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HORIZONS

Key ecological challenges in sustainable algal biofuels production

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Algae have significant potential as a renewable biofuels feedstock, but their promise is unproven at a scale that actually competes with the existing use of fossil fuels. The success of global algal biofuels initiatives will depend upon our ability to produce algal crops in a reliable, cost-effective and sustainable manner. Although the science of aquatic ecology *per se* has unfortunately been given insufficient emphasis to date in this nascent field, careful applications of its principles can play a vitally important role (1) by informing the rates and ratios of nutrients supplied to algal cultivation systems, (2) by guiding efforts to design and construct biotic communities that will help to maximize algal biomass yields and minimize grazing losses, (3) by guiding efforts to minimize biomass losses to infectious disease, (4) by applying decades of past experience in optimal harvesting theory to help guide the magnitude and frequency of algal crop harvests and (5) by helping to create biologically adaptive algal biomass production systems that are both resistant and resilient to future climate change. These general principles also should be broadly relevant to many other algal mass culture efforts, including those associated with aquaculture.

KEYWORDS: algal biofuels; bottom-up control; crop protection; disease control; optimum yield; polyculture; top-down control

INTRODUCTION

High energy prices, coupled with increasing energy imports, uncertainties about future petroleum supplies and an increasing recognition of the environmental

impacts of fossil fuels, are driving strong worldwide interest in the development of renewable biofuels (Hill *et al.*, 2006). For example, eukaryotic microalgae and prokaryotic cyanobacteria (collectively referred to here as *algae*)

are considered to have immense promise as a feedstock for the production of liquid transportation fuels (Pienkos and Darzins, 2009). The history, challenges and productivity potential of algal biofuels (Grobbeelaar, 2010; Hannon *et al.*, 2010; Scott *et al.*, 2010; U.S. DOE, 2010; National Research Council, 2012; Flynn *et al.*, 2013; Pate, 2013; Moody *et al.*, 2014) will not be re-reviewed here. However, the full promise of algal biofuels has not yet been realized, and the ultimate success of algal biofuels initiatives will depend upon our ability to reliably and predictably produce massive algal crops which can in turn be harvested and processed into biofuels in a cost-effective and sustainable manner.

Algal biomass cultivation in open pond arrays is currently one of the most cost-effective system designs for large-scale biofuels production (Benemann, 2013; McBride and Merrick, 2014). In this Horizons article, we assert that there is a critically important role for aquatic ecologists to help improve the operation and performance of these engineered biosystems. Although space does not permit an exhaustive review, we focus briefly on five key areas in which aquatic ecology can play a key role in the future development of sustainable algal biofuels.

Nutrient controls and nutrient demands of algal biomass production

More than 40 years of eutrophication science confirms that the availability of mineral nutrients sets the upper limit both for the productivity and for the standing crops that can be attained in algal biomass cultivation facilities (cf. Sakamoto, 1966; Vollenweider, 1976; Smith, 1979). Nitrogen (N) supply concentrations for mass algal cultures range from 25 to 5000 mg N L⁻¹, and variations in the supply concentrations of phosphorus (P) have been reported to range from 0.98 to 179 mg P L⁻¹ in the algal cultivation medium (Mostert and Grobbelaar, 1987). Both of these ranges greatly exceed the water column N and P concentrations that are typically observed in natural water bodies.

As in commercial agriculture (Goulding *et al.*, 2008), optimizing nutrient supply rates and supply ratios will be essential if algae-derived biofuels are to be economically and environmentally sustainable. Fig. 1A demonstrates that the biomass of microalgae in hyper-enriched ponds and artificial algal cultivation systems responds predictably to increasing concentrations of total phosphorus (TP), just as has been observed in nutrient-enriched lakes, reservoirs and estuaries worldwide (Smith, 2009). The highest growing season average algal biomass attainable in outdoor ponds appears to be ~3 mg L⁻¹ chlorophyll *a*, corresponding to an ice-free period average of

