Model parameterization for the growth of three submerged aquatic macrophytes

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ABSTRACT

The development of an aquatic community can reflect the anthropogenic influence on adjacent areas of a freshwater system. The understanding of growth rates of a key species is useful for planning management activities. In this study, we used a kinetics model to evaluate growth of three submerged macrophytes: Brazilian elodea (*Egeria densa* Planch.), narrowleaf elodea (*Egeria najas* Planch.), and coontail (*Ceratophyllum demersum* L.) under laboratory conditions that simulate the *in situ* condition in a Neotropical, constructed lake ecosystem (Jupiá Reservoir, Brazil). Incubations were prepared with healthy apical tips of Brazilian elodea, narrowleaf elodea, and coontail ($n = 40$; 5.0 cm long) in 40 polystyrene pots filled with sediment from the reservoir. A set of 10 pots were placed in a glass tank with 6.5 L of water from the reservoir. The fitting of the data indicated that the growth of macrophytes exhibited an average doubling time (t_d) between 11.6 (Brazilian elodea) and 23.9 d (coontail) and yields varied between 8.6 ($\equiv$ 52.9 mg; Brazilian elodea) and 19.6 cm ($\equiv$ 217.8 mg; coontail). The growth parameters suggest that these plants have a close niche; however, in Neotropical aquatic systems, these species coexist and compete with other native and aliens submerged species. The floating genus can also present a t_d with the same order of magnitude as that presented by *Egeria* and *Ceratophyllum*. In this case, the floating plants have an advantage in that light is not a limiting factor nor is the shadowing effect that is imposed on submerged species.

Key words: aquatic plants, growth model, Neotropical reservoir, vegetative reproduction.

INTRODUCTION

Aquatic macrophytes appear in seven plant divisions that are widespread in the major biogeography areas, with the largest species diversity in the Neotropical region (Chambers et al. 2008). Their ability to adapt in both morphological and physiological characteristics allowed these plants to develop distinct ecological types (i.e., as floating, emergent, or submerged life forms), with the macrophyte assemblage being distributed according to several factors, such as

environmental factors and biological interactions. The growth of submerged macrophytes, for instance, is regulated by such factors as the substrate grain size (Li et al. 2012), the dissolved inorganic carbon available (James 2008, Freitas and Thomaz 2011), the subsurface irradiance (Dale 1986, Rørslett and Johansen 1995, Zhu et al. 2008), the concentrations of nutrients such as phosphorous and nitrogen (Madsen and Cedergreen 2002, Zhu et al. 2008), the interaction with other organisms (Ozimek et al. 1991), and the colonization depth (Middelboe and Markager 1997, Caffrey et al. 2007).

Although many factors affect the growth of aquatic macrophytes, during summer in temperate regions and in all seasons in the tropics, such plants usually present doubling times (t_d) ranging typically from days (e.g., 3.1 d; Vermaat and Hanif 1998) to weeks (e.g., 17.1 d; Téllez et al. 2008), depending on the aquatic system trophic status, displaying a great potential to generate large populations and, consequently, interfering in the multiple uses of freshwater systems (Dodds et al. 2009).

In artificial reservoirs, ponds situated within floodplains, and lakes, the littoral regions are usually colonized by different species of macrophytes with distinct ecological types (Thomaz et al. 2008), depending on the (1) topography, (2) hydraulic regime (water level, flow, velocity), (3) light intensity, (4) action of wind (speed and direction), (5) temperature, and (6) availability of nutrients (water and sediment) (Chambers et al. 2008, Sousa et al. 2009, Freitas and Thomaz 2011, Martins et al. 2013). In such environments, the macrophytes often exhibit high productivity (Best et al. 2001), which means that after senescence, they become important autochthonous sources of detritus (Murray and Hodson 1986), mediating the transfer of carbon and nutrients for heterotrophic community (Pieczynska 1993, Cronin et al. 1998) and mediating the processes related to diagenesis (Mitsch and Gosselink 1993; Reddy and DeLaune 2008).

In addition to natural forcing functions, anthropogenic influence is also relevant for aquatic communities (Martins et al. 2013); therefore, understanding growth rates of a key species, including aquatic plants, is useful for environmental management planning. The approach based on modeling experimental data allows for testing hypotheses about strategies of macrophyte growth, which may elucidate ecological trends in a particular environment (Straškraba 1973). It also facilitates comparison of growth and decomposition processes in ecosystems. Indeed, growth coefficients for macrophytes can be used to describe colonization dynamics in ecosystems. Furthermore, mathematic model-

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ing may have general applicability to other aquatic environments, thus contributing significantly to the decisions of macrophyte control (Hu et al. 1998). In this context, contrary to the empirical procedures usually adopted to control the incidence of aquatic plants (e.g., harvest time frame or harvest until a specific cover ratio or some biomass yield) or to schedule their eradication, using the growth rate constant (or the t_d of macrophyte growth) makes it possible to derive more precisely the harvest frequency or the temporal function of removing biomass to reach a desired goal (Mahujchariyawong and Ikeda 2001).

Macrophyte growth models are valuable tools to improve the understanding of macrophyte responses to anthropogenic stressors with parameterization being used to predict future states (Best et al. 2001). In this study, we investigate the growth of three submerged macrophytes under laboratory conditions simulating the *in situ* condition in which these plants occur in a Neotropical, constructed lake ecosystem. We also compare the potential expansion of these macrophytes using the parameterization of growth process, namely, the daily growth rates, number of vegetative budding, yields, and growth rate constants. Our hypothesis is that the native Neotropical species (*Egeria*) that occurs in South American reservoirs present under the experimental conditions, have a greater growth performance than do similar cosmopolitan species (*Ceratophyllum*) because of their greater adaptive value.

