

Crop diversification can contribute to disease risk control in sustainable biofuels production

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Global demand for transportation fuels will increase rapidly during the upcoming decades, and concerns about fossil-fuel consumption have stimulated research on renewable biofuels that can be sustainably produced from biological feedstocks. However, if unchecked, pathogens and parasites are likely to infect these cultivated biofuel feedstocks, greatly reducing crop yields and potentially threatening the sustainability of renewable bioenergy production efforts. In particular, clonal biofuel crops grown as monocultures at industrial scales will be confronted both by an accumulation of specialist pathogens over time, and by the rapid evolution of those pathogens. We propose possible solutions to these important sustainability problems, with a focus on managing disease risk through crop rotations and the cultivation of multi-species polycultures.

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Ethanol and other liquid fuels used throughout the 20th century were critical in the development of early internal combustion engines and automobiles (Simpson *et al.* 2008), and today's transportation sector is served by a very large and reliable liquid fuel infrastructure (Melaina *et al.* 2013). However, global demands for transportation fuels can be expected to increase rapidly in the future, and concerns about fossil-fuel consumption have stimulated research on renewable liquid fuels that can be sustainably produced from biological feedstocks (Hill *et al.* 2006). Currently, the two most prevalent biofuels are ethanol, which is currently produced from sugar or starch crops, and biodiesel. World production of ethanol alone more than doubled between 2000 and 2005, while the global production of biodiesel quadrupled over the same time period (Worldwatch Institute 2006). Biodiesel fuels in particular have received major attention worldwide, both as blending components and as direct replacements for petroleum diesel in vehicle engines (Demirbas 2009). However, in order to be competitive, all renewable fuels

must offer cost, convenience, and reliability comparable to today's fuel supply system (Ogden and Anderson 2011). Moreover, renewable fuels should be derived from biomass feedstocks that have much lower life-cycle greenhouse-gas emissions than fossil fuels, and should be produced with little or no competition with food production (Tilman *et al.* 2009).

What will these biofuel feedstocks be? Annual and perennial plants can be grown and harvested for the production of both biodiesel and ethanol fuels, and the fermentation of waste products such as stems, stalks, or woody components of plants can be used to produce ethanol (Dale *et al.* 2010). In addition, algae are being explored as renewable biofuel sources, and the cultivation of microalgal biomass is already transitioning to commercial-scale production systems (Trentacoste *et al.* 2014). Algae offer many potential advantages over traditional terrestrial biofuel crops, including higher lipid production rates, a lack of competition for arable land, year-round cultivation, the potential to use saline and low-quality water sources, and a viable substitute for existing liquid fuels (Moody *et al.* 2014). Nevertheless, algal biofuels face many unresolved sustainability challenges, and scaling up the production of microalgae to meet even a modest percentage of US transportation fuel demands could strain water, energy, and nutrient resources (Pate 2013). Although improved genetics and cultivation methods can potentially enhance the sustainability and yields of both terrestrial and algal feedstocks, many questions remain about how best to produce biofuels without causing new and unanticipated environmental impacts (Duke *et al.* 2013).

The purpose of this paper is to highlight specific challenges that the biofuels industry could face if large-scale monocultures of either algae or vascular plants are used as a primary biofuels feedstock. Clonal biofuel crops grown at industrial scales might be confronted both by an accumulation of specialist pathogens, and by rapid evolution of these pathogens (McDonald 2014). If unchecked, dis-

In a nutshell:

- The world is experiencing unprecedented demands for energy
- Global energy demands can potentially be met in part through the production of biofuels derived from cultivated terrestrial plants and algae
- Minimizing crop losses to disease organisms will be critically important to the future success of renewable bioenergy
- Evolution- and ecology-based approaches can help to reduce pathogen prevalence and transmission in both terrestrial and aquatic biofuel crops

