Algal Research 25 (2017) 431–438

Contents lists available at ScienceDirect

Algal Research

journal homepage: www.elsevier.com/locate/algal

Applying principles of resource competition theory to microalgae biomass production: A more refined relationship between species richness and productivity

Daniel L. Roelke

Texas A & M University, Department of Wildlife and Fisheries Sciences, Department of Oceanography, 2258 TAMUS, College Station, TX 77843-2258, United States

ARTICLE INFO

Keywords:
Microalgae
Phytoplankton
Inorganic nutrients
Productivity
Biodiversity
Equilibrium resource competition theory

ABSTRACT

Ecosystem productivity is commonly greater when biodiversity is high, an observation that extends to artificial systems, such as microalgae production systems employing polycultures. Regarding these, when functional diversity within polycultures is also high, the stability of production is increased. There are various strategies to designing biomass production systems; some differentiate between ways in which nutrients are resupplied to production chambers after harvesting. Here, a mathematical model is developed that depicts a microalgae biomass production facility. Simulation analyses are then performed to explore optimization strategies that consider production magnitude and functional diversity within polycultures. Two nutrient resupply strategies are explored. The first involves using the same concentrations of nutrients with each resupply after harvesting. The second involves using alternating nutrient concentrations of varied proportions (relative to each other) for the resupply after harvesting. The first nutrient resupply strategy is best depicted by an ecological paradigm described by the resource-saturation limitation (RSL) model. The second nutrient resupply strategy is best depicted by another ecological paradigm described by the resource-ratio (RR) model. Findings suggest that if confidence is high that the polycultures being employed are resilient, then designing a biomass production system following the RSL-model approach is best. In such a system, the complementarity of the polyculture being employed should be maximized, as this will produce the highest biomass production. But if confidence is low that the polycultures are resilient, then designing a biomass production system following the RR-model approach is best. In this case, designing the resource supply fluctuations with intermediate proportional alternations, and employing polycultures of lesser complementarity, is best. This will maximize functional diversity, and therefore production stability.

1. Introduction

Ecosystem productivity is commonly greater when biodiversity is high, as observed in many environments and spanning multiple trophic levels [3,5]. Included in these are ecosystems primarily fueled from microalgae, such as plankton environments [23,37,39]. This biodiversity-productivity relationship extends to artificial systems as well, such as microalgal production ponds and phytoplankton microcosms. In these systems, increases in the stability of biomass production have also been observed with higher biodiversity [1,7,29,30,37,39,43]. For these reasons, artificial systems employing polycultures for biomass production seem more promising than monoculture systems [6,33]. But biodiversity, per se, may not necessarily lead to enhanced biomass production and production stability, as it is the diversity of functional groups that appears to drive the biodiversity-productivity relationship [30,34,38]. Maintaining high functional group diversity in an artificial system, then, is a challenge faced in microalgal biomass production.

Application of classic equilibrium resource competition (ERC) theory developed for plant and microalgae ecosystems [40,41] provides a useful framework for evaluating approaches to maintaining high functional group diversity in artificial systems. In ERC theory, a species' growth rate (μ) at a resource concentration can be estimated with knowledge of two life history traits; the species' maximum growth rate (μ_{max}) and half-saturation coefficient for resource-limited growth (k_S). The function that describes this relationship, i.e., the Monod equation [22], shows μ increasing nearly linearly with increases in resource concentration over the low range of resource concentrations. Over the higher range of resource concentrations, the function shows μ asymptotically approaching μ_{max} as resource concentrations increase (Fig. 1A). The ERC theory can also be used to estimate above what resource concentration microalgae biomass will accumulate. At this resource concentration, coined R*, the summed rate of losses to a

---

E-mail address: droelke@tamu.edu.

http://dx.doi.org/10.1016/j.algal.2017.06.002
Received 22 March 2017; Received in revised form 11 May 2017; Accepted 6 June 2017

