chl *a* content was calculated based on light absorbance at 630, 664, and 730 nm (Lobban 1988).

Productivity was determined by measuring photosynthesis using an oxygen electrode (YSI model 5720a probe, YSI model 58 meter, Yellow Springs Instruments, Yellow Springs, Ohio) in 300-mL

biological oxygen demand (BOD) bottles (Wheaton, Millville, New Jersey) at 12°C. Eelgrass segments (with the epiphytic community intact) were mounted through slits in short segments of fiber optic strands to keep them upright. All photosynthetic measurements were made with measured photon flux densities of 1250 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Measurements were carried out in BOD bottles placed in a temperature-controlled aquarium for ~1 h at a fixed distance from a light source to provide constant photon flux density and temperature (12°C). Prior to productivity measurements on experimental organisms, photosynthesis versus photon flux density curves were determined for eelgrass segments with the epiphytic community intact and removed. Photosynthesis was saturated at 500 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and was not photo-inhibited at 1500 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for both eelgrass and epiphytes.

The reduction in light reaching the eelgrass blade was estimated by scraping a given mass of epiphytes onto a glass slide and comparing absorbance of a clean slide with treated slides. Scraping with a glass slide removed virtually all of the epiphytic community. The area of the glass slide over which the epiphytes were spread was at most equal to the area from which they had been removed. Even with epiphytic biomasses much higher (up to 6 times) than those observed in this portion of the study, a photon flux density of 1250 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ reaching the epiphytic community was sufficient to photosynthetically light-saturate the underlying blade.

Posttreatment productivity of the eelgrass segment with and without attached epiphytes was determined. Productivity of the epiphytic community was then calculated as the difference between the two measurements. This calculation assumes that the productivity of the eelgrass segment was the same with and without epiphytes. Light reduction has been ruled out as a factor reducing eelgrass productivity in the presence of epiphytes. However, algal epiphytes may limit eelgrass productivity by reducing HCO_3^- availability. Vigorous mixing of the seawater in the BOD bottles should have prevented depletion of HCO_3^- in the water adjacent to the blade. Oxygen evolution is not usually used as a method of measuring eelgrass photosynthesis because of the presence of gases stored in the plant's aerenchyma tissues. In this case, however, the leaf segments had been submerged for at least 10 days, the aerenchyma tissue appeared completely flooded, and no gases were trapped in the tissue.

Analysis of variance (ANOVA) was used to test for differences between mean biomass and productivity at the three snail densities. If significant differences ($\alpha = 0.05$) were found, Ryan's Q multiple comparison test was used to distinguish specific treatment means (Day and Quinn 1989). If no significant difference was found, the power of the test (i.e., the probability of not failing to reject a false hypothesis) was calculated.

Productivity of epiphytes at different epiphytic densities. To test the functional form of the first term in equation (1a), the effect of biomass on productivity in intact epiphytic communities was examined. The eelgrass segments collected from the microcosms described earlier provided measures of productivity for epiphytic communities at a variety of densities (mean ± 1 SD is 0.0411 ± 0.0454 g dry weight [gdw]·[10 cm eelgrass] $^{-1}$, $N = 56$). Four replicates with no detectable biomass following treatment in the microcosms were removed from this analysis.

The models listed in Table 1A were evaluated for fit (r^2), normality of error terms, and constancy and random distribution of variance. The exponential model assumes that productivity is proportional to biomass and is evaluated via linear regression. The proposed logistic model can be converted to a multiple linear regression model as:

$$P = r_e E - (r_e/K_e)E^2 \quad (2)$$

All other models were fit using nonlinear regression (Gauss-Newton method, Neter et al. 1983). Normality of error terms was evaluated for all models using D'Agostino's test (Zar 1984). Homogeneity of variance was evaluated by Spearman's rank correlation (Zar 1984) performed on both the actual and absolute values of residuals versus epiphytic biomass. A "runs" test was per-

TABLE 1. Alternative forms of model terms.

Model	Form
A. Epiphyte growth models	
Logistic (Pielou 1969, May 1973)	$P = r_e E(1 - E/K_e)$
Exponential (Lotka 1925)	$P = r_e E$
Smith (1963)	$P = r_e E(K_e - E)/(K_e + \epsilon E)$
Schoener (1972)	$P = r_e E[(K_e/E) - 1]$
Gompertz (1825)	$P = (r_e E) \ln(K_e/E)$
B. Grazing rate models	
Holling (1959, 1966)	$F = \tau E/(E + \alpha)$
Takahashi (1964)	$F = \tau E^2/(E^2 + \alpha^2)$
Constant	$F = \tau$
Linear (Lotka 1925)	$F = aE$
Rosenzweig (1971)	$F = aE^2$
Iyev (1961)	$F = \tau[1 - \exp(-cE)]$
Watt I (1959)	$F = \tau[1 - \exp(-cHG^{1-b})]$
Watt II (1959)	$F = \tau[1 - \exp(-cHG^{1-b})]$

formed on the residuals to determine if they were randomly distributed (Neter et al. 1983).