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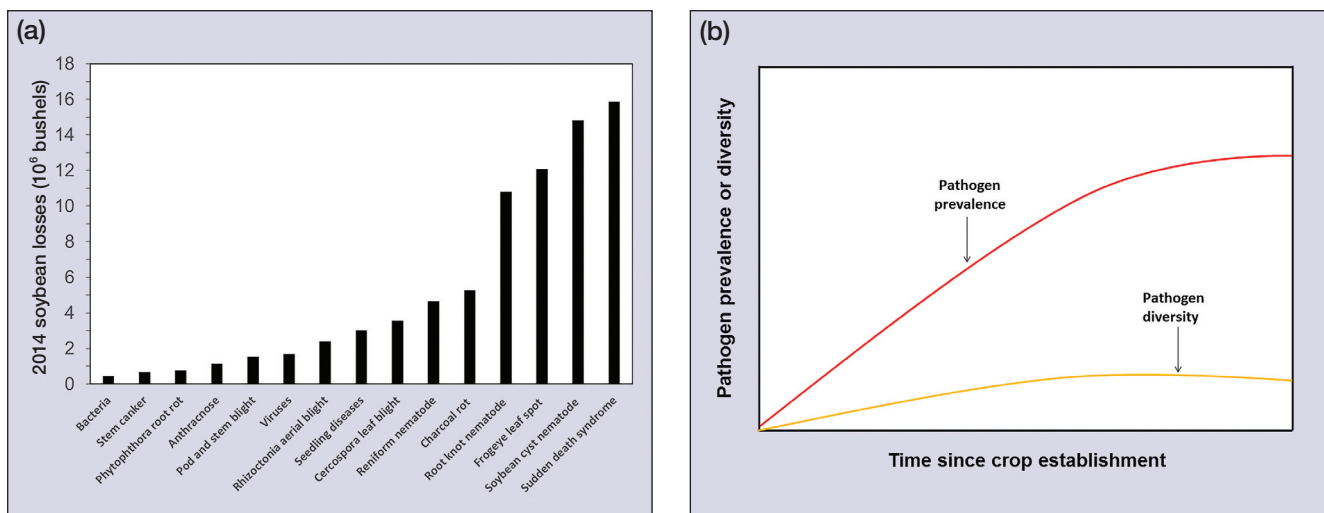


Figure 1. (a) Losses of soybean production to 15 groups of pathogens in the mid-southern US (Arkansas, Louisiana, Mississippi, Missouri, and Tennessee) in 2014; the total estimated annual value of this lost yield was \$886 500 000. Data from <http://mssoy.org/blog/soybean-yield-loss-to-diseases-in-the-mid-southern-us-2>. (b) Hypothesized trends in pathogen prevalence and pathogen diversity over ecological time after the establishment of a biofuel crop monoculture.

ease organisms could harm yields and impede the intended use of these crops (Mekete *et al.* 2009). Minimizing crop losses to pathogens and parasites is therefore important for the future success of renewable biofuel production.

We suggest that the problems historically faced by agriculture can help to inform the development of commercial-scale biofuel feedstocks. In agro-ecosystems, disease development depends upon interactions in time and space between host plants, pathogens, the environment, and humans (Bousset and Chèvre 2012). For example, McDonald (2014) noted that pathogen transmission was facilitated as a result of the increased density and genetic uniformity of host plant populations in agro-ecosystems relative to natural ecosystems, enabling an increase in pathogen virulence. Large population sizes of pathogens also led to greater genetic diversity by increasing the total number of mutations available at the field level, while simultaneously decreasing the effects of genetic drift. Over time, pathogen evolutionary potential has likely increased as fungi, bacteria, and viruses have become adapted to the agro-ecosystem environment and to the most widely cultivated crop genotypes.