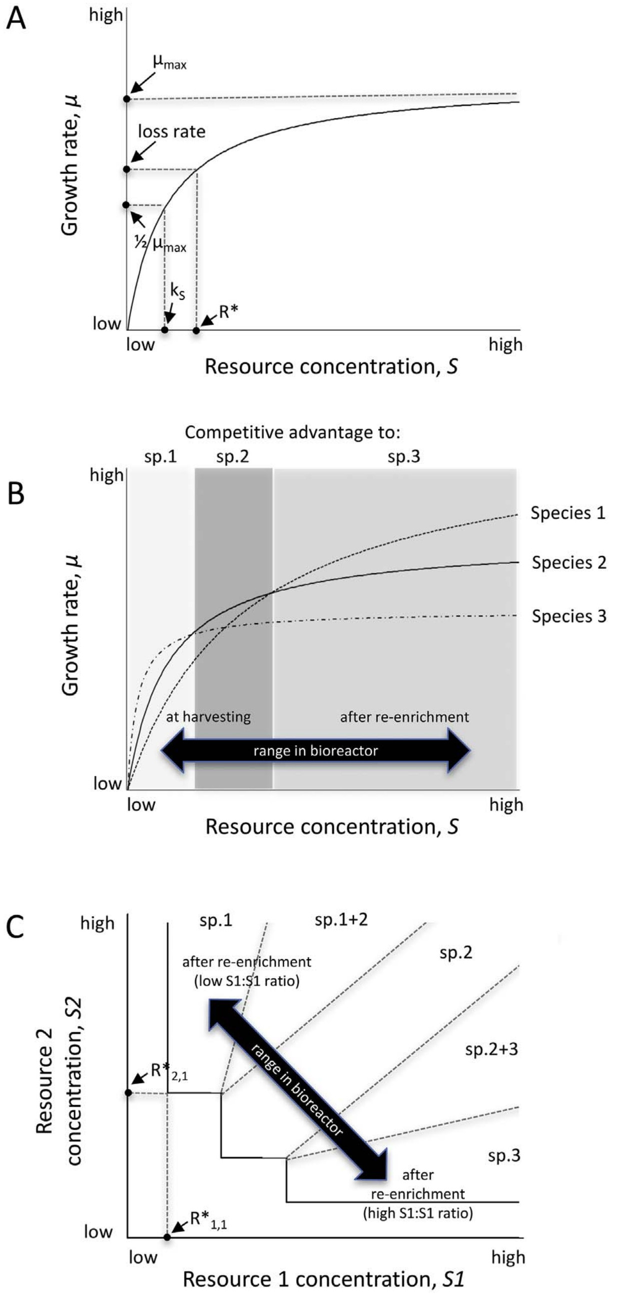

Fig. 1. Classic equilibrium resource competition (ERC) theory as it applies to approaches to microalgae production. A species' growth rate (μ) at a resource concentration (S) can be estimated with knowledge of the species' maximum growth rate (μ_{max}) and half-saturation coefficient for resource-limited growth (k_S). The resource concentration above which biomass will accumulate (R*) can also be determined when the summed rate of losses to a population is known (A). Regarding microalgae production operations, when resources are added to the re-claimed water at a fixed ratio, a variant of ERC theory called the resource saturation-limitation (RSL) model (B) shows how species with high μ_{max} gain a competitive advantage when resource concentrations are high, and how species with a high $\mu_{max}/2^*k_S$ (slope of the initial portion of the species-specific Monod function) gain a competitive advantage when resource concentrations are low (B). When resources are added to the re-claimed water alternating in ratio between harvesting cycles, another variant of ERC theory called the resource ratio (RR) model illustrates how species' combined μ_{max} and k_S (which determines R* when losses are considered) for multiple resources determines at which resource ratios competitive advantages will be gained (C).

microalgae population equal μ (Fig. 1A). When applying ERC theory to polycultures, knowledge of species-specific μ_{max}'s and k_S's enables an estimation of competitive abilities at specific resource concentrations, as discussed below.