MATERIALS AND METHODS

Sampling area

The construction of Engineer Souza Dias Hydroelectric Power Plant (Jupiá) was completed in 1974. It is located on the Paraná River, between the cities of Andradina and Castilho (São Paulo State) and Três Lagoas (Mato Grosso do Sul State), Brazil (20°50′S; 51°43′W).

Besides the Paraná River, the reservoir has as tributaries the Tietê and Sucuriú rivers. During normal operation (280 m above sea level), the reservoir has an area of 330 km² with an accumulated water volume of $3,680 \times 10^6$ m³, a total length in the longitudinal axis of 54.95 km, an average width of 6.0 km, a mean residence time of 6.9 d, a mean depth of 11.2 m, and is 20.0 m at maximum depth. It is classified as a tropical system, with medium anthropogenic pressures and a small (10^6 to 10^8 km²) to medium (10^2–10^4 km²) and rapidly flowing through system (i.e., retention time less than 2 wks; Straškraba 1999). In addition to the large occurrence of southern cattail (*Typha domingensis* Pers.), the reservoir presents major infestations of submersed aquatic plants, such as Brazilian elodea (*Egeria densa* Planch.), narrowleaf elodea (*Egeria najas* Planch.), and coontail (*Ceratophyllum demersum* L.) along the dammed stretch of the river Tietê and in areas of the Paraná River with higher water transparency (Velini et al. 2005).

During the past 3 yr—August 2010 to May 2012; quarterly sampling at 4 sites: (1) 20°24′44.6″S; 51°22′51.2″W; (2) 20°36′01.6″S; 51°51′09.5″W; (3) 20°41′33.0″S; 51°23′14.3″W; (4) 20°45′25.4″S; 51°38′11.3″W; and 3 depths: (1) surface, (2) middle, and (3) bottom—the reservoir had a large variation in total phosphorus concentrations (minimum: 5 µg L⁻¹; maximum: 187 µg L⁻¹) and was classified as mesotrophic (average concentration: 25.3 µg L⁻¹) according to Vollenweider (1968) and Companhia Energética de São Paulo (unpub. data). The annual variation in water temperature ranged from 20.0 C (August 2010) to 29.8 C (November 2011). According to limnological assessments performed by CESP between 2010 and 2012, this reservoir had high concentrations of dissolved oxygen (average ± SD: 6.8 ± 1.1 mg L⁻¹), with an average water pH and electric conductivity of 7.41 ± 0.95 and 53.2 ± 31.9 µS cm⁻¹, respectively. The turbidity was usually low (3.0 ± 2.5 nephelometric turbidity units [NTU]) and the average water transparency, as measured by Secchi disk, was 4.3 ± 1.9 m. The alkalinity concentrations varied from 12 (August 2011) to 45 mg L⁻¹ (May 2012). The average concentrations of total solids and total organic nitrogen were, respectively, 2.3 mg L⁻¹ and 135 µg L⁻¹, and inorganics were the most prevalent form of solid (approximately 86%). On average, the sediments contained 1.3% of organic matter, and the sand fraction (70%) prevailed over silt (18%) and clay (12%) fractions.

Sampling procedures and experimental design

To determine the growth patterns of the macrophytes, the following species were selected: Brazilian elodea, narrowleaf elodea, and coontail. The choice of species was based on the sizes of their incidence areas in the Jupiá Reservoir and because of their interference to the operation of the hydropower plant by accumulating in protection grids and blocking the water intake of generating units (Marcondes et al. 2003).

Stem samples (apical fragments) of Brazilian elodea and narrowleaf elodea were collected (July 2009; winter season) from Jupiá Reservoir at approximately 2.0 km upstream of the dam (20°46′01.4″S; 51°36′01.9″W). Samples of coontail were harvested (January 2010; summer season) in the littoral zone (depth: 1.5 m) of the Tietê River embayment (20°41′33.0″S; 51°23′14.3″W). At the sampling sites, the extinction coefficient, measured at the time of collection, was relatively low (0.45 m⁻¹), presenting an euphotic zone for at least for 10 m; the photosynthetically active radiation (PAR) was estimated with underwater radiation sensor.[1] In the sampling areas, water and sediment were obtained with a Van Dorn bottle[2] and an Ekman-Birge dredge,[3] respectively. In the laboratory, the stems were washed with tap and distilled water to remove adhered particles. The relation between the average of fresh plant length and dry mass (Brazilian elodea, $n = 11$; narrowleaf elodea, $n = 10$; coontail, $n = 12$) was determined by ruler and gravimetric measurements (Goodman et al. 2010). After the fresh mass determination, the stems were dried at 40 C, until constant weight, and dry masses were determined by gravimetry (Brazilian elodea, $n = 122$; narrowleaf elodea, $n = 119$; coontail, $n = 140$); Wetzel and Likens (1990). To set up incubations, healthy apical tips of Brazilian elodea, narrowleaf elodea, and coontail stem fragments ($n = 40$, 5.0 cm long) were fixed in 40 polystyrene pots (diameter = 4.5 cm, height = 4.0 cm, volume = 40 ml) that were filled with sediment from the reservoir (approximately 30 ml). To avoid

TABLE 1. AVERAGE VALUES (SD) OF PHYSICAL AND CHEMICAL VARIABLES DURING THE GROWTH EXPERIMENTS WITH BRAZILIAN ELODEA, NARROWLEAF ELODEA, AND COONTAIL FROM JUPIÁ RESERVOIR.