By way of example, the negative impacts of a highly diverse set of pathogens on US soybean production in 2014 are illustrated in our Figure 1a, and potential global losses to pathogens for six major terrestrial crops are summarized in Table 1 of Oerke (2006). Even non-food terrestrial biofuel crops such as camelina (*Camelina sativa*), elephant grass (*Pennisetum purpureum*), jatropha (*Jatropha curcas*), and switchgrass (*Panicum virgatum*) are susceptible to a diversity of disease agents. Moreover, proposed genetic modifications of terrestrial crops for biofuels production may increase their susceptibility to viral infection and crop losses (Schrotenboer *et al.* 2011).

Algal populations can be similarly plagued by patho-

genic bacteria, fungi, protozoa, and viruses, and can experience major disease outbreaks in both natural and artificial populations. Gachon *et al.* (2010) recently reviewed the effects of pathogens on aquatic primary producers in both freshwater and marine ecosystems, including their socioeconomic and ecological impacts. Infectious diseases therefore potentially pose a major problem in the algal biofuels arena as well (Carney and Lane 2014; Smith and McBride 2015).

The accumulation of host-specific soil pathogens can rapidly reduce the productivity of individual species in terrestrial plant communities (Bever *et al.* 2012). It therefore seems plausible that increasing pathogen abundance and diversity over time (Figure 1b), as well as evolutionary changes that promote pathogen virulence, could impede sustainable low-cost biofuels production in commercial-scale biomass cultivation systems, whether the biofuel feedstock is obtained from terrestrial plants or from algae. Within vascular plant monocultures, changes in the abundance and composition of otherwise beneficial microbes such as rhizosphere bacteria and mycorrhizal fungi can reduce plant growth (Bever 2002), and microbial negative-feedback mechanisms can make terrestrial biomass yield declines in plant monocultures highly predictable. For example, an accumulation of fungal soil pathogens at the expense of plant-beneficial fungi accompanied the consecutive cultivation of peanut monocultures in China (Li *et al.* 2014), and the biodiversity of major soil pathogens increased over time (X Wang *pers comm*). Similarly, with regard to algal biofuels, strains of eukaryotic microalgae grown outdoors by Sapphire Energy, Inc. were susceptible to substantial disease-related losses (Figure 2a). Such open pond systems tend to become more contaminated over time because of continuous biological invasions from the surrounding environment: fungal pathogens increased in abundance