Grazing rate at various epiphytic densities. The models described in Table 1B were tested by measuring the feeding rate of *Lacuna variegata* in response to a varying density of epiphytes. Snails were collected from the Brown Island site on 11 August 1992. Ten snails were placed in 20 replicate 500-mL polystyrene cell culture flasks (Sigma Scientific Products, St. Louis, Missouri) (mean ± 1 SD = 0.113 gdw ± 0.0195 gdw snails per microcosm, $N = 20$). Five 10 cm sections of eelgrass blades were placed in each microcosm. Air was pumped into the medium via Tygon tubing passed through a hole drilled in the top of the flask. Care was taken to provide a variety of epiphytic densities among microcosms. Average epiphytic biomass per microcosm was 0.165 ± 0.194 gdw, $N = 20$, calculated by adding the quantity consumed by snails (see below) to the remaining epiphytic biomass at the end of the treatment. Microcosms were incubated for approximately 24 h at 11°C (the temperature of the seawater in which the snails were collected). Following incubation, the snails, eelgrass, epiphytes, and snail feces were removed, dried to constant weight, and incinerated. The mass of food consumed was calculated based on the quantity of feces produced and the ash content of the feces and food as follows:

$$\text{food consumed} = (\text{ash content of feces}) \times (\text{weight of feces}) \times (\text{ash content of food})^{-1} \quad (3)$$

Each model was then fit to the data using linear or nonlinear least-squares regression and was evaluated for fit, normality of error terms, and homogeneity and random distribution of variance using the methods described previously.

The range of snail biomass was limited. This is trivial when testing most models, because most assume that the grazing rate is proportional to grazer biomass. However, feeding rate per unit of grazer biomass decreases as snail biomass increases in Watt's (1959) models. Thus, while these models may seem appropriate for the range of snail biomasses tested, they may fail at higher or lower biomasses.

The models tested for the second term in equation (1a) are also appropriate for the second term in equation (1b) if assimilation efficiency is not related to the density of epiphytes or snails. The procedure described provides the ash content of the epiphytes and feces. The assimilation efficiency can be calculated (following Parsons et al. 1988) as:

$$\text{assimilation efficiency} = 1 - [(\text{epiphyte ash content}) \times (\text{fecal ash content})^{-1}] \quad (4)$$

Assimilation efficiency was regressed against the biomass of snails and epiphytes (separately) to test for potential correlation.

Proportion of the epiphytic community on the oldest leaf at various densities of epiphytes and snails. To test for relationships between epiphyte or snail density and the proportion of the epiphytic com-

TABLE 2. Effects of snail density on measures of eelgrass and epiphyte community function.

Community function	Snail density ^a (snails per microcosm)		
	0	5	10
Epiphyte areal production *** (mg O ₂ ·h ⁻¹ ·[10 cm eelgrass] ⁻¹)	1.66 ± 1.33	0.745 ± 0.741	0.242 ± 0.287
Epiphyte biomass-specific production (NS) (mg O ₂ ·h ⁻¹ ·[gdw epiphytes] ⁻¹)	51.6 ± 89.7	63.3 ± 170	63.1 ± 131
<i>Zostera</i> productivity NS (mg O ₂ ·h ⁻¹ ·[10 cm] ⁻¹)	0.126 ± 0.176	0.160 ± 0.139	0.186 ± 0.123
Epiphyte biomass (mg dry weight·[10 cm eelgrass] ⁻¹)***	75.3 ± 55.2	36.6 ± 30.3	11.3 ± 15.7
(µg Chl <i>a</i> ·[10 cm eelgrass] ⁻¹)***	162 ± 127	60.4 ± 82.3	10.9 ± 16.4

^a Values are treatment means ± 1 SD, with N = 20. *, **, and *** indicate that treatment means differed significantly across all treatment levels at P = 0.05, 0.01, and 0.001, respectively. NS indicates that treatment means are not significantly different. In all cases where treatment means differed significantly, the 5- and 10-snail treatments were not significantly different from each other, but the 0-snail treatment was significantly different than treatments with snails.

munity on the oldest leaf of a shoot, eelgrass shoots were collected from Argyle Lagoon, San Juan Island, Washington (Fig. 1, 48°31' N, 123°01' W) and the Brown Island site, At Argyle Lagoon, grazers were markedly absent and the heavy epiphytic load was composed primarily of diatoms. The Brown Island site had abundant gastropod grazers (*Lacuna vincta* Montague and *L. variegata*) and less epiphytic cover. Epiphytes were removed from 20 shoots collected randomly along a transect parallel to the long axis of the eelgrass meadow at each site. The epiphytic community was first scraped off the oldest blade with a microscope slide onto a piece of preweighed filter paper. This treatment removes virtually all epiphytes, including tightly-adhering diatom species (e.g. *Cocconeis scutellum*). The age structure of the blades can be determined because *Zostera* produces alternate new leaves at the center of the shoot. This procedure was repeated for the remaining blades. The samples were dried to constant weight. The averages of the portion of epiphytic biomass on the oldest blade at each site were compared with Student's *t*-test on square root arcsine-transformed data (where $x' = \arcsin \sqrt{x}$, Zar 1984) to examine the effect of snail abundance. The proportion on the oldest blade was regressed on total epiphytic biomass per shoot (following the transformation of data) to test for any effect of epiphytic density.