Variables	n	Brazilian Elodea	Narrowleaf Elodea	Blank[1]	n	Coontail	Blank[2]
EC (μS cm^{-1})	130	83.5 (25.6)	70.6 (20.8)	53.5 (1.9)	140	149.9 (36.8)	172.4 (4.2)
N-NH$_4^+$ (μg L^{-1})	24	166.0 (114.5)	138.6 (98.7)	28.8 (1.4)	24	22.4 (30.2)	21.7 (1.1)
N-NO$_3^-$ (μg L^{-1})	24	13.8 (15.8)	22.2 (19.5)	43.5 (2.5)	24	32.4 (7.3)	41.8 (1.1)
N-NO$_2^-$ (μg L^{-1})	24	1.5 (1.2)	2.1 (1.9)	3.7 (0.2)	24	1.97 (0.4)	2.54 (0.2)
N-organic (μg L^{-1})	24	841.3 (90.3)	1075.7 (154.3)	740.0 (103.9)	24	852.1 (149.9)	711.6 (56.6)
TP (μg L^{-1})	24	18.2 (5.3)	17.7 (7.1)	21.2 (5.3)	24	28.4 (4.3)	16.8 (3.7)
TDP (μg L^{-1})	24	8.9 (4.5)	7.7 (2.1)	11.5 (4.1)	24	9.5 (2.4)	7.6 (0.1)

Where: SD = standard deviation; EC = electrical conductivity; TP = total phosphorus; TDP = total dissolved phosphorus; Blank[1] = sample of water collected in July 2009 at 20°46′01.4″S; 51°36′01.9″W; and Blank[2] = sample of water collected in January 2010 at 20°41′33.0″S; 51°23′14.3″W); n = number of samples.

increases in turbidity, a thin layer (approximately 1 cm) of calcinated sand (2 h at 550 C) was added to the surfaces of the pots. A set of 10 pots were placed in a glass tank (diameter = 20 cm, height = 24 cm) with 6.5 L of water from Jupiá Reservoir (height of water column = approximately 20 cm).

The glass tanks ($n = 12$) and their respective controls (bottles [vol: 5.0 L] with only water samples from the reservoir) were incubated (in a germination chamber[4]) under controlled conditions: 21 C and PAR = 47.25 μmol m^{-2} s^{-1} with a light/dark light regime of 12/12 h. PAR was estimated with an underwater radiation sensor.[1] Periodically, the electrical conductivity and the concentrations of nitrogen (organic N [Organic-N], ammonium nitrogen [NH$_4^+$-N], nitrite nitrogen [NO$_2^-$-N], nitrate nitrogen [NO$_3^-$-N]) and phosphorus (total P and dissolved P) were determined in incubations. The electrical conductivity measurements were made with conductivimeter.[5] Analytical determinations were performed according to the American Public Health Association standards (APHA et al. 1998). During 3 mo (Brazilian elodea and narrowleaf elodea) and 4 mo (coontail), the stem lengths were measured approximately every 4 d, and the reservoir water was replaced weekly. Bud counts and length measurements were also made at this time. The criterion adopted to conclude the experiment was when the daily rates achieved approximately 0.05 cm d^{-1} (i.e., near the stabilization of cultures). During the measurement procedure, the yellow (senescent) stems were considered detritus. The senescent fragments of the stems (and buds) or the fallen fragments were not considered in the calculated length. Only green and healthy structures were considered for the length measurements. The adoption of these criteria was simple because, after becoming senescent (yellow), decomposition of this kind of resource is quick and clear (Chiba de Castro et al. 2013).

The temporal variations the cultures yielded (stems lengths + buds lengths) were fitted to a logistic model (Vogels et al. 1975; Equation 1). To achieve the mean parameters of each culture, the fittings were performed with length averages ($n = 40$). In addition, the growth of each plant was fitted to obtain the dispersion of parameters within the model (μ and K). These kinetics parameters were obtained by nonlinear regressions, calculated with the iterative algorithm of Levenberg-Marquardt (Press et al. 2007).

$$\frac{dN}{dt} = \mu N \left(1 - \frac{N}{K}\right) \qquad (1)$$

where N is the length (cm), μ is the growth rate constant (d^{-1}), K is the maximum value of the length (yield) of the culture (equivalent to the maximum value of biomass under selected experimental conditions).

The t_d was estimated according to Equation 2 (Mitchell 1974):

$$t_d = \frac{\ln 2}{\mu} \qquad (2)$$

The biomass of the macrophytes was calculated by linear regression using length and dry mass (Equation 3):

$$\text{Dry mass(mg)} = m \times [\text{fresh plant length(cm)}] \qquad (3)$$

where m is the slope of the straight line calculated with the least-squares method, with x (fresh plant length) as 0 and y (dry mass) as 0 (i.e., linear coefficient = 0). The following values were obtained for m: 6.15 (Brazilian elodea), 10.04 (narrowleaf elodea), and 11.11 (coontail). A comparison between fresh and dry plant biomass led to water content for Brazilian elodea, narrowleaf elodea, and coontail of 87.9 ($n = 122$), 90.4 ($n = 119$), and 90.9% ($n = 140$), respectively.

The frequency distributions of the following parameters were evaluated: yield (length), growth rate constant; doubling time, and the number of buds of the cultures. These parameters were submitted to the normality test (Shapiro and Wilk 1965), at a significance level of 0.05. The time changes of the yields (i.e., the growth curves) were submitted to the Kolmogorov-Smirnov test to check distribution normality and to the Bartlett test to verify homoscedasticity. Because these conditions were satisfied, the variables were tested using repeated measures ANOVA. The differences among the curves were compared using the Tukey test with a significance level of 0.01. The software used in the statistical analyses was PAST version 2.16 (Hammer et al. 2001).