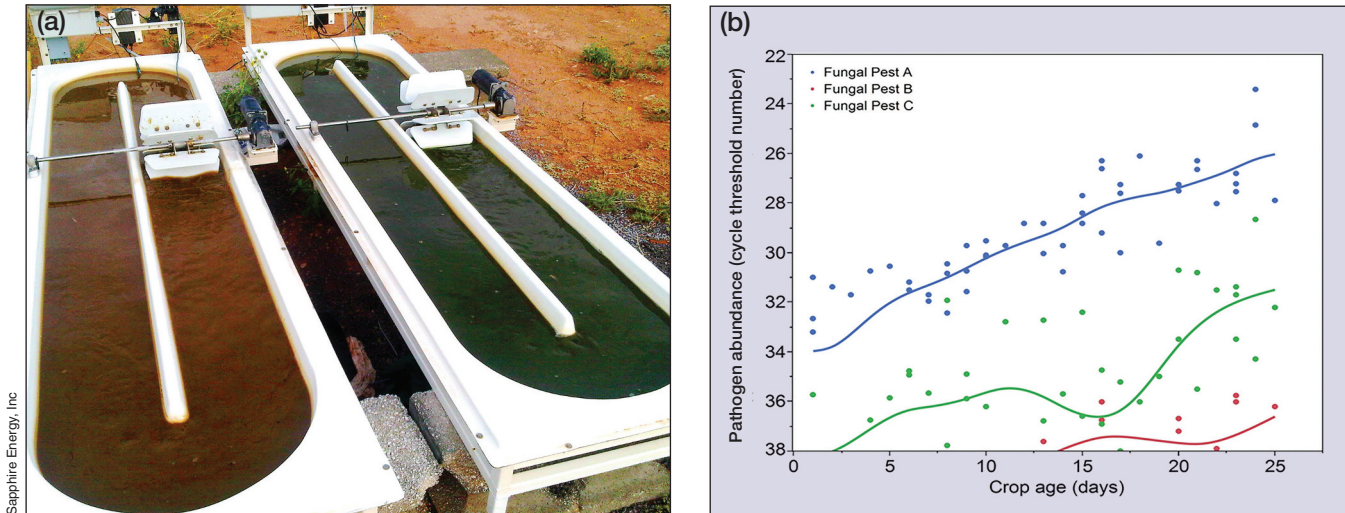


Figure 2. (a) Open mini-ponds operated by Sapphire Energy, Inc. The mini-pond on the left shows the near-total algal crop loss to a chytrid pathogen, whereas the mini-pond on the right illustrates what a productive pond looks like. (b) Both the abundance and diversity of pathogen strains were observed to increase over time in an open raceway pond operated by Sapphire Energy, Inc, using a polymerase chain reaction (PCR) approach. Note: the “cycle threshold number” decreases as fungal pathogen abundance increases. Fungal pest A (blue dots and trendline) is *Amoebophilidium protococcarum*, and fungal pest B (red dots and trendline) is *Amoebophilidium occidentale*; fungal pest C (green dots and trendline) is currently unknown but is genetically distinct from the first two pests.

in the water column and pathogen diversity increased with time since inoculation (Figure 2b).

The high crop densities of commercial-scale biofuel production systems may also result in pathogen-driven negative feedbacks. Introducing vascular plant biofuel crops from other continents could initially reduce the rate of negative feedbacks by escaping the crops’ co-evolved natural enemies. However, this release from negative feedbacks may be transitory, because generalist pathogens of abundant host species may acquire greater virulence over time through natural selection (Thrall *et al.* 2011), and specialist pathogens from the native region may eventually colonize the host’s introduced range. As a result, negative feedbacks on naturalized plant species increase steadily after invasion of previously unoccupied areas (Diez *et al.* 2010): an effect that is particularly well documented in the agricultural sector for rice (see Cassman *et al.* 2003).

Even with phytosanitary measures in place, specialist crop pests have typically accompanied the movement of their plant hosts, with serious consequences; the Great Irish Potato Famine is a prime example (Donnelly 2005). Diseases have already been observed in non-native biofuel species such as elephant grass and jatropha, and their pathogens are expected to become more abundant and more diverse if these plant species are cultivated extensively. Smith and Crews (2014) emphasized that by the middle- to late-20th century, terrestrial plant breeders became highly successful in the development and application of resistance genes designed to stop or slow disease proliferation; however, in mass cultivation the genetic uniformity of these disease-resistant varieties promoted pathogen evolution and subsequent crop resistance failures. We

believe that these agricultural experiences also have important implications for the production of algal biofuels: avoiding genetic uniformity in cultivated crops is likely to be a wise strategy (Smith and Crews 2014).

We predict that the continuous cultivation and harvesting of single-strain biofuel monocultures will favor the accumulation of pathogenic organisms that will progressively reduce crop yields over time (Figure 3a). In the sections below we propose possible solutions to this problem.

■ Biological methods of disease control: the importance of crop diversity

Evidence from commercial agriculture operations suggests that managing disease risk in monocultures using pesticides and standard cultivation and breeding practices can have limited success (see Figure 1a), and can also become progressively more expensive over time, undermining the economic feasibility of biofuels. Managing plant disease risk by enhancing crop diversity offers the potential benefits of stable yields, as theoretically illustrated in Figure 3b.