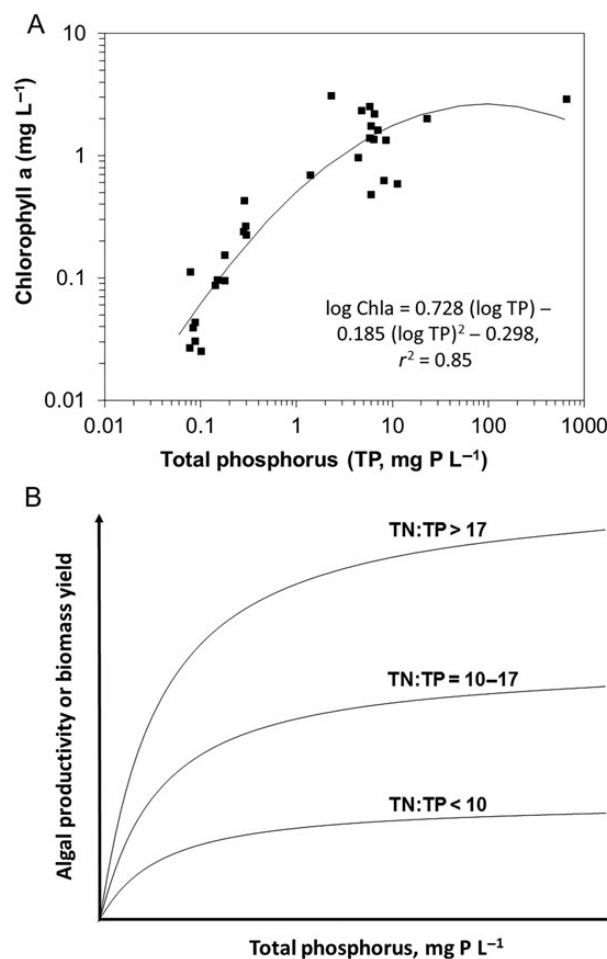


Fig. 1. The nitrogen and phosphorus dependence of algal biomass yield. **(A)** Hyperbolic relationship between growing season average concentrations of TP and algal biomass (measured here as the photosynthetic pigment chlorophyll *a*) in shallow hypertrophic ponds worldwide. **(B)** Algal biomass at a given water column concentration of TP is predicted to increase with an increase in the total nitrogen:total phosphorus mass ratio (TN:TP) (see text).

~200 mg dry wt. L⁻¹ of total suspended solids in the water column (cf. Fallowfield *et al.*, 1999).

Because supplying N and P to microalgal cultivation systems can have significant capital costs, the data in Fig. 1A suggest that creating target water column TP concentrations exceeding 3–5 mg P L⁻¹ is neither necessary nor cost-effective. Moreover, it can be expected that the algal biomass yields produced at any given water column TP concentration will be influenced in part by the total nitrogen:total phosphorus (TN:TP) ratio of the nutrients that are supplied to algal cultivation systems (Fig. 1B; see Smith, 1979, 1982). Although the demonstrated effects of N:P ratios on phytoplankton growth and species composition have been the focus of extensive research in both freshwater and marine ecology for almost four decades

(Rhee, 1978; Sterner and Elser, 2002; Klausmeier *et al.*, 2004), N:P ratios are explicitly considered in relatively few papers in the algal biofuels arena (for recent exceptions, see Mayers *et al.*, 2014; Rasdi and Qin, 2015). We therefore strongly suggest that extensive research is warranted on the effects of resource supply ratios on biomass yields, species composition and quality of biomass produced by large-scale algal cultivation facilities, whether they use closed photobioreactors or open pond-based systems.

We further suggest that the core principles of nutrient physiology and ecological stoichiometry (Sterner and Elser, 2002) can help contribute significantly to analyses of resource sustainability in algal biofuels production. It has been known for more than four decades that the specific growth rate (μ , day^{-1}) of a cultivated algal population is a function of the intracellular nutrient quota, Q , of the individual algal cells (Droop, 1974; see also Leadbeater, 2006 and Pahlow and Oschlies, 2013). In turn, the inverse of cell quota ($1/Q$) is the Nutrient Use Efficiency of the algal cells (NUE, 1 mg of algal biomass produced per 1 mg of cellular nutrients). The value of NUE is exceptionally important because it provides a direct, quantitative measure of the nutrient demands of algal production and thus also provides a measure of the nutrient-associated economic costs of biomass cultivation.

The value of NUE is known to vary widely among different algae, but for any given algal species or strain, the magnitude of NUE is highly sensitive to variations in local environmental conditions (National Research Council, 2012; Shurin *et al.*, 2013). For example, the classic continuous culture experiments performed by Rhee and Gotham (1981b) demonstrated that the intracellular stoichiometry of N-limited algal cells changed with light availability, resulting in a significant decline in Nitrogen Use Efficiency when the incident light was reduced from 17.1 to 11.8 W m^{-2} (Fig. 1C). As a result, the associated daily nitrogen costs of algal production ($\text{mg N L}^{-1} \text{d}^{-1}$) increased at all chemostat dilution rates. Variations in environmental temperature also can have strong effects on cell nutrient quota (Rhee and Gotham, 1981a) and thus can similarly affect resource costs. The mechanistic model incorporating dynamic multi-nutrient, light and temperature interactions in phytoplankton communities developed by Flynn (2001) is also directly relevant to questions related to the resource control and elemental nutrient demands of algal biomass production.

We thus very strongly urge that the biofuels industry pay greater attention to environmentally induced variation in Nutrient Use Efficiency of cultivated algal crops and request that both researchers and modelers discontinue assuming a fixed Redfield Ratio stoichiometry of 106C:16N:1P by atoms for the elemental content of algal

cells. We also suggest that there is a critically important need for the routine analysis and sharing of data on the elemental composition of the algal biomass that is produced, because these data can be used to guide future modeling and facility design efforts. The economic implications of variations in the resource costs of algal biomass production will be addressed briefly below, in the section on Optimal Harvesting Theory.

