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Review article

Assessing the potential of polyculture to accelerate algal biofuel production

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ABSTRACT

To date, the algal biofuel industry has focused on the cultivation of monocultures of highly productive algal strains, but scaling up production remains challenging. Algal monocultures are difficult to maintain because they are easily contaminated by wild algal strains, grazers, and pathogens. In contrast, theory suggests that polycultures (multispecies assemblages) can promote both ecosystem stability and productivity. A greater understanding of species interactions and how communities change with time needs to be developed. Ultimately a predictive model of community interactions is needed to harness the capacity of biodiversity to enhance productivity of algal polycultures at industrial scales. Here we review the agricultural and ecological literature to explore opportunities for increased annual biomass production through the use of algal polycultures. We discuss case studies where algal polycultures have been successfully maintained for industries other than the biofuel industry, as well as the few studies that have compared biomass production of algal polycultures to that of monocultures. Assemblages that include species with complementary traits are of particular promise. These assemblages have the potential to increase crop productivity and stability presumably by utilizing natural resources (e.g. light, nutrients, and water) more efficiently via tighter niche packing. Therefore, algal polycultures show promise for enhancing biomass productivity, enabling sustainable production and reducing overall production costs.

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1. Introduction

Algae hold much promise as a viable feedstock for biofuels but there is still much discussion over how to make production more cost effective [1–7]. High biomass and lipid yields are achievable from algae cultured under controlled laboratory conditions at the bench scale or in incubators (e.g., photobioreactors). However, cultivation in outdoor pond facilities may be the only cost-effective way to produce algal biomass at the scales needed for the biofuel industry [3–9]. To date, the algal biofuel industry has focused on selecting for (or genetically modifying) algal strains that have rapid growth rates or high lipid contents in order to maximize lipid yields [3,4]. While this strategy can be effective at smaller scales and in the short term, shifting production from the laboratory to outdoor ponds raises a number of ecological challenges [10].

Monocultures are exceedingly difficult to maintain in outdoor settings, because they are easily contaminated through aerial colonization by wild algal strains, grazers, and pathogens [11–13]. In terrestrial systems, the agriculture industry has had to develop multiple layers of defense against such invaders (e.g. herbicides, fungicides, pesticides, genetically engineered organisms, etc.) to optimize yields of monoculture crops. Because aquatic systems are readily invaded by a host of microbes and invertebrates, algal crops are more susceptible to losses due to invading species. Specific interactions of concern include competition, predation (i.e., grazing pressure), and pathogenic interactions. Competition for nutrients and allelopathy (chemical warfare) with non-target algal strains can significantly reduce production rates and/or alter the quality of the biomass produced [14,15]. Predation by grazers or invasion by algal pathogens can decrease the stability of production by destroying mass cultures in a matter of days [16]. It has been estimated that 10 to 30% of annual production in open ponds is lost due to pond crashes induced via consumption of the algal crop by a contaminating grazer or invasion by a crop specific pathogen [11,17]. Additionally, these interactions can influence the temporal consistency of algal biomass production and/or cellular lipid content, thereby affecting the stability of the algal culture. Clearly, crop protection and management will be a critical need for maintaining predictable and stable crop production for the algal biofuel industry as production begins scaling up.

In contrast to the monocultures grown for the biofuel industry, algae in natural ecosystems exist in diverse multispecies assemblages [12], where species abundance can fluctuate as environmental conditions change. Such changes are driven by spatial and temporal heterogeneity in resources such as light and nutrient availability that can change rapidly over time and with depth in the water column, creating multiple niches for species with different optimum light or nutrient conditions. In addition, the landscape of biotic interactions can also vary as grazers or pathogens can often be very selective for an algal strain or group of algae. When these stressors affect an algal population, other algal species within the assemblage can quickly multiply to fill the newly available niche. Although typically no single species in these complex natural system assemblages dominates for any extended period of time, overall algal production can stay relatively stable as long as nutrient concentrations are sufficient and algal species diversity is maintained.

There is much evidence from the agricultural and ecological literature that species diversity can promote both ecosystem stability and productivity [18–20]. These principles have recently been applied to biofuel production of grassland plants and algae with promising results—higher diversity can lead to higher biomass and lipid production than monocultures [21,22]. In addition to providing crop protection from losses due to grazing and infection, there is evidence that algae polycultures can provide a more stable crop [23]. Further, polycultures that effectively combine species with complimentary traits such as for nutrient and light utilization have greater potential for overyielding (i.e., higher productivity or increased biomass quality in the polyculture relative to the most productive monoculture strain [24]).

These studies provide encouraging indications that use of algal polycultures may be an effective approach to enhancing algal biomass production. Applying these principles to long-term, larger-scale production efforts will require a greater systematic understanding of species interactions and how algal communities change with time. Indeed, complex microbial communities are a reality of algal biofuel production at industrial scales. However, diversity is no guarantee of high productivity or stability as only a subset of species combinations display these desirable properties, and only under particular environmental contexts. Identifying consortia of species that consistently yield biomass with useful biochemical composition, and the conditions under which they outperform single species, is therefore a research priority.

In this review, opportunities that algal polycultures offer the biofuels industry for increasing algal biomass yields are highlighted. Specifically, the basic ecological principles that support the theoretical basis for increasing species diversity to increase crop stability and productivity are highlighted and examples are provided of studies that have shown promise for application to the industry. Recent advances in harvesting, extraction, and conversion technologies that make use of algal polycultures, and in turn make their cultivation a more viable solution than previously considered, are also described. Finally, the challenges and potential for improved biomass productivity and stability through implementation of a polyculture strategy are considered.

2. Ecological principles and polycultures

The relationship between ecological diversity and stability has been a subject of debate within the scientific community [25–28]. Theory predicts a positive correlation between diversity and stability in ecological communities [29], but there has been much discussion about how these factors should be defined and quantified. Definitions for ecological stability in the literature can broadly be broken into three categories: (1) the ability to stay unchanged (constancy), (2) the ability to return to the reference state after perturbance (resilience), and (3) persistence through time, and approaches to quantifying stability vary accordingly [30]. For example, biomass productivity may be maintained as the environment fluctuates if species that decline in abundance are replaced by others with different tolerances. Simply increasing the number of species does not necessarily increase the stability of a system if species are functionally equivalent or respond to the environment in a common fashion. That is, species must respond differently to environmental fluctuations or interact in ways that cause their populations to vary asynchronously in order for diversity to enhance ecosystem stability. The species that are present and what role they play in the ecosystem (i.e., functional diversity) is at least as important in determining both ecosystem stability and productivity [22,31].

Likewise, the relationship between diversity and productivity can be positive, either because diverse communities will randomly include highly productive species, or because in the face of fluctuating environmental conditions, diverse assemblages provide greater assurance that at least one species will grow well [32,33]. Within the planktonic (i.e., free floating) algae in natural aquatic ecosystems, the relationship between diversity and productivity is generally positive [12], even though maximum productivity can be seen during low diversity blooms that escape predation [34] which may not be sustainable over longer time periods. The algal biofuel industry will be faced with the trade-off between maximum productivity and crop stability for the long-term, sustained production of algal biomass [10].

Research has shown that polycultures can vary in productivity with respect to their respective monocultures [24], but that higher productivities (i.e., overyielding) are possible with polycultures [10,23,24,31,35]. Underyielding (i.e., when a polyculture yields less than the average of its component monocultures) can result, for example, when a polyculture is dominated by a fast-growing, low-yielding species [14,24] or due to allelopathy, where a secondary metabolite produced by one species is toxic to another [36]. In order to

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