A central tenet of epidemiology is that both the number of diseases and the incidence of disease should rise as host abundance increases (Lin 2011). Improving the diversity of cultivated species can reduce pathogen infection rate and loss of yield in two ways. First, populations of specialist crop pathogens tend to flourish when low crop diversity increases the absolute abundance of their preferred host species, making pathogen transmission more probable (Pagán *et al.* 2012). This effect is consistent with Root’s (1973) resource-concentration hypothesis, in which the abundance of specialist arthropod herbi-

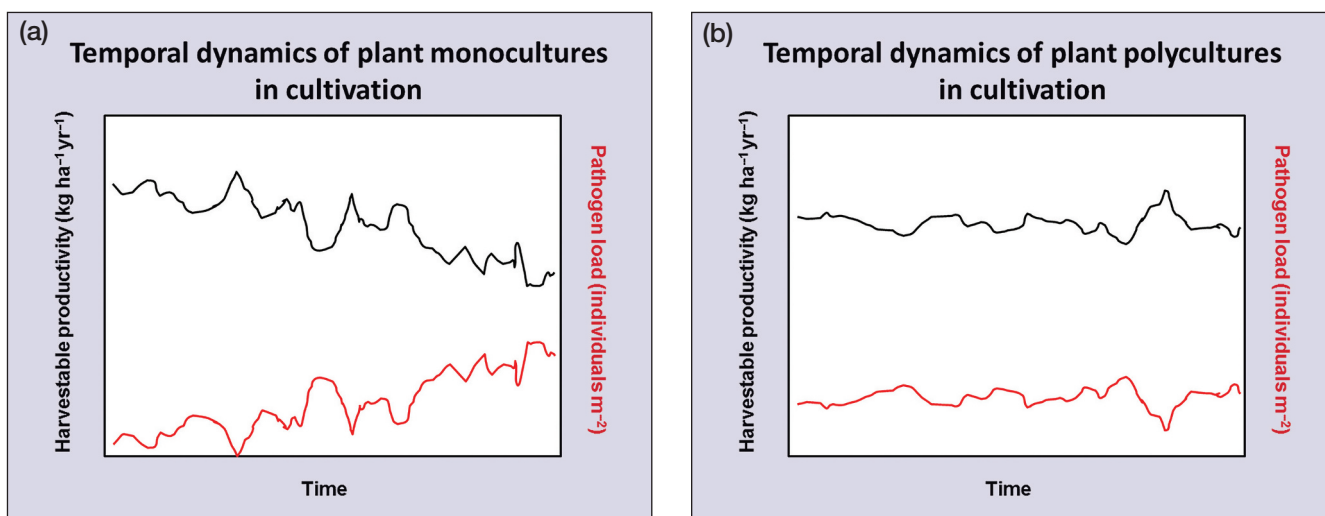


Figure 3. (a) Net productivity in crop monocultures is hypothesized to decline as the total pathogen load increases over time. The conceptual time trends represent the maximum potential productivity and minimum potential pathogen loads that might be expected if chemical disease management strategies are deployed, but these crop protection strategies will also contribute substantially to total production costs. (b) The cultivation of carefully assembled crop polycultures is predicted to provide pathogen load control benefits, and thus more consistent productivity levels – but with lower capital and operating costs, and with potentially greater long-term effectiveness.

vores on plants (defined as density per unit mass of the host-plant species) is expected to decline at progressively higher levels of plant community diversity. Root's hypothesis thus predicts a negative correlation between crop biodiversity and disease risk (Pagán *et al.* 2012). The resource-concentration hypothesis has endured over time, but more complex outcomes from various field experiments may be relevant to the management of biofuel systems. For example, Otway *et al.* (2005) found a positive relationship between successful colonization of a specialized herbivore on a host plant and that plant's abundance, a finding consistent with the resource-concentration hypothesis. However, the authors discovered that once the host plants were colonized by herbivores, there was a negative relationship between herbivore load and host-plant abundance. They called this a "resource dilution" effect because the low-diversity systems essentially diluted the herbivore load with greater host abundances. Rapid microbial growth rates may make resource dilution less likely to occur with pathogens, but further research on particular crop compositions will be necessary to explore this effect in biofuel systems.