RESULTS AND DISCUSSION

The average values of physical and chemical variables measured during the growth experiments are presented in Table 1. The culture media were kept under the same proportions between variables that were observed in the controls. However, some values (i.e., electrical conductivity,

organic N, and N–NH$_4^+$ concentrations) observed in the incubations were higher because of the addition of sediment for attachment of the plants. In all incubations, the average concentrations of N–NO$_3^-$ and N–NO$_2^-$ were lower than those seen in the blanks. The average concentrations of total and dissolved phosphorus were lower than those of blanks in incubations with *Egeria*. The average value of electrical conductivity was only lower than that of the control (87%) in incubations with coontail. From the initial 40 plants used in each experiment, 62.5% survived in the Brazilian elodea culture, 75% in the culture of narrowleaf elodea, and all plants in the coontail culture.

Two approaches were adopted to compare the growth of the three species. The first one comprised the use of the biomass average values for the estimations of the yield (K) of the culture and the growth rate constant (μ); in the second approach, the fit of biomass of each exemplar was made to achieve the dispersion values of parameters K and μ. This strategy was also applied to the buds analysis (the use of mean values to compare the number of buds and the buds' daily rates of formation, and the number of buds of each specimen to achieve the dispersions frequency). Figures 1–3 depict the growth rates and yields for each macrophyte species. On average, the increase in biomass of *Egeria* had higher rates in the second and third weeks; after which, the daily rates tended to decrease. For Brazilian elodea, the highest average value was measured on the 14th d (0.19 cm d^{-1} ≡ 1.24 mg d^{-1}) and for narrowleaf elodea the highest average value was measured on the 11th d (0.53 cm d^{-1} ≡ 5.32 mg d^{-1}). The increase in biomass of coontail had higher rates during the second month (31st to 60th d). The highest average value was measured on the 45th d (0.19 cm d^{-1} ≡ 2.11 mg d^{-1}). The temporal changes of daily rates, as verified in our experiments, are characteristics of growths in all environments. The integration of daily rates defines the logistic growth curve, and consequently, the kinetic parameters μ and K (Vogels et al. 1975). These changes derive from the intrinsic metabolic characteristics of plants (which define μ) and environmental (or experimental) conditions (which define the K values; e.g., competition for space, self-shading, and nutrients availability), and in Jupiá Reservoir, basically, the corresponding factors drive the growth of macrophytes.

The average number of narrowleaf elodea vegetative budding was 4.0 per branch, with the highest rates observed in the first month. For Brazilian elodea, the average number of buds was 1.6 per branch while for coontail it was 0.75. The highest average daily rates of bud occurred on the 14th day for Brazilian elodea cultures and on the 35th day for coontail, with the highest rates observed at the same time of the highest growth rates. At the end of the experiment, the number of vegetative budding did not show a normal distribution at a 0.05 significance level; in most of the cases, the plants presented 0 to 6 buds, as shown in Figures 1–3. The vegetative budding was effective to increase the biomass of these macrophytes because the daily rates for sprouting and growth were similar. The differences in daily rates for sprouting and the final number of buds suggest different growth strategies adopted by each species. Another interesting feature was the large standard deviation in the results. More than a mere dispersion in the data, these results pointed to a high variability of Brazilian elodea, narrowleaf elodea, and coontail, which then required a large number of samples to obtain the biometric curves.

The parameters from fitting the data in Figures 1–3 showed that under the experimental conditions used, on average, the macrophytes' growth exhibited a t_d time between 11.6 (Brazilian elodea) and 23.9 d (coontail) and a yield between 8.6 (≡ 52.9 mg; Brazilian elodea) and 19.6 cm (≡ 217.8 mg; coontail). The yield of cultures with *Egeria* presented a normal distribution (at a 0.05 significance level), but that did not apply to the yield of coontail cultures. Because the μ is a intrinsic (physiological) parameter of the plants species and the yield derives from environmental conditions, the carrying capacity (i.e., the length or biomass; K parameter, Equation 1) obtained from laboratory experiments should not be indiscriminately used to simulate plants growth in the environment because this value is the result of conditions that do not always have close correspondence with natural conditions. For this purpose, the macrophyte assessment is particularly relevant for mapping the incidence areas and the proposition of carrying capacity (e.g., Caffrey et al. 2007). The incidence area, carrying capacity (i.e., density), and the growth rate constant of the macrophytes are essential data for implementing any program of harvesting those plants, whereas the rates of biomass removal derive from the product of those three parameters (Gutiérrez et al. 2001). Thus, considering the densities of any macrophyte species and their incidence areas, the μ values shown in Table 2 permits an *a priori* definition of efforts (e.g., costs, material resources, harvest schedule, etc.) to be adopted in planning a specific physical control program.