RESULTS

Effects of Lacuna density on epiphytic community function. The presence of snails at low and high densities significantly altered epiphytic biomass in microcosms ($F_{2,56} = 14.51$, $P < 0.001$). Mean epiphytic dry weight was 62% and 94% lower in low and high snail density treatments, respectively (Table 2). Mean biomass measured as Chl *a* was 49% and 84% lower, respectively, in the low and high snail density treatments ($F_{2,56} = 15.13$, $P < 0.001$). The two treatments with snails were not significantly different from each other but had significantly lower epiphytic biomass than the ungrazed treatment (Table 2).

Epiphytic productivity decreased significantly with increasing snail density ($F_{2,56} = 12.78$, $P < 0.001$; Table 2). Mean biomass-specific productivity, however, tended to increase with the presence of grazers (Table 2). Although this trend was not significant ($F_{2,56} = 0.046$, $P > 0.50$), the power of the test was very low (<30%).

Mean light-saturated photosynthesis of the *Zostera* leaf segment beneath the epiphytic community tended to increase with increasing snail biomass

(Table 2). Again, this trend was not significant ($F_{2,56} = 0.820$, $P > 0.50$), but the power was low (<30%). Following the ~10 day incubation period, segments from the grazed treatments were greener and had fewer necrotic regions than segments from the ungrazed treatments.

Productivity of epiphytes at different epiphytic densities. Epiphytic productivity increased with increasing epiphytic biomass, although biomass-specific productivity tended to drop as biomass increased (Fig. 2). The logistic, exponential, Smith (1963), and Gompertz (1825) growth models performed equally well based on fit and residual analyses (Fig. 2, Table 3, $r^2 = 55\%$ for all). Schoener's (1972) form did not fit these data as well ($r^2 = 37\%$). Residuals were randomly distributed for all models except Schoener's (1972) model ($P = 0.0002$). Residuals were not normally distributed in the exponential model ($0.02 \geq P \geq 0.01$) and Schoener's (1972) model ($P \leq 0.01$). In all models tested, there was a trend for increasing variance of residuals with increasing epiphytic biomass (Fig. 2, Table 3). This pattern suggests that the models may be inappropriate or that samples were drawn from a multimodal population or separate populations.

For the models that fit the data best and had appropriately distributed residuals, predicted values for r_c varied from 5.68 ± 2.51 mg O₂·(gdw epiphytes)⁻¹·h⁻¹ using Smith's (1963) model to 27.1 ± 6.24 mg O₂·(gdw epiphytes)⁻¹·h⁻¹ using Gompertz's model (1825) (N = 56 for all means ± standard deviations, see Table 4). Using the proposed logistic model, r_c was 24.1 ± 3.77 mg O₂·(gdw epiphytes)⁻¹·h⁻¹ and the predicted carrying capacity (K_c) was 0.429 ± 0.205 gdw·(10 cm eelgrass)⁻¹. This value was 2.5 times greater than the maximum epiphytic biomass and 10.5 times greater than the average epiphytic biomass observed on the tested eelgrass segments. Predicted carrying capacities were even higher for Gompertz's (1825) model (2.29 ± 3.11 gdw·[10 cm eelgrass]⁻¹) and Smith's (1963) model (1405 ± 921 gdw·[10 cm eelgrass]⁻¹) (N = 56 for all means ± standard deviation, see Table 4).