Planktonic community structure and consumer controls of algal production

Existing algal biomass production systems range in areal extent from ~ 0.5 to ~ 400 hectares (Borowitzka, 2005), but algal cultivation facilities will have to be scaled up by many orders of magnitude in order to attain the production targets that will be necessary for algal biofuels to contribute significantly to global renewable energy needs (Wigmosta *et al.*, 2011). Three different views of algal cultivation systems are shown in Fig. 2, which contrasts an idealized algal monoculture (Fig. 2A) grown in a hypothetically “contamination-proof” biomass cultivation system with two views of more “real-world” systems that acknowledge the presence of other species (Figure 2B and C). Indeed, carefully controlled laboratory-scale monocultures can quickly experience contamination (Huisman *et al.*, 1999; Verschoor *et al.*, 2013), and even in closed photobioreactors, the complete destruction of microalgal crops has been recorded within 48 h of the first detection of an aggressive invading protozoan grazer (Forehead and O’Kelly, 2013). Although a few exceptions have been reported (e.g. Moheimani and Borowitzka, 2006), a majority of the published literature suggests that maintaining single-species mass populations of microalgae will be exceptionally difficult (Persoone and Claus, 1980; De Pauw and De Leenheer, 1985). We are convinced that contamination of open, large-scale algal production systems will be essentially certain during long-term continuous operation (>4 – 6 months), because they will be constantly exposed to potential invasions by other species from the local and regional environment (Smith and Crews, 2014).

Biotic contamination thus can have strong detrimental effects on production and can be considered to be a major potential bottleneck in microalgal cultivation in open systems (Mooij *et al.*, 2015). In particular, open ponds will be constantly exposed to immigration by a diverse set of aquatic consumers that range from crustacean zooplankton to insect larvae, rotifers and protozoa (De Pauw and De Leenheer, 1985). The diversity of herbivorous consumers can be expected to scale positively with the surface area of the pond (Smith and Crews, 2014), and their grazing can be expected to cause strong and undesirable oscillations in algal biomass yield and