In contrast to what was observed for coontail, the *Egeria* growth rates did not show a normal distribution at a 0.05 significance level. Normal distributions of t_d were observed for *Egeria* but not for coontail. The r^2 values derived from fitting the model to Equation 1 were high and so were the standard deviations, as shown in Figures 1–3. According to the determination coefficients (r^2), the model adopted was robust in describing growth for Brazilian elodea, narrowleaf elodea, and coontail. In the parameterization of Brazilian elodea growth, the average biomass data used included only the first 49 d because after that, time mass loss (i.e., death and decomposition of leaves) prevailed, as seen in Figure 1. ANOVA–repeated measures tests showed significant differences ($P < 0.01$) between the three growth curves (samples size = 26; average values). When using data from the first 49 d, avoiding interference from Brazilian elodea mass loss (samples size = 14; average values), similar growth was observed for Brazilian elodea and coontail ($P = 0.97$); this result only partially supports the hypothesis because of the higher growth rate of Brazilian elodea ($P < 0.01$). Another factor that tends to compete with the hypothesis (i.e., the greater adaptive value of indigenous species) is the closeness of the values obtained for the average growth rates; on the other hand, the most frequent values for the growth rate constant tended to be higher for the two *Egeria* species. The growth rate constant of the macrophytes were close, and there was little relative difference between their minimum and maximum values (Table 2). Those parameters suggest
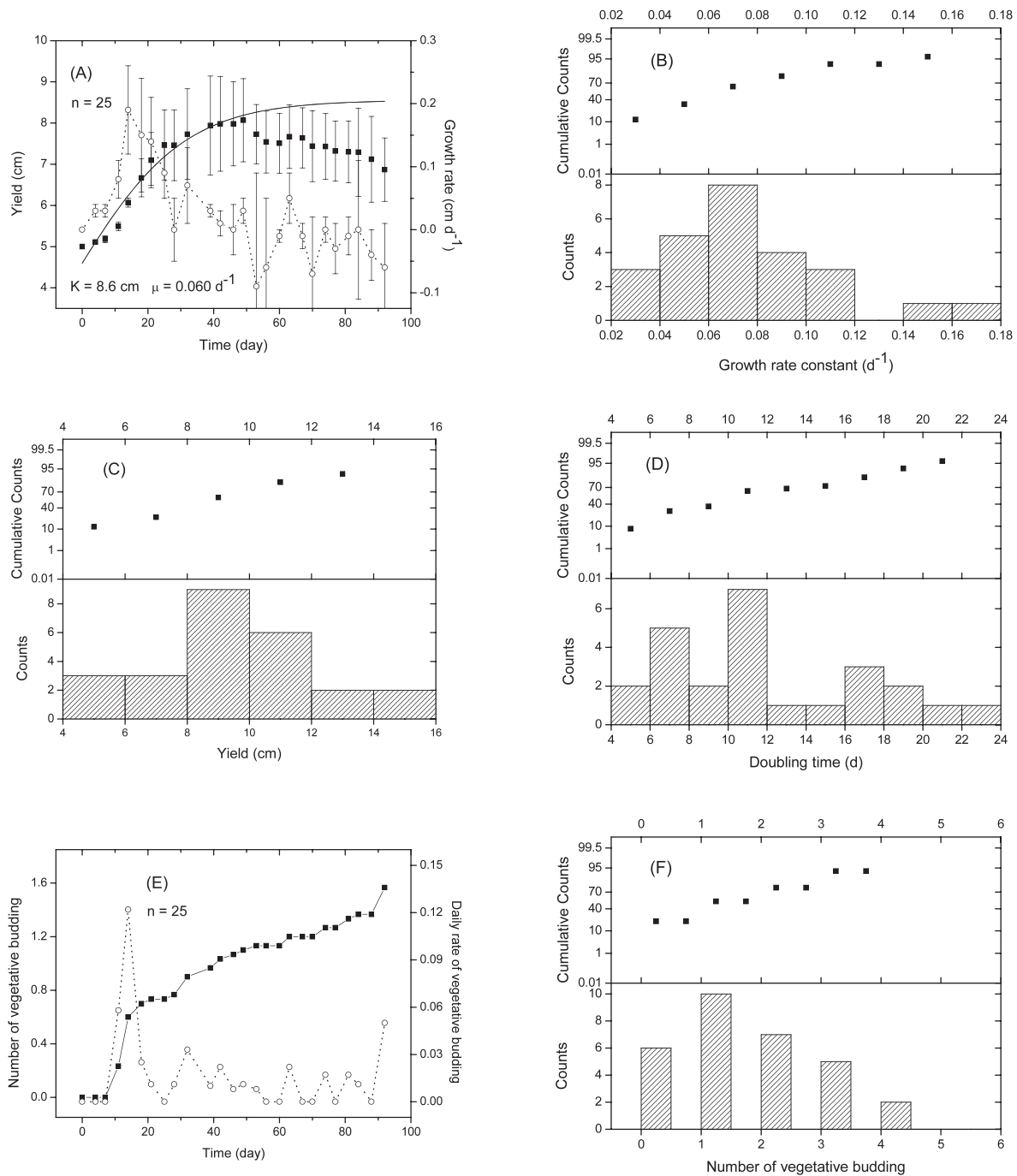
Figure 1. The average growth of Brazilian elodea under controlled conditions (cumulative yield [cm] and daily growth rate [cm d^{-1}]. (A) where cumulative yield = closed symbols; growth daily rate = open symbols; standard deviations = bars. (B) The frequencies of growth rate constant (d^{-1}). (C) Final yield (cm). (D) Doubling time (d). (E) Temporal variation in the average number of buds (cumulative number and daily rate [bud d^{-1}]. (F) The frequency of number of buds at the end of experiment.

the possibility of intense competition among the species. Thus, the closeness of growth rate constants constitutes an advantage for the cosmopolitan species.