The second way in which enhancing the diversity of cultivated species can reduce pathogen infection rate is by reducing the rate of evolution of crop-pathogen virulence, thereby elevating the long-term efficacy of resistant crop varieties. The use of polycultures (co-cultivating susceptible crop varieties or species among resistant crop varieties or species) is therefore predicted to slow the evolution of resistance mechanisms in crop pathogens (Thrall *et al.* 2011). For instance, to slow or prevent pest organisms from evading *Bacillus thuringiensis* (Bt) resistance genes inserted into single-trait transgenic corn hybrids, farmers are required to plant 20% refugia, in order to maintain Bt

susceptibility within the pest population (Cullen *et al.* 2008); these refugia provide separate areas of toxin-free crop for susceptible pest organisms. Intra- or interspecifically diverse crop communities are also less likely to facilitate rapid evolution of virulent pathogens, which may invade the biofuel production system from wild or weedy populations (Burdon and Thrall 2008).

The importance of diversity in disease control is clearly evident in an experiment by Mitchell *et al.* (2002), which directly manipulated grassland plant species richness and composition. In this study, the average pathogen load was almost three times greater in the single-species monocultures than in plots planted with 24 grassland plant species (Figure 4). Eleven individual plant diseases increased in severity (measured as the percentage of leaf area infected by a single disease) with a decrease in plant species richness, and the severity of only one disease was positively correlated with diversity.

The value of using of mixed-species plant assemblages (multiline cultivars and cultivar mixtures) for disease management has been well demonstrated in the field (Mundt 2014). In agroecosystems, disease-susceptible rice varieties planted in mixtures with resistant varieties produced 89% greater yield, and rice blast disease was 94% less severe, than when grown in monoculture (Zhu *et al.* 2000). Similarly, in a comparative analysis of large-scale intercropping experiments on 15 302 ha of farmland, Li *et al.* (2009) demonstrated the advantages of intercropping for enhanced agricultural yields and disease prevention. Rottstock *et al.* (2014) recently confirmed that pathogen incidence and severity, and thus overall infection, decreased with increasing plant species diversity in experimentally manipulated European grasslands; co-infection of individual plants by two or more pathogen

groups were less likely with increasing plant community diversity. Additional benefits of species diversity for vascular plant disease and pest control were reviewed by Ratnadass *et al.* (2012).

We are therefore confident that the dual benefits of improved protection against disease (Figure 4; see Mitchell *et al.* 2002) and enhanced biomass yields (Tilman *et al.* 2006; Shurin *et al.* 2013) can be expected to occur in high-diversity biofuel crop communities, whether they comprise vascular plants or algae. The presence of alternative hosts will tend to reduce disease incidence by increasing the number of disease-resistant species, thereby buffering the mixed-species community from infection (the “host diversity dilution effect”; see Keesing *et al.* 2010). Moreover, because each of the multiple species being grown within the biofuel production system will respond differently to other kinds of physical, chemical, and biological variation in the local environment, maintaining a high species and trait diversity in the production system will help to offset negative impacts associated with environmental fluctuations, and to ensure the maintenance of functional capacity against human management failures (Lin 2011).

We therefore suggest that manipulating biodiversity at multiple temporal and spatial scales will be critical to the stability of future bioenergy systems based on microalgae. First, high crop diversity within a pond may dilute disease spread and may also maintain pond productivity when one species is infected with pathogens and experiences population declines. Compensatory dynamics occur when other species in the same community increase in abundance due to competitive release and replace the productivity lost to epidemics. Second, diversity may be important to a strategy of crop rotation or turnover in cultivated algal species through time. Pathogens that accumulate in the water column may reduce the fitness of cultivated strains so that productivity cannot be maintained in the long term. In addition, seasonal niches may allow species to maintain productivity, for instance, when cold-season species replace those that are most productive in warmer months. Finally, algae are typically grown in arrays of multiple ponds, and the productivity of an entire array may be at risk if only one algal strain is grown and a specialized pathogen sweeps through one or more pond arrays. Thus, we argue that the domestication of algal strains for the production of bioenergy will necessarily involve the deployment of a diverse suite of potential taxa to maintain stable productivity. Polyculture-based strategies that explicitly harness the complementary traits of algae that lead to over-yielding, and to resilience against disease and consumers, will be much more likely to result in commercially viable bioenergy production systems.