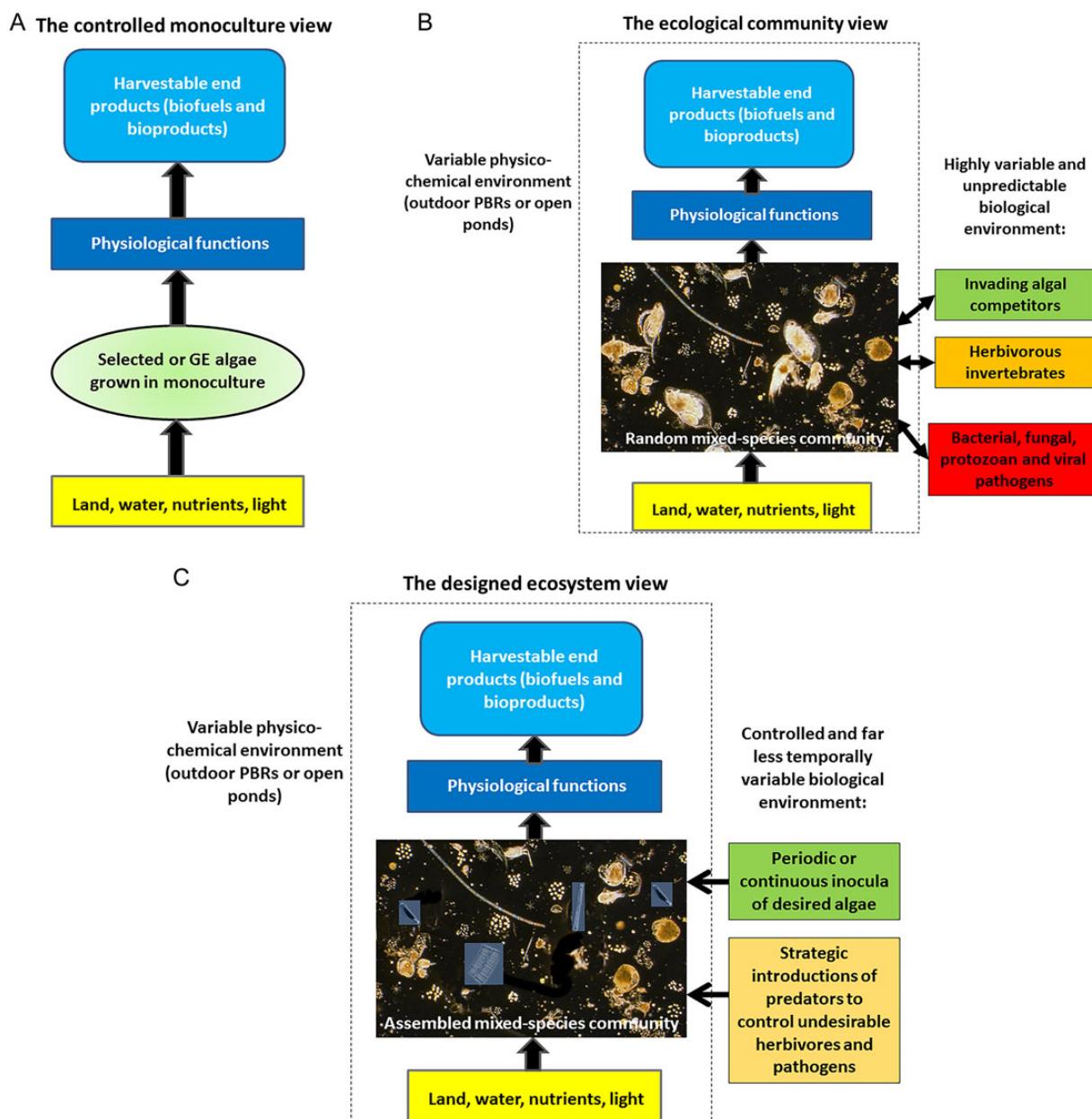


Fig. 2. Three different views of large-scale algal cultivation systems (see text).

species composition. It will therefore be essential to regulate top-down interactions in large-scale biomass cultivation systems (Smith *et al.*, 2010; Kazamia *et al.*, 2012, 2014; Nalley *et al.*, 2014) in order to avoid potentially devastating losses to herbivores, and to maximize algal biomass yields.

Acknowledging that contamination is almost certain if open ponds are used for cultivation, we suggest that commercial-scale algal biomass production may perhaps best be accomplished using carefully designed mixed-species assemblages (Fig. 2C). For a number of reasons,

including the phenomenon of biomass over-yielding in multi-species assemblages, the polyculture cultivation approach has strong advocates (Smith *et al.*, 2010; Kazamia *et al.*, 2012, 2014; Shurin *et al.*, 2013; Stockenreiter *et al.*, 2013; Nalley *et al.*, 2014). Moreover, it is important to note that Plötner *et al.* (2015) have recently reported that the presence of heterotrophic flagellates (micrograzers) may enhance nutrient availability and thus may increase microalgal yield in bioreactors much in the same way as heterotrophic protists can enhance microalgal growth in natural food webs. Nonetheless, we acknowledge that

polycultures can be expected to exhibit significant temporal variations in crop species composition, yield and quality. For example, [Regan and Ivancik \(1984\)](#) found that species composition and dominance in open outdoor cultures of marine microalgae depended upon multiple factors, including the species composition of the inoculum, resource limitation, the hydraulic retention time of the system and local variations in temperature and salinity.

Despite potential complications, we believe that the concept of commercial-scale algal polyculture is likely to be a viable one, and we strongly urge intensive new research into the relative costs and benefits of monoculture-based versus polyculture-based algal production systems. A number of key questions must be addressed, however, including: Can temporal variability in aquatic community structure be predicted and controlled? Can crop rotation in space and in time help to reduce or stabilize this temporal variability ([Liebman and Dyck, 1993](#); [Lin, 2011](#))? We note in this regard that [Kenney and Flynn \(2015\)](#) suggest the selection of different crops to suit the variation in dilution rates, nutrient loading, and incident light regimes that can occur throughout the course of a year. Will the exceptionally high nutrient loading that is supplied to algal biofuel production systems reduce the stabilizing effects of biodiversity ([Hautier et al., 2014](#))? Will variation in community composition significantly affect harvesting and/or downstream processing of the algal biomass, as well as the molecular composition of the algal biofuels that are produced from this biomass?

Disease ecology and the control of algal pathogens

[Stentiford et al. \(2012\)](#) have argued that disease can potentially limit future food supplies produced by the global crustacean fishery and aquaculture sectors, and we have very strong concerns that the same may likely be true of algal biofuels production. For example, both cyanobacteria and eukaryotic algae are susceptible to infection by a wide range of bacterial, fungal, and viral pathogens ([Smith and Crews, 2014](#); [Carney and Lane, 2014](#)), and there are published reports of open pond systems being decimated by disease within days of initial inoculation ([Letcher et al., 2013](#)).