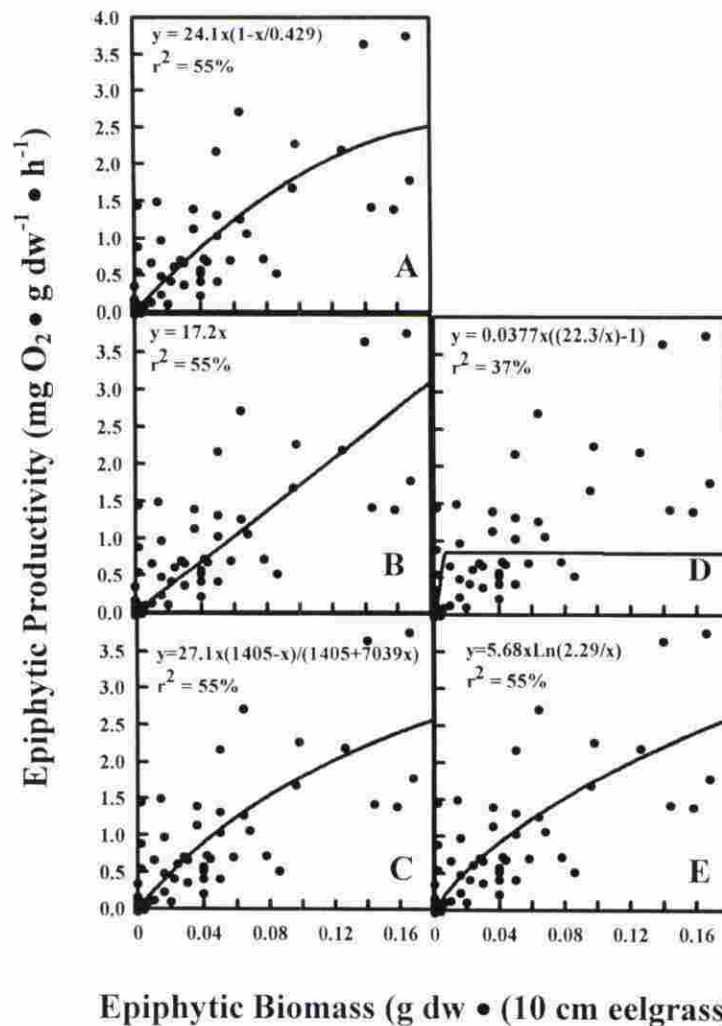


FIG. 2. Plot of epiphytic photosynthesis versus biomass. Lines in A-E represent fits based on the A) logistic (Pielou 1969, May 1973), B) exponential (Lotka 1925), C) Smith (1963), D) Schoener (1972), and E) Gompertz (1825) models.

Grazing rate at various epiphytic densities. Grazing rate increased with increasing epiphyte biomass. If feeding rate were constant over various epiphytic densities, then the regression coefficient of a linear regression of feeding rate on epiphytic biomass would be zero (Fig. 3). The data indicate that this coefficient is significantly greater than zero ($t = 4.63$, d.f. = 18, $P < 0.0005$). The linear model, however, does not provide a satisfactory fit to the data ($r^2 = 38\%$), and the residuals are not distributed normally ($P < 0.05$). Watt's (1959) second-model form also shows a worse fit than the other models considered ($r^2 = 62\%$), and residuals show a trend toward heterogeneity of variance ($P \approx 0.08$). Least-squares regression indicates the value of the parameter b in this model is negative and thus out of the intended and biologically meaningful bounds of this model. All of the other models showed reasonable fits to the data (Fig. 3, Table 3; $68\% \leq r^2 \leq 73\%$). The Holling (1966) model had the highest r^2 value. The absolute values of the residuals demonstrated a

trend toward heteroscedasticity ($P \approx 0.09$) under the Takahashi (1964) model, and the signed values of the residuals showed a similar trend ($P \approx 0.09$) under the Rosenzweig (1971) model.

The three models that are most appropriate (Holling 1966, Ivlev 1961, and Watt's first model [1959]) predict that feeding rate will increase with increasing epiphytic biomass until some maximum rate (τ) is reached. The predicted value of τ for these models ranges from 0.250 ± 0.024 gdw consumed \cdot (gdw snails) $^{-1} \cdot d^{-1}$ under Watt's (1959) first model to 0.301 ± 0.037 gdw consumed \cdot (gdw snails) $^{-1} \cdot d^{-1}$ under the Holling (1966) model (Table 5). The Holling (1966) model explicitly employs a half-saturation constant (α) indicating the epiphytic density at which the feeding rate is expected to be half the maximum rate. An equivalent value can be calculated from the other two models being considered. For the Watt (1959) form, a value for grazer biomass must be known. For comparative purposes, that value will be assumed to be the mean

TABLE 3. Summary of fit and appropriateness of alternative model forms for epiphyte growth and grazing.^a

Model	Fit (r^2)	Constancy of variance			
		(Absolute values)	(Signed values)	Normality	Randomness
Epiphyte growth models					
Logistic (May 1973)	55%	***	*	NS	NS
Exponential (Lotka 1925)	55%	***	NS	*	NS
Smith (1963)	55%	**	*	NS	NS
Schoener (1972)	37%	***	***	**	***
Gompertz (1825)	55%	***	*	NS	NS
Grazing models					
Holling (1959, 1966)	73%	NS	NS	NS	NS
Takahashi (1964)	68%	B	NS	NS	NS
Linear (Lotka 1925)	0%	NS	NS	*	NS
Rosenzweig (1971)	68%	NS	B	NS	NS
Iyev (1961)	72%	NS	NS	NS	NS
Watt I (1959)	72%	NS	NS	NS	NS
Watt II (1959)	62%	B	NS	NS	NS

*, **, and *** indicate departures from the null hypothesis of a given test at $P = 0.05$, 0.01, and 0.001, respectively. B indicates borderline cases ($0.1 > P > 0.05$). NS indicates no significant departure from the null hypothesis ($P < 0.1$).

grazer biomass used in this study, 0.113 gdw. Because of this assumption, a standard deviation cannot be calculated for this form. The calculated half-saturation constants varied from 0.0649 gdw epiphytes under Watt's (1959) first model to 0.0880 ± 0.0298 gdw epiphytes under the Holling (1966) model.