Different macrophyte life forms (e.g., emergent, submerged, and floating) and changes in environmental variables (i.e., forcing functions) interfere in different ways with the growth rate constants (Barko et al., 1986). The responses of macrophytes to abiotic factors, together with

the effects of intraspecific and interspecific relationships, determine the basis of the diversity and abundance of communities (Santamaría 2002, Lacoul and Freedman 2006). Considering the predominance of bottom-up control (e.g., the growth regulated by nutrient availability; Glibert 1998), using the logistic model, the effects from forcing functions (e.g., light, temperature, nutrients; Sand-Jensen and Madsen 1991, van der Heide et al. 2006, Moss et al. 2013)
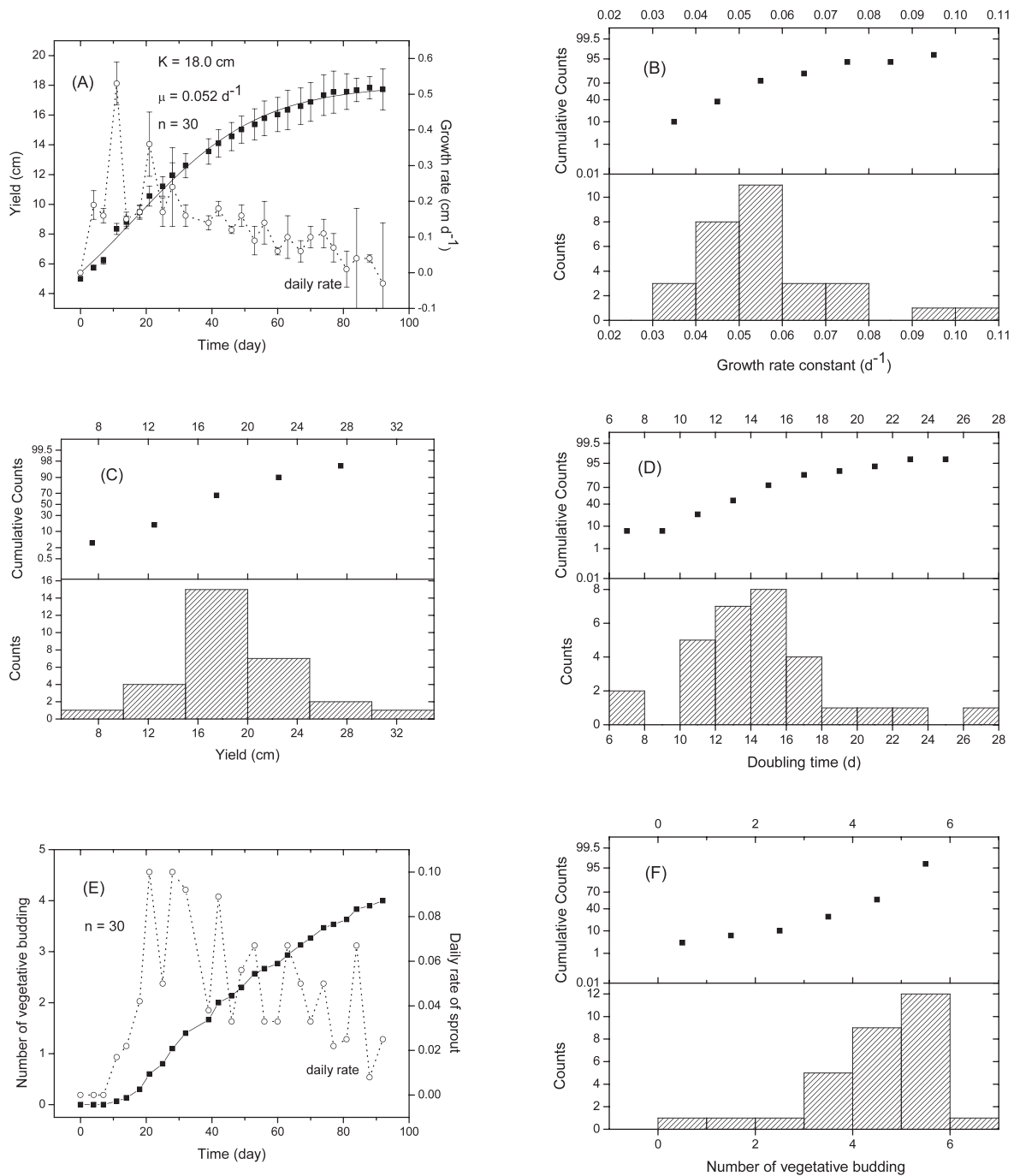
Figure 2. The average growth of narrowleaf elodea under controlled conditions (cumulative yield [cm] and growth daily rate [cm d^{-1}]. (A) where cumulative yield = closed symbols; growth daily rate = open symbols; standard deviations = bars. (B) The frequencies of growth rate constant (d^{-1}). (C) Final yield (cm). (D) Doubling time (d). (E) Temporal variation in the average number of buds (cumulative number and daily rate [bud d^{-1}]. (F) The frequency of number of buds at the end of experiment.

are typically manifested by changes in the growth rate constants (Jørgensen 1980, Bowie et al. 1985). Those rate constants may also include other processes, such as respiration, excretion, abrasion/export, and nonpredatory mortality (decomposition) (Canale and Auer 1982). The fittings for plant growth led to average rate constants (Brazilian elodea: 0.06 d^{-1}; narrowleaf elodea: 0.052 d^{-1};