Nutrient enrichment has strong effects on the incidence and the severity of aquatic diseases ([Johnson et al., 2010](#)), and we thus hypothesize that the extremely high nutrient loading to algal biomass cultivation systems will influence the within-host and between-host population dynamics of most if not all infectious disease agents in the algal cultivation system (Fig. 3). For example, the nutrient-rich open pond cultivation systems operated by Sapphire

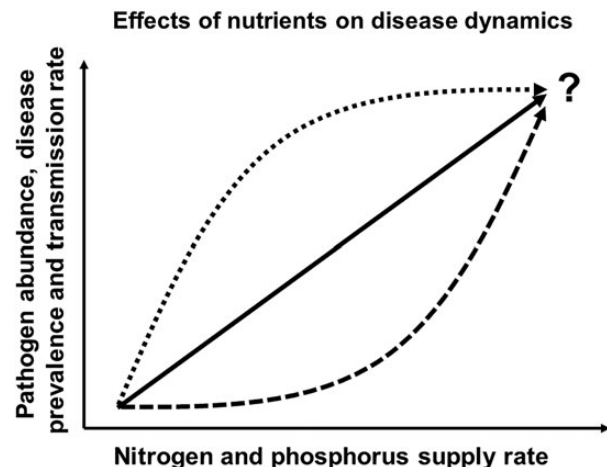


Fig. 3. Increasing nutrient availability may potentially increase the intensity and dynamics of infectious diseases in algal biomass cultivation systems (see text).

Energy, Inc., frequently experience major infections by basal fungi that, if unmanaged, can cause highly undesirable oscillations in the algal standing crop ([Shurin et al., 2013](#); [McBride and Merrick, 2014](#)).

Because large-scale algal cultivation systems can be expected to experience periodic and sometimes catastrophic losses to pathogens, disease prevention and control will be essential to the success of future algal biofuels production. As in commercial agriculture, the use of chemical agents is one potential solution to this dilemma. However, their intensive use will add to operating expenses, and many chemical control strategies have not been successful at scale for extended periods of time in open ponds used for biofuel production ([McBride and Merrick, 2014](#)). In addition, monitoring for the inevitable appearance of resistance among the targeted pathogens will be essential ([Port et al., 2014](#)). In order to help minimize the need for biocides, we invite aquatic microbial ecologists to explore alternative disease control measures that focus upon strong and reliable biological controls of algal pathogens. For example, biocontrol efforts have been deployed that take advantage of trophic interactions by introducing rotifers into *Arthrospira* cultures to consume contaminating green algae ([Mitchell and Richmond, 1987](#)), and we speculate that carefully designed introductions of rotifers or ciliates might perhaps be used successfully to reduce the abundance of infectious stages of fungal pathogens (see [Schmeller et al., 2014](#)). As in commercial agriculture, we urge aquatic ecologists to evaluate the effects of both species diversity ([Ratnadass et al., 2012](#)) and genetic diversity ([Heal et al., 2004](#)) on disease resistance, as well as the potential value of crop rotation (e.g. [Hwang et al., 2009](#)), in reducing disease risk and disease intensity in large-scale algal biomass cultivation systems.

Optimal harvesting theory

Sustainable long-term harvesting has been a key goal of fisheries science for more than half a century, and this concept was formalized with the development of simple but extremely useful mathematical models by Milner Schaefer of the Scripps Institution of Oceanography (Schaefer, 1954; see Zabel *et al.*, 2003). The theory of maximum sustainable yield was originally developed for marine fisheries, and not surprisingly, this concept has been infrequently cited in the algal biofuels literature until recently (e.g. Xu and Boeing, 2015; Bartley *et al.*, 2015). Nonetheless, we believe that harvesting theory is exceptionally relevant to the sustainable future production of algal biofuels, whether the algal production facility is run as a batch culture (e.g. large-scale heterotrophic production of *Chlorella*; see Barclay *et al.*, 2013), as a continuous culture (e.g. the computer-modeled facility analyzed by Rogers *et al.*, 2014), as a semi-continuous culture open pond (e.g. Sapphire Energy's Columbus site: www.sapphire.com) or as a hybrid system comprised of semi-continuous culture PBRs linked to batch culture ponds (e.g. Cellana's ALDUO™ system: Huntley *et al.*, 2015). In particular, it will be important to optimize both the fraction of culture volume that is removed per harvest and the harvesting frequency.

An important general feature of sustainable yield models for any harvested organism is recognition that its population size strongly determines its growth rate (Zabel *et al.*, 2003). The population growth rate (expressed as the number or biomass of new organisms that is produced per unit time) is low when its population size is small, and competition for potentially growth-limiting resources is very low. At progressively higher population densities, the growth rate slows to zero as the population nears its maximum abundance (the environmentally controlled carrying capacity), because the organism's growth and reproduction are increasingly constrained by density-dependent processes such as resource competition. Intermediate-sized populations therefore have the greatest ability to produce the most harvestable fish per year, and the maximum sustainable yield (Y_{msy}) from a harvested population is obtained at an intermediate level of harvesting effort (H ; in this case, the fraction of the total population harvested at any given time).