The assimilation efficiency observed averaged 37.1% of the total food ingested and did not appear to vary predictably with either snail ($r^2 = 1.1\%$, $F_{15,1,0.05} = 0.96$, $P = 0.343$) or epiphytic biomass ($r^2 = 3.6\%$, $F_{15,1,0.05} = 0.59$, $P = 0.454$) (Fig. 4). Because the diatomaceous diet of the snail has an extremely high ash content (55%), the assimilation efficiency appears low. The assimilation efficiency of organic matter averaged 70%.

Proportion of the epiphytic community on the oldest leaf at various densities of epiphytes and snails. Despite differences in epiphyte and snail biomass at Brown Island and Argyle Lagoon, the proportion of the epiphytic community on the oldest leaf of a shoot was similar for the two sites. Total epiphytic biomass was greater at Argyle Lagoon, averaging 0.545 ± 0.282 gdw-shoot⁻¹, than at Brown Island, which averaged 0.351 ± 0.330 gdw-shoot⁻¹ ($N = 20$ for both sites, $t = -2.00$, d.f. = 37, $P = 0.053$). Shoots at Argyle Lagoon and Brown Island had 52.9% and 47.2%, respectively, of the epiphytic community on the oldest leaf. There was not a significant difference between the average proportion of the epiphytic community on the oldest leaf at the two sites ($t = 1.12$, d.f. = 34, $P = 0.27$). The variance in the proportion of the epiphytic community on the oldest leaf, although higher at the Argyle Lagoon site (0.018 at Brown Island vs. 0.033 at Argyle Lagoon), was not

TABLE 4. Estimated parameter values for epiphyte growth models.^a

Model	Intrinsic growth rate r_1 (mg O ₂ gdw ⁻¹ h ⁻¹)	Carrying capacity K (gdw)
Logistic (May 1973)	24.1 ± 3.77	0.429 ± 0.205
Exponential (Lotka 1925)	17.2 ± 1.33	NA
Smith (1963)	27.1 ± 6.23	1405 ± 921
Schoener (1972)	0.0377 ± 2.54	22.3 ± 1416
Gompertz (1825)	5.68 ± 2.51	2.29 ± 3.11

^aAll values are means \pm 1 SD with a sample size of $N = 56$. NA indicates a parameter that was not used in the model.

significantly different ($F = 1.85$, d.f. = 19, 19, $P \approx 0.200$) between the sites.

The proposed linear relationship between epiphytic biomass on the oldest leaf and epiphytic biomass appears appropriate (Fig. 5, $r^2 = 88\%$). The proportion of the epiphytic community on the oldest leaf is not affected by total epiphytic biomass. Regression of the proportion of the epiphytic community on the oldest leaf on the total epiphytic biomass per shoot showed no pattern at the Brown Island site. The slope of the line was not significantly different from zero ($t = 0.72$, d.f. = 18, $P = 0.478$), and the regression explained almost none of the variance in the dependent variable ($r^2 = 0.281\%$). At the Argyle Lagoon site, the regression also failed to explain the majority of the variance ($r^2 = 20.5\%$), but the slope was significantly different than zero (slope = 0.215, $t = -2.15$, d.f. = 18, $P = 0.045$). However, three of the data points had much higher epiphytic biomasses than the others, which gave them inordinate influence on the regression results. If these three points are removed, the slope of the best-fit line is not significantly different from zero ($t = -1.39$, d.f. = 15, $P = 0.186$, $r^2 = 11.4\%$). Because the mean and variance are not significantly different for the two sites, the data were combined. Using this combined data set, no correlation between epiphytic biomass and the proportion of the epiphytic community on the oldest leaf could be detected ($t = -0.07$, d.f. = 15, $P = 0.944$, $r^2 = 0.00\%$).

DISCUSSION

Effects of Lacuna density on epiphytic community function. That snails in the genus *Lacuna* can reduce epiphytic biomass is suggested by the observation that, in meadows with abundant snails (Brown Island in August 1988 and August 1992), the epiphytic fouling of eelgrass blades appeared minimal (Nelson 1995). Two meadows that lacked *Lacuna* (Turn Cove in 1988 and Argyle Lagoon in 1992) had large quantities of epiphytes (Nelson 1995, see also King 1965). This site-specific difference occurs over a relatively small geographic scale (no two study sites were more than 1.5 km apart). The data presented from microcosm studies support the hypothesis that high densities of *Lacuna variegata* can dramatically reduce epiphytic biomass.

