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Seasonal growth of submersed macrophytes in lakes: The effects of biomass density and light competition

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Abstract

The long-term growth and succession of aquatic plant species in lakes have been documented in many field studies, but there has been little insight to quantify the mechanisms which determine the outcome of competitive growth. In this paper, a process-based macrophyte growth model is formulated and used to investigate the light limited growth of individual macrophyte species and of two species in competition. Closed form solutions for integral biomass production over 1 day are derived, reducing the time and depth resolution required for seasonal growth calculations. For growth in monoculture, seasonal biomass production is found to be most sensitive to the base growth and respiration rate coefficients and the temperature dependence of growth, and relatively insensitive to biomass density, and the half-saturation constant for light. The sensitivity of seasonal biomass production to basic physiological, morphological, and physical lake parameters is found to be significantly higher for growth in competition compared to growth in monoculture. For published growth parameter values, invasive species are predicted to suppress the growth of native species over a well-defined range of water depths and turbidities, largely by reaching the water surface early in the season and subsequently forming a dense surface canopy.

Keywords: Lake; Macrophyte; Growth model; Photosynthesis; Invasive; Competition

1. Introduction

Invasive aquatic plant species are a major issue in lake management. Invasive plants such as *Hydrilla verticillata* (Hydrilla) and *Myriophyllum spicatum* (Eurasian Watermilfoil) are capable of taking over the littoral area of lakes in a few years, suppressing or eliminating native plant species. The resulting dense, monoculture macrophyte beds are less suitable habitat and food sources for waterfowl and fish, and interfere with recreation usage of lakes and reservoirs. Dense plant monocultures can also lead to seasonal water quality problems, as the plants simultaneously senesce, decay and introduce pulses of nutrients and oxygen demand to a lake system.

There are many potential causes for the dominance of invasive species over native species, including lower grazing pressure, reproduction strategies, carbon

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Nomenclature

b	layer thickness (m)
b_c	canopy thickness (m)
Chl	phytoplankton concentration as chlorophyll (mg/L)
d	water depth (m)
DL	photic period (h)
h	macrophyte stand height (m)
h_0	initial stand height (m)
I	irradiance ($\mu E/m^2/s$)
I_d	irradiance at lake bottom ($\mu E/m^2/s$)
$\bar{I}_d$	average irradiance at lake bottom ($\mu E/m^2/s$)
I_{dp}	peak irradiance at lake bottom ($\mu E/m^2/s$)
I_m	irradiance at top of macrophytes ($\mu E/m^2/s$)
$\bar{I}_m$	average irradiance at plant top ($\mu E/m^2/s$)
I_{mp}	peak irradiance at plant top ($\mu E/m^2/s$)
I_0	irradiance at water surface ($\mu E/m^2/s$)
$\bar{I}_0$	average irradiance at water surface ($\mu E/m^2/s$)
k_m	specific light attenuation coefficient for macrophytes ($m^{-1}/kg/m^3$)
k_1	half-saturation constant for light ($\mu E/m^2/s$)
K_{wt}	light attenuation coefficient for water + phytoplankton
P	biomass density (g DW/m^3)
P_s	sub-surface biomass density (g DW/m^3)
t	time (days)
T	water temperature (°C)
T_b	base temperature (°C)
W	integral macrophyte biomass (kg/m^2)
W_p	peak biomass (kg/m^2)
W_0	initial biomass (kg/m^2)
z	depth (m)

Greek letters

Γ	daily integral production rate ($kg/m^2/day$)
δ	loss rate (day^{-1})
θ_g	Arrhenius constant for growth
θ_r	Arrhenius constant for respiration
λ	respiration rate (day^{-1})
λ_0	base respiration rate (day^{-1})
μ	growth rate (day^{-1})
μ_T	light saturated growth rate (day^{-1})
μ_0	base growth rate (day^{-1})
π	peak biomass sensitivity coefficient

Subscripts

a	species *a*
a(b)	species *a* in competition with *b*
b	species *b*
b(a)	species *b* in competition with *a*
c	canopy
g	growth
i	layer number
m	macrophyte
p	peak
r	respiration
s	subsurface
t	total
T	temperature-dependent
w	water
0	initial or base

uptake mechanisms, allelopathy, and light competition (Madsen, 1989; Smith and Barko, 1990; Pieterse and Murphy, 1990). Growth morphology has been recognized as an important factor in aquatic macrophyte growth behavior and competition (Duarte and Kalff, 1990; McCreary, 1991). Invasive aquatic plants such as *M. spicatum* are often associated with a growth form that includes low density shoots rapidly growing to the water surface by utilizing stored carbohydrates, followed by formation of a dense, continuous surface canopy.

The results of competition between native and invasive species have been documented in numerous field studies, but there is relatively little information on the processes that control the results. Titus and Adams (1979) identified parameters associated with light competition (light half-saturation constant, specific attenuation coefficient and plant morphology) which influenced the coexistence of an invasive species (*M. spicatum*) and a native species (*Vallisneria americana*) in a lake. The study included growth modeling of each species alone, but not in competition. Field studies of Madsen and Boylen (1990) showed consistent differences in growth parameters between typical