These concepts are illustrated in Fig. 4 using data from Droop's (1974) classic chemostat studies of the marine microalga *Monochrysis lutheri*. As can be seen in Fig. 4A, there is a strong inverse relationship between algal biomass (in this example, measured as cell density B_{cell} , cells mL⁻¹) and the dilution rate (D , day⁻¹) of the continuous cultures. Moreover, because each harvested algal cell contains a cell quota (Q , nmol cell⁻¹) of essential

chemical elements such as carbon, nitrogen and phosphorus, the resource costs per unit volume of algal production ($Y_{nutrient}$, mol L⁻¹ d⁻¹) increase with dilution rate D (equation 1):

$$Y_{nutrient} = D \times B_{cell} \times Q. \quad (1)$$

The example shown in Fig. 4B illustrates the particulate phosphorus requirements of algal production (Y_P , μmol P L⁻¹ d⁻¹) for a wide range of dilution rates; we stress, however, that this value is not necessarily the total phosphorus cost of production, because unabsorbed dissolved inorganic and organic P will be exported in the harvested outflow as well. Significant monetary costs may result from meeting these and other nutrient requirements of algal biomass production, and we note later in this section that these resource-associated costs will contribute to total production costs at any given harvesting effort H and therefore will influence the maximum economic yield of a production facility. However, we also stress that there may be significant environmental costs as well. The continuous application of fertilizers to feed ever-increasing human demands for food and energy production has the potential to result in the nutrient pollution of global terrestrial, aquatic and atmospheric environments, and it is critically important that solutions be found that will allow us to meet future energy demands in an environmentally sustainable manner that allow the production of greater energy yields with fewer land, energy and resource inputs (Germaine *et al.*, 2010; National Research Council, 2012; Pate, 2013).

The production of algal biomass (Y_{cell} , cells L⁻¹ d⁻¹) at any given dilution rate D can be calculated using the following equation:

$$Y_{cell} = D \times B_{cell}, \quad (2)$$

and Schaefer's (1954) model predicts that the relationship between algal biomass yield Y and harvesting effort H should exhibit a humped curve:

$$Y = aH - bH^2. \quad (3)$$

The maximum sustainable yield (Y_{msy}) of algal biomass grown in continuous culture is predicted to be obtained at an intermediate harvesting effort that is equal to one-half of the maximum per capita growth rate (μ_{max} , day⁻¹) that is exhibited by the target species under a given set of environmental conditions (temperature, nutrient and light availability).

Consistent with the general predictions of equation 3, Fig. 4C confirms a strongly humped relationship between total biomass yield and harvesting effort H , which was equal to the chemostat dilution rate in Droop's (1974)