Several species of mesograzers are reported to in-

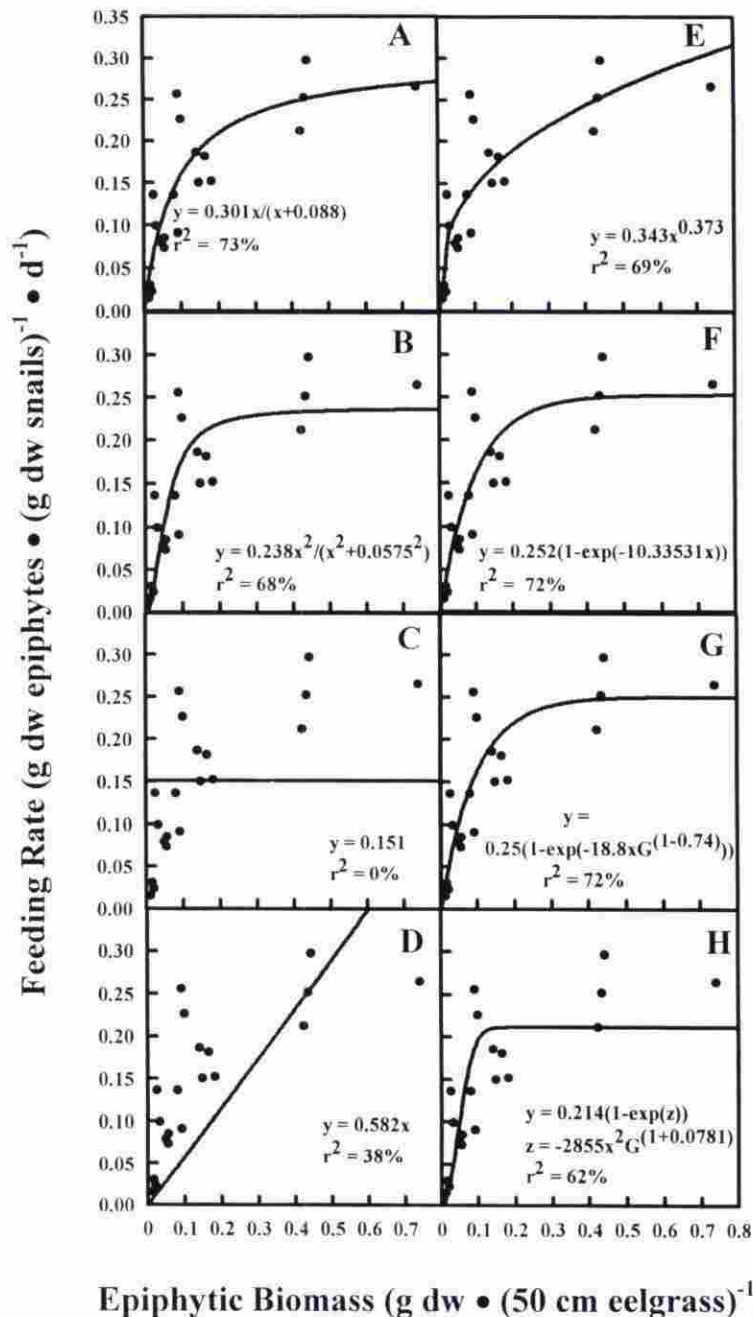


FIG. 3. Plot of grazing rate versus epiphyte biomass. Lines in A-H represent fits based on the A) Holling (1959, 1966), B) Takahashi (1964), C) constant grazing rate, D) linear (Lotka 1925), E) Rosenzweig (1971), F) Ivlev (1961), and G & H) Wait (1959) models.

crease *Zostera marina* growth by reducing epiphytic biomass (reviewed in Jernakoff et al. 1996). If algal epiphytes have a net negative effect on the growth of subtidal eelgrass, as suggested in the literature (reviewed in Harlin 1980, Orth and van Montfrans 1984, van Montfrans et al. 1984, Jernakoff et al. 1996), then *L. variegata* should indirectly increase the fitness of *Z. marina*. A large epiphytic load is thought to accelerate senescence in seagrass blades (Bulthuis and Woelkerling 1983). The presence of a large quantity of epiphytes in the treatment with

no grazers may account for the loss of eelgrass productivity and the necrotic appearance of the blade segments in this treatment. Although not statistically significant, this loss of productivity is an enduring result of the presence of epiphytes: the epiphytic community was removed prior to measuring the photosynthetic capability of the blade. The eelgrass segments appeared to be degraded permanently by the presence of a dense epiphytic community in this treatment.