coontail: 0.029 d^{-1}) and μ_{max}/μ_{min} relations (Brazilian elodea: 5.1; narrowleaf elodea: 3.9; coontail: 3.3) similar to other species (cf. Table 2). The proximity of the rate constants suggests that these plants have a close niche, which could explain the changes in daily rates for sprouting and for the final number of buds. However, in Jupiá Reservoir, as in several other Neotropical aquatic ecosystems, these species
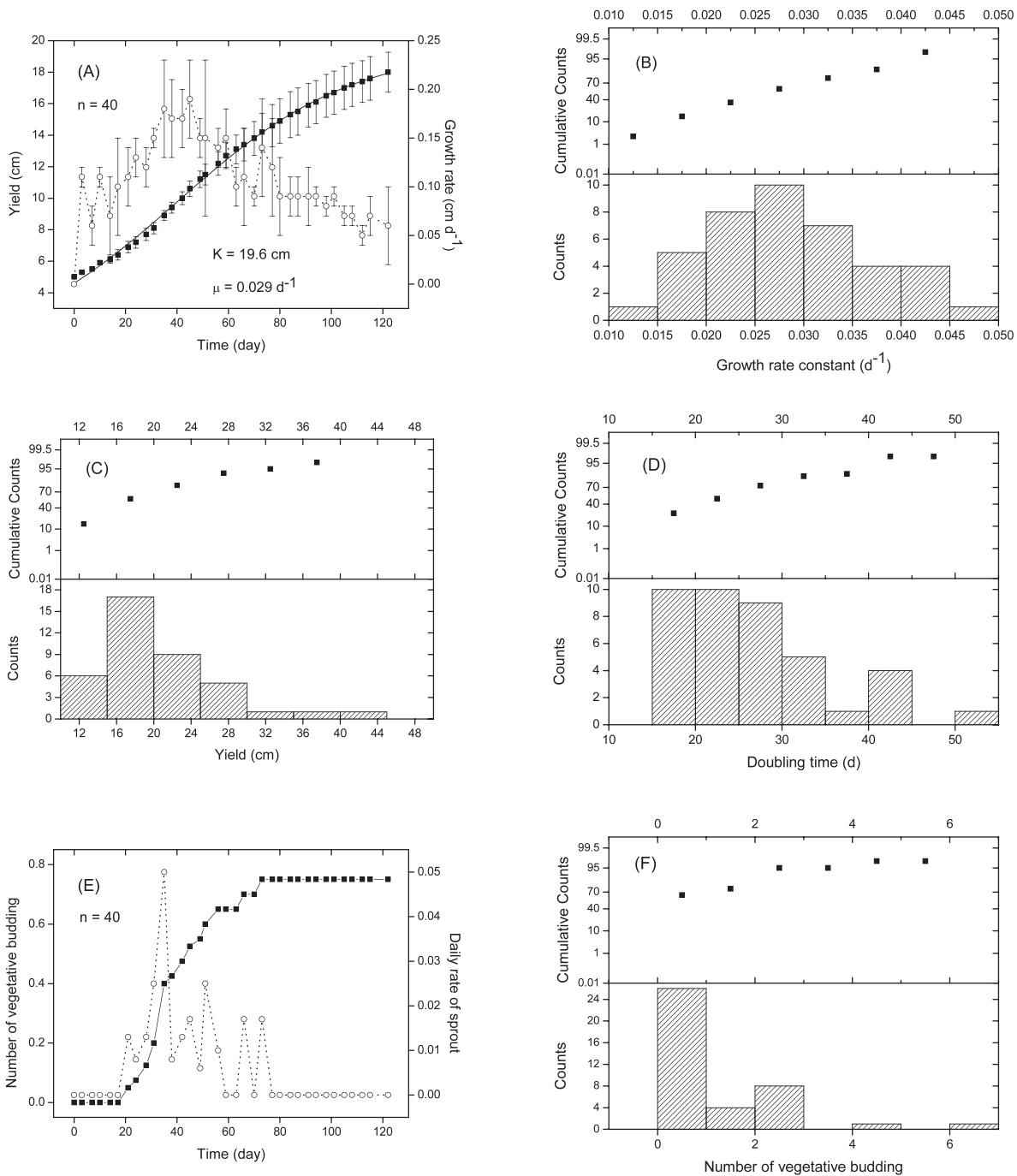
Figure 3. The average growth of coontail under controlled conditions (cumulative yield [cm] and growth daily rate [cm d^{-1}]. (A) where cumulative yield = closed symbols; growth daily rate = open symbols; standard deviations = bars. (B) The frequencies of growth rate constant (d^{-1}). (C) Final yield (cm). (D) Doubling time (d). (E) Temporal variation in the average number of buds (cumulative number and daily rate [bud d^{-1}]). (F) The frequency of number of buds at the end of experiment.

coexist. It is possible that, through this growth strategy, Brazilian elodea, narrowleaf elodea, and coontail also compete with other native and alien submerged species. For example, bladderwort (*Utricularia* L.), fanwort (*Cabomba* Aubl.), pondweed (*Potamogeton* L.), and hydrilla [*Hydrilla verticillata* (L. f.) Royle] were recently reported in the Paraná River, downstream of Jupiá Reservoir (Sousa et al. 2009),

which has average t_d lower (i.e., 7 d; Table 2) than that presented by Brazilian elodea, narrowleaf elodea, and coontail. The floating genus, especially the small ones, such as mosquitofern (*Azolla* Lam.), smaller duckweeds (*Lemna* L.), larger duckweeds (*Spirodela* Schleid.), salvinia (*Salvinia* Ség.), and watermeal (*Wolffia* Horkel ex Schleid.), can also present a t_d that is smaller or is of the same order of magnitude as

Table 2. Minimum (μ_{MIN}), maximum (μ_{MAX}), and average (μ) growth rate constants (d^{-1}) and average doubling times (T_D; d) of various genus of aquatic plant under different experimental or environmental conditions. Where: μ_{MAX}/μ_{MIN} = relation between the maximum and minimum growth rate constants of genus.