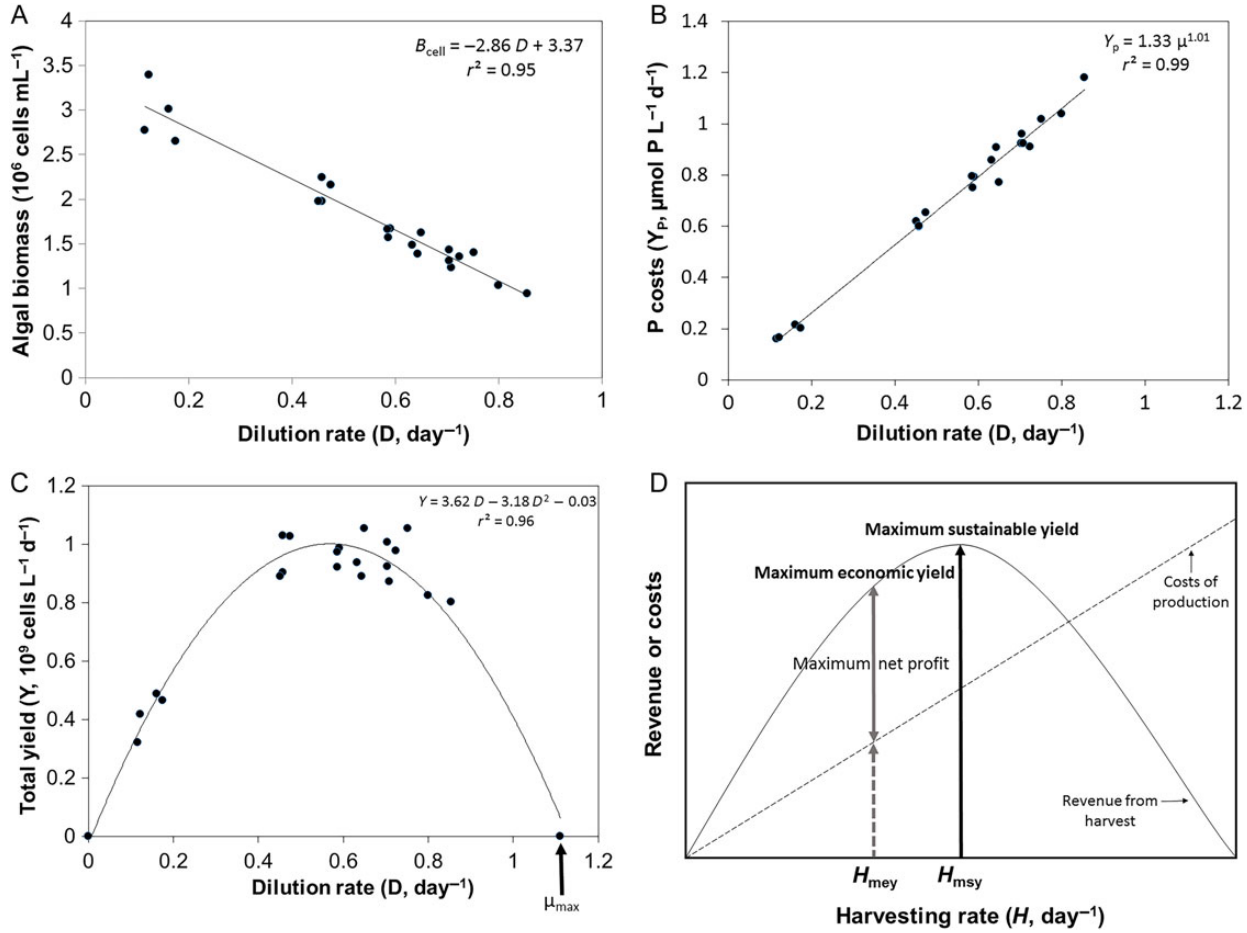


Fig. 4. Optimal Harvesting Theory for algal biomass cultivation systems. (A) Linear inverse relationship between algal biomass and dilution rate for chemostat-grown algal cells (data from Droop, 1974). (B) Positive relationship between the phosphorus costs of algal biomass production and dilution rate for chemostat-grown algal cells (data from Droop, 1974). (C) Humped relationship between algal biomass production rate and dilution rate for chemostat-grown algal cells (data from Droop, 1974). (D) A simple fixed-price model for profit and cost in an open-access algal biomass production system operated at different harvesting rates (modified from Fig. 1 in McManus, 1995).

study. Moreover, the hump occurs at a dilution rate that is one-half of the physiological maximum growth rate of the algal cells (μ_{max}). It is important to note that the *in silico* experiments performed by Flynn *et al.* (2013) also revealed humped relationships between dilution rate and the areal rates of both algal biomass and biofuel production. Expanding upon this important work, Kenney and Flynn (2015) have used computer models to explore the optimization of algal biomass and biofuel production through careful selection of dilution regimes, strain characteristics, system optical depth and nutrient supplies across a wide range of geographic and seasonal light conditions.

Because the commercial production of algal biofuels will be a for-profit enterprise, we present a simple fixed-price model for profit and cost in an open-access production system in Fig. 4D. In this conceptual model, maximum sustainable yield coincides with the point of maximum gross

profit. However, maximum net profit occurs at the fractional harvesting rate that results in maximum economic yield (H_{mey}), which occurs at the point of greatest difference between the gross profit derived from the harvested product and the total costs of harvesting (modified from Fig. 1 in McManus, 1995). As shown in Fig. 4D, maximum profit typically occurs at a harvesting rate that is lower than the value of H that results in maximum sustainable yield (H_{msy}).

We are convinced that the algal biofuels industry will substantially benefit from the integration of direct experimentation with mathematical modeling efforts designed to assess different harvesting strategies under a wide variety of environmental conditions. For example, in the USA, the Algae Testbed Public-Private Partnership (www.atp3.org) operates a collaborative network of cultivation facilities designed to help standardize production methods and

optimize algal biomass yields. Since 2014, parallel experiments have been run at each of five geographically diverse sites in replicated open mini-ponds that are operated as semi-continuous cultures. In 2015, these mini-ponds are being used to test methods to improve productivities and reduce production costs. Whether the algal crop being cultivated is grown as a monoculture or as a mixed-species polyculture, real-world experiments such as those currently being performed by ATP³ should be coupled with *in silico* modeling efforts such as [Flynn et al. \(2013\)](#) in order to assess how variation in local environmental and climatic factors can influence the optimal harvesting effort (H) and frequency of harvesting (n) that is being applied to the biomass production system. Consideration of bioeconomic models of aquaculture (e.g. [Pascoe et al., 2002](#)), and models for the commercial harvesting of marine macroalgae ([Lukeman et al., 2012](#)), also may provide helpful guidance.