The observed pattern of an increase in the epi-

TABLE 5. Estimated parameter values for snail grazing models.^a

Model	Maximum grazing rate (τ or a) (gdw·gdw ⁻¹ ·d ⁻¹)	Half saturation constant (α or equivalent) (gdw)
Holling (1959, 1966)	0.301 ± 0.037	0.0880 ± 0.0298
Takahashi (1964)	0.238 ± 0.022	0.0575 ± 0.0120
Linear (Lotka 1925)	0.582 ± 0.085	NA
Rosenzweig (1971)	0.343 ± 0.041	NA
Ivlev (1961)	0.252 ± 0.024	0.0670 ± 0.02099
Watt I (1959)	0.250 ± 0.024	0.0649
Watt II (1959)	0.214 ± 0.018	0.00392

^aAll values are means ± 1 SD with a sample size of N = 20. NA indicates a parameter that was not used in the model.

phytic biomass-specific productivity and a decrease in areal productivity with increased grazing activity is consistent with the model's assumption that there will be reduced competition at lower epiphytic biomass and that this increase cannot make up for the effect of the missing biomass on areal productivity. Similarly, Rosemond et al. (1993) found that high levels of grazing by snails reduced both biomass and areal productivity in stream periphyton. In contrast, Power (1990) noted that "moderate" levels of grazing by armored catfish increased stream periphyton areal and biomass-specific productivity by increasing light availability. High grazing levels, however, reduced both measures of productivity.

Productivity of epiphytes at different epiphytic densities. Two of the tested models can be ruled out due to poor fit or lack of normality in the residuals (Schoener's [1972] form and the exponential form). Of the three remaining models, the logistic model provides a minor improvement in r^2 (55.3% vs. 55.0%) over the exponential and Gompertz (1825) models, although the difference appears trivial. All models were flawed in that variance tended to increase with increasing biomass. This is not unexpected: errors

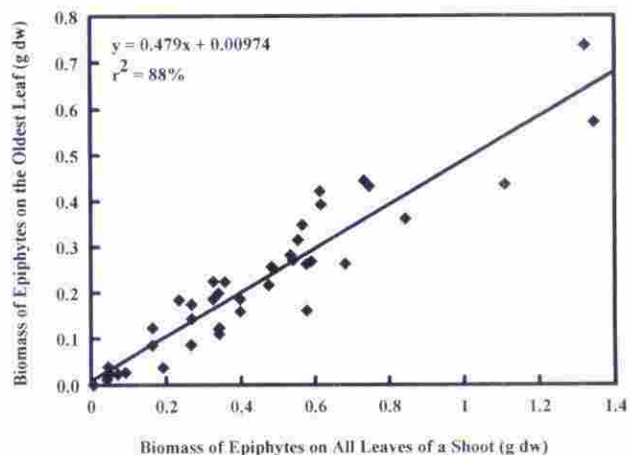


FIG. 5. The linear relationship between epiphytic biomass on the oldest leaf of an eelgrass shoot versus total epiphytic biomass per shoot can be seen in this figure.

in predicting productivity based on a function of biomass might reasonably be expected to increase as biomass increases.

Smith's (1963) model, although fitting the data well, results in biologically unfeasible parameter values. It makes an unrealistic prediction that the carrying capacity of epiphytes on a 10-cm segment of eelgrass is 1405 gdw. During the 2 years a local meadow was monitored, the maximum epiphytic biomass was less than 200 gdw·m⁻² (Nelson 1995, Nelson and Waaland 1997). Thus only Gompertz's (1825) model and the logistic model remain as the best fits explored here. The predicted carrying capacity under Gompertz's model is improbably high. Because the logistic form is also commonly used to model population growth rates (May 1973), it seems the more reasonable choice.

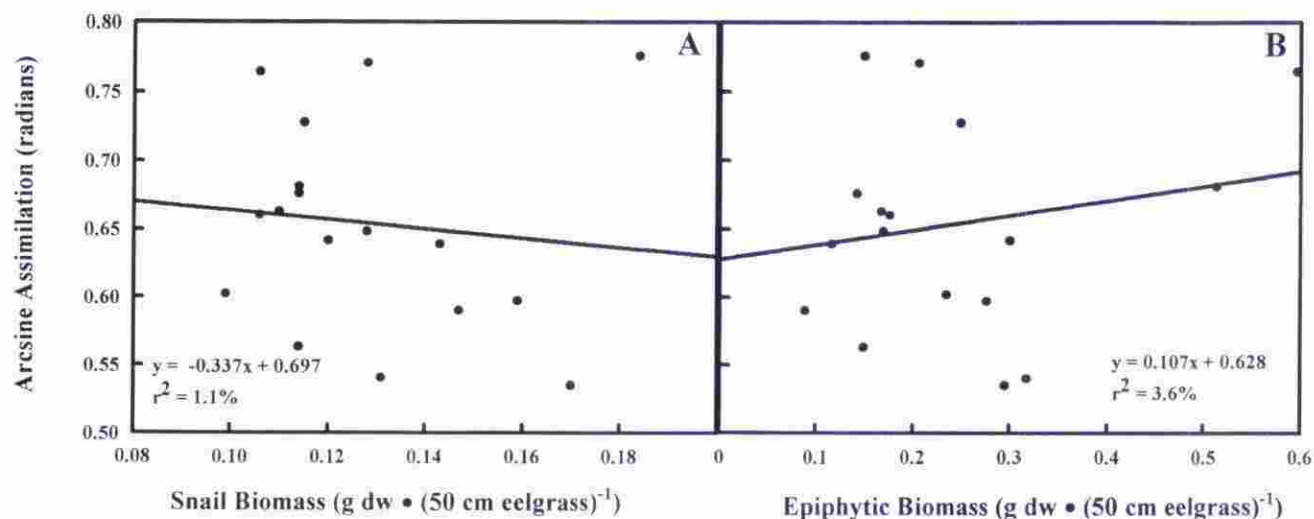


FIG. 4. Plot of assimilation efficiency versus snail biomass (A) and epiphytic biomass (B). The quantity of ingested material assimilated by the snails does not vary predictably with either epiphytic biomass or snail biomass. (Assimilation efficiency data were arcsine-transformed prior to the analysis.)