Macrophyte	Common name	μ_{min} (d^{-1})	μ_{max} (d^{-1})	μ_{mean} (d^{-1})	t_D (d)	μ_{max}/μ_{min}	Source*
Aldrovanda	waterwheel	0.032	0.083	0.057	12.1	2.6	1
Azolla	mosquito fern	0.104	0.189	0.141	4.9	1.8	2, 3, 11, 12, 14, 16, 24, 25, 28, 31, 33, 48, 49, 54, 55
Batrachium	water crowfoot	-	-	0.097	7.1	-	35
Cabomba	fanwort	0.048	0.080	0.064	10.8	1.7	53
Callitriche	water starwort	0.060	0.066	0.063	11.0	1.1	32
Ceratophyllum	coontail	-	-	0.043	16.1	-	4
Egeria	common waterweed	0.030	0.065	0.049	14.3	2.2	5, 8, 9, 15, 19, 41, 42, 51, 56
Eichhornia	water hyacinth	0.021	0.087	0.051	13.6	4.1	7, 10, 17, 18, 21, 22, 23, 39, 44, 47, 50, 51
Elodea	elodea	0.038	0.042	0.063	11.0	1.1	32, 35
Hydrilla	hydrilla	0.079	0.183	0.099	7.0	2.3	6, 29
Lemna	duckweed	0.147	0.315	0.182	3.8	2.1	26, 54, 55
Littorella	shoreweed	-	-	0.009	77.0	-	35
Lobelia	cardinal flower	-	-	0.007	99.0	-	35
Myriophyllum	parrot feather	0.069	0.069	0.069	10.0	-	29
Pistia	water lettuce	-	-	0.084	8.3	-	20, 21, 40, 44
Potamogeton	pondweeds	0.037	0.038	0.066	10.5	1.0	32, 35
Ranunculus	water buttercup	-	-	0.046	15.1	-	32
Salvinia	giant salvinia	0.048	0.148	0.118	5.9	3.1	13, 20, 23, 34, 36, 37, 38, 43, 45, 46, 51, 52, 54
Sparganium	bur-reed	-	-	0.042	16.5	-	35
Spirodela	giant duckweed	0.149	0.352	0.260	2.7	2.4	27, 30, 55
Utricularia	bladderwort	0.021	0.076	0.049	14.3	3.6	1
Wolffia	watermeal	0.060	0.170	0.115	6.0	2.8	55
Average		0.064	0.145	0.098	7.1	2.3	

(*) 1 Adamec and Kovářová (2006); 2 Arora and Singh (2003); 3 Arora and Saxena (2005); 4 Batterson (1977); 5 Bianchini Jr. et al. (2006); 6 Bianchini Jr. et al. (2010); 7 Bravo et al. (1992); 8 Carrillo et al. (2006); 9 Carvalho et al. (2003); 10 Center and Spencer (1981); 11 Chakrabortty and Kushari (1986); 12 Costa et al. (1999); 13 Finlayson (1984); 14 Forni et al. (2001); 15 Freitas and Thomaz (2011); 16 Garcia-Murillo et al. (2007); 17 Greco and Freitas (2002); 18 Gutiérrez et al. (2001); 19 Haramoto and Ikusima (1988); 20 Henry-Silva et al. (2002); 21 Henry-Silva and Camargo (2005); 22 Henry-Silva et al. (2008); 23 Holm and Yeo (1980); 24 Jayakumar et al. (2002); 25 Kathiresan (2007); 26 Kim and Kwon (2006); 27 Kinnear et al. (2007); 28 Kitoh et al. (1993); 29 Lembi and Netherland (1990); 30 Loveson and Sivalingam (2012); 31 Lumpkin and Plucknett (1982); 32 Madsen and Cedergreen (2002); 33 Maejima et al. (2001); 34 Mitchell and Tur (1975); 35 Nielsen and Sand-Jensen (1991); 36 Olguín et al. (2007); 37 Oliver (1993); 38 Panigatti and Maine (2003); 39 Penfound and Earle (1948); 40 Pereira (2004); 41 Pezzato (2007); 42 Pistori et al. (2004); 43 Pistori et al. (2010); 44 Reddy and DeBusk (1984); 45 Rubim and Camargo (2001); 46 Sale et al. (1985); 47 Silva (2008); 48, 49 Sood et al. (2008; 2012); 50 Téllez et al. (2008); 51 Thomaz et al. (1999); 52 Usha Rani and Bhambie (1983); 53 Valletta (2007); 54 van der Heide et al. (2006); 55 Vermaat and Hanif (1998); 56 Yarrow et al. (2009).

Brazilian elodea (t_d = 5 to 22 d), narrowleaf elodea (t_d = 7 to 27 d), and coontail (t_d = 15 to 51 d). In this case, the floating species have an advantage because light is not a limiting effect for these plants nor is the shadowing effect that is imposed on submerged species.

SOURCES OF MATERIALS

[1] Model LI-193SA underwater radiation sensor, LI-COR, 4647 Superior Street, Lincoln, NE 68504.

[2] Van Dorn bottle, **Limnotec**, Rua José Missali 707, São Carlos (SP), Brasil, 13562-060.

[3] Ekman-Birge dredge, **Limnotec**, Rua José Missali 707, São Carlos (SP), Brasil, 13562-060.

[4] Tecnal Model TE-401 germination chamber, Tecnal, Rua João Leonardo Fustaino 325, Piracicaba (SP), Brasil, 13413-102.

[5] Model DM3 conductivimeter, Digimed, Rua Marianos 227, São Paulo (SP), Brasil, 04691-110.

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