A variant of ERC theory is the resource saturation-limitation (RSL) model. The RSL model is a useful framework of understanding when a single resource limits microalgae growth at any point in time, and the limiting resource does not change over time. Under such conditions, the microalgal species in polyculture with the greatest μ_{max} will have the highest μ when resource concentrations are high (Fig. 1B). If a generalized loss term is introduced, such as hydraulic displacement that would occur in a flow-through microalgae biomass production system, and resource concentrations remain high, the species with the greatest μ_{max} will eventually competitively exclude other species in the polyculture, leaving only a monoculture. Conversely, the microalgal species in polyculture with the greatest $\mu_{max}/2^*k_S$ (initial slope of the species–specific Monod curve) will have the highest μ when resource concentrations are low (Fig. 1B). Again, if a generalized loss term is introduced and resource concentrations remain low, the species with the greatest $\mu_{max}/2^*k_S$ will eventually competitively exclude other species in the polyculture, again leaving only a monoculture.

When the concentration of the limiting resource fluctuates over time, but the ratio between resources remains the same (so still, only one resource limits microalgae growth), the RSL model can be used to illustrate how polycultures can persist. For example, as the concentration of the growth-limiting resource goes from high to low concentration, a succession of species will occur. In this case, the succession will be from the species with the highest μ_{max} through species with intermediate μ_{max} and $\mu_{max}/2^*k_S$, eventually to the species with the greatest $\mu_{max}/2^*k_S$. In Fig. 1B, this sequence of succession is species 1 to species 2 to species 3. When the concentration of the growth-limiting resource goes from low to high concentration, a succession of species will occur in the opposite sequence. When the concentration of the growth-limiting resource fluctuates recurrently, going from high to low to high, etc. (Fig. 1B), co-existence of many species of varying life history traits (μ_{max} and k_S combinations) becomes possible [17,32,35]. Here, the variance in life history traits within the polyculture (the range of μ_{max} and k_S combinations) and the number of *co*-existing species defines the polyculture's functional group diversity.

In many systems, however, the resource that limits microalgae growth changes over time. In this case, the concentrations of potentially growth-limiting resources and the ratio between these resources fluctuate over time. Another variant of ERC theory, called the resource ratio (RR) model, is a useful framework of understanding for such systems. In the RR model, a species' combined μ_{max} and k_S for multiple resources determines at which resource ratios competitive advantages will be gained (Fig. 1C). Essential to this model are the R* values for each resource for each co-existing species. Knowledge of a species optimal resource ratio, i.e., the R* for one resource divided by the R* for another resource (R2*/R1*), influences the species' resource consumption vector in regards to the two resources. In turn, the consumption vectors of species in polyculture influences the boundaries between regions where species gain competitive advantages over other microalgae (Fig. 1C). Should the concentrations of resources remain fixed for an extended period of time, competitive exclusion will occur. For example, in the polyculture shown in Fig. 1C, species 1 gains a competitive advantage at a high ratio of resource 2 to resource 1 (S_2/S_1). A monoculture will eventually result if S_2/S_1 remains high for an extended period of time. Conversely, at a low S_2/S_1 species 3 gains a competitive advantage over other species in polyculture. Again, a monoculture will eventually result if S_2/S_1 remains low for an extended period of time.

As before, co-existence in a RR model framework become possible if the resource ratio fluctuates over time [35,41]. For the polyculture shown in Fig. 1C, as S_2/S_1 decreases a succession sequence will occur from species 1 to species 2 to species 3. As S_2/S_1 increases a succession sequence will occur from species 3 to species 2 to species 1. When the S_2/S_1 fluctuation is recurrent, co-existence of species of varying life history traits (μ_{max} and multiple nutrient specific k_S's) becomes possible. Again, the variance in life history traits within the polyculture and the number of *co*-existing species defines the polyculture's functional group diversity.