The measure of productivity used in this study is light-saturated photosynthesis. The usefulness of light-saturated photosynthesis as an estimate of overall productivity can be argued. At less than saturating photon flux densities, the higher Chl *a* content seen in high biomass communities might be advantageous, leading to higher productivity. However, epiphytic biomass appears to respond more to changes in the quantity of time spent under light-saturated conditions than to changes in photon flux density (Nelson and Waaland 1997).

Grazing rate at various epiphytic densities. The analyses of snail grazing rate versus epiphytic availability demonstrate that grazing rate increases initially with increasing epiphytic density, asymptotically approaching some saturation rate. Based on poor fit and residual analysis, five models can be ruled out (constant, linear, Takahashi [1964], Rosenzweig [1971], Watt's second model [1959]). The Holling (1966) equation provides the best fit to the data. However, the Ivlev (1961) form and Watts' first model (1959) should not be rejected out of hand, because they provide a reasonable fit and are supported by examination of the residuals. The Holling (1966) form is used more commonly than alternative forms (May 1973) and is easier to interpret biologically than the two other forms that the data support.

Cattaneo and Mousseau (1995) have demonstrated that grazing rate increases with increasing food density for a wide variety of freshwater periphyton grazers, although they note that crowding can decrease the grazing rate. Power (1992) similarly notes that the Holling (1966) and related forms will be inappropriate if predators employ interference competition when crowded. *Lacuna* does not appear to employ overt interference competition: when resources are limiting, individuals will remove periphyton from the shells of other snails without obvious aggression. Power (1992) provides several other conditions under which the proposed grazing term would be inappropriate: 1) if predators compete for resources other than food, 2) if predators cause prey to hide or become better defended, or 3) if there is a time lag for predator response. The first two possibilities are unlikely for snails of the genus *Lacuna* and their algal prey. There may be a time lag for the predator population to respond, because the life cycle of the snail includes a planktonic veliger stage. However, eggs are laid throughout most of the year, and a ready supply of veligers is always at hand. The exception might be in late winter and early spring, prior to observed spring epiphytic blooms (King 1965, Nelson 1995), when eggs are not always laid. Because assimilation efficiency appears to be constant over changes in epiphytic biomass or snail biomass, the same functional form can be used for grazing terms in both model equations (1a) and (1b).

Proportion of the epiphytic community on the oldest leaf at various densities of epiphytes and snails. Harlin

(1980) notes that leaf sloughing and grazing are mechanisms that reduce the epiphytic load on eelgrass blades. Because the presence or absence of snails had no effect on the proportion of the epiphytic community on the oldest leaf, it appears that *Lacuna* density does not influence the effectiveness of eelgrass sloughing as a means of removing epiphytes. This also suggests that the sloughing term used in the mathematical model should be independent of grazer biomass. Similarly, the data indicate that epiphytic biomass does not affect the proportion of the epiphytic community on the oldest leaf. However, the biomass of epiphytes or grazers may influence the rate at which eelgrass leaves are sloughed. Further research is necessary to address this question.

Conclusions. Grazing snails in the genus *Lacuna* are critical to the productivity and biomass of epiphytes and eelgrass. They are capable of removing large quantities of epiphytes at densities well below their maximum observed field density, which reduces not only epiphytic biomass, but areal productivity as well. Biomass-specific productivity may increase with increasing grazer density, as competition within the epiphytic community is reduced. The host plant appears healthier in the presence of the snails.

The model proposed to describe the interaction between epiphytes and grazers is the most promising of all tested models. Although not all alternative forms can be ruled out definitively, the form proposed in equations (1a) and (1b) provides the best fit under the conditions tested. This model may not be appropriate at times when high epiphytic biomass increases the sloughing rate of eelgrass leaves or for snail densities much higher or lower than the range considered here. Grazers may remove periphyton by mechanisms other than ingestion (e.g. "bulldozing") (Cattaneo and Mousseau 1995). If such removal is significant, and if it does not follow the same functional form as ingestion, then the model should be altered to account for this activity. The precision of predictions of epiphytic productivity decreases with increasing epiphytic biomass in most of the models tested. Although data transformations (e.g. log transforms) may remove this problem from the statistical analysis, the inability to predict epiphytic productivity precisely will still be problematic.

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