Algal biofuels production in a changing environment

Just as future global change will force us modify the agricultural methods used to produce food, cultivation systems for biofuels production also are likely to be strongly influenced by changes in local environmental conditions. Understanding how biofuel production will be affected by future changes in climate is important for achieving a sustainable biofuels economy, and [Tulbure et al. \(2012\)](#) recently used a climate envelope approach to explore the responses of switchgrass, a terrestrial bioenergy crop, to future climate change. Similarly, we expect that the algal species and the cultivation conditions that are optimal today for biofuels production may not be optimal in future decades. Shallow waterbodies are particularly sensitive to environmental change ([Meerhoff et al., 2012](#)), and we predict that the exceptionally shallow (typically 15–30 cm operating depth) ponds used in algal biomass cultivation will be extremely susceptible to changes in key climatic variables such as temperature. Changes in water temperature can be expected to act upon the resident pond biota through changes in species composition, growth, and reproduction ([Daufresne et al., 2009](#)). In addition, [Schabhuettel et al. \(2013\)](#) concluded that algal species richness is an important factor in determining phytoplankton community performance under varying temperature conditions. However, the details and the practical implications of these temperature effects are neither fully known, nor currently predictable. We thus urge plankton ecologists to assist the emerging algal biofuels production industry in recognizing, responding to and coping with the possible consequences of future climate change.

There are many key climate-related questions that need to be answered. For example, in what ways will

plankton dynamics in algal biomass cultivation systems be modified by warming, and will the direction and magnitude of such dynamical changes differ among pond facilities that are being operating at different geographical locations? How, and to what degree, will changes in local seasonal variation (longer, hotter summers; shorter, warmer winters) alter cultivation system performance at any given location? Because warming alters the metabolic balance of ecosystems ([Yvon-Durocher et al., 2010](#)), will warming-driven increases in cellular respiration relative to photosynthesis have net negative effects upon net primary productivity and achievable algal biomass yields? Based upon the results of mesocosm studies performed by [Yvon-Durocher et al. \(2011\)](#), could warming increase the proportion of primary production emitted from the algal cultivation ponds as methane (a greenhouse gas that is 25 times more potent per mole than CO₂)? Will warming alter the nutrient requirements and/or the energy content of the harvested biomass, and if so, in what direction(s)? Will the invasion risk and subsequent proliferation of low-lipid cyanobacteria increase with warming in open algal mass cultivation systems, paralleling trends observed in lakes ([Paerl and Huisman, 2008](#); [Wagner and Adrian, 2009](#); [Kosten et al., 2012](#))? Will warmer water temperatures significantly alter the effects of grazers or pathogens on algal standing crops ([O'Connor et al., 2009](#); [Hoekman, 2010](#); [Ibelings et al., 2011](#); [Ewald et al., 2013](#))? Attempts to address these and other emerging questions should be made not only through dedicated research programs but also through the organization of ecological colloquia analogous to those that resulted in the March 2013 special issue of *Freshwater Biology*, which was dedicated to the topic of *Plankton Dynamics in a Fast Changing World*.

In agricultural systems, it has been argued that crop diversification can improve resilience in a variety of ways: (i) by engendering a greater ability to suppress pest outbreaks and dampen pathogen transmission, which may worsen under future climate scenarios, as well as (ii) by buffering crop production from the effects of greater climate variability and extreme events ([Lin, 2011](#)). Similarly, we suggest that crop diversification may potentially benefit large-scale algal biomass production efforts as well.

We also very strongly urge that data obtained from careful monitoring and experimentation should be examined for evidence of threshold responses to environmental change, because two additional questions are extremely relevant ([Meyer et al., 1999](#)): (i) Will algal cultivation systems change slowly with respect to changing environmental conditions until some ecological threshold is reached, after which sudden and dramatic changes in system state will occur? (ii) will internal variability within

these systems increase as these thresholds are approached? Many aquatic ecosystem changes are non-linear with temperature and exhibit rapid and abrupt responses (Moss, 2012). We therefore suggest that it will be very important to apply state-of-the-art biomonitoring tools and analytical methods (Brock and Carpenter, 2012) to help detect and respond appropriately to early warnings of undesirable regime shifts in algal mass cultivation systems.

CONCLUSIONS

Plankton ecology is a core discipline of freshwater and marine science, and it encompasses all aspects of the biotic and abiotic interactions determining the abundances and distributions of planktonic aquatic organisms (Lüring and de Senerpont Domis, 2013). In particular, the successful large-scale implementation of algal biofuels will require the reliable operation of very large algal cultivation systems whose internal biological dynamics and biomaterial outputs will be strongly governed by predictable and well-established principles of ecology. We strongly believe that applying these principles to algal biomass production will help provide solutions to the environmental challenges that will accompany a growing human population (e.g. CO₂ dynamics and global climate change, aquaculture and edible protein production, sustainable use of nitrogen and phosphorus fertilizers, and wastewater reuse and remediation).

In this Horizons article, we have only discussed a subset of the potential areas in which we believe that aquatic scientists can make important contributions, and we predict that many more population-, community- and ecosystem ecology-related issues will emerge as algal biomass cultivation systems expand from the pilot to the commercial scale during the next several decades. We strongly urge aquatic ecologists to partner closely with colleagues in the biofuels industry in order to help address these future issues as we work together to help meet the world's renewable energy needs.

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