Investing in monocultures of genetically engineered or genetically selected species carries additional risks associated with the loss of an essential trait. In algal biofuel pro-

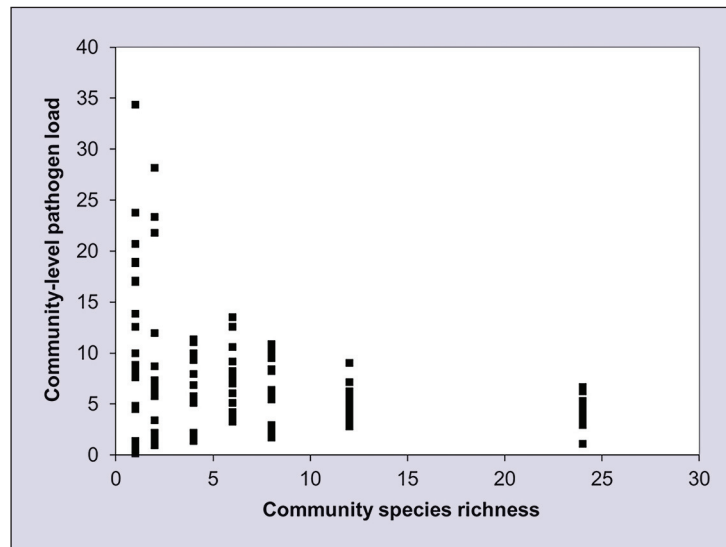


Figure 4. Strong suppressive effects of increasing vascular plant diversity on pathogen load, as measured by community-wide disease severity, have been confirmed in experimentally manipulated grassland communities. The inverse relationship between plant diversity and pathogen load is highly significant ($P < 0.001$). Data replotted from Figure 1a in Mitchell *et al.* (2002).

duction systems, the crop could become dominated by mutant algal strains that no longer invest energy in the production of lipids, because the mutants would likely be better resource competitors than the original high-lipid strains. Zevenboom *et al.* (1981), for instance, observed that a mutant cyanobacterium that did not fix nitrogen (N) rapidly outcompeted the original N-fixing strain in a light-limited continuous culture. Nitrogen fixation is energy expensive, and by giving up N fixation in an environment in which inorganic N was not growth-limiting, the mutant cyanobacterial strain was able to continue increasing in abundance under low light conditions that prevented any further growth of the N-fixing strain. Similarly, because algal allocation to lipids is energy expensive and provides no fitness benefit under rapid culture conditions, genetic mutants that spontaneously lose this capability would likely increase rapidly in the cultivation system and would thereby reduce net bioenergy production.

■ Conclusions

The complexity of bioenergy production systems will require considerable research to achieve renewable energy solutions that are truly sustainable (Greenwell *et al.* 2012), and we agree with Robertson *et al.* (2008) that the identification of potential problems early in the development of renewable biofuel strategies will help to avoid costly mistakes. Although homogeneity of biofuel inputs may facilitate biofuel processing, monoculture-based biofuel production may ultimately prove to be unsustainable.

Growth in modern agricultural productivity has been underpinned to a large extent by the use of effective

strategies to control disease (Burdon *et al.* 2014). A future in which biofuel crops form a substantial component of human landscapes will pose important challenges in pest control, and it will therefore be crucially important to conduct targeted, preemptive research on disease management as part of the “proof of concept” and risk assessment for new biofuel crops (Fitt 2010). These efforts will create the opportunity to design production systems in a manner that both anticipates and minimizes the negative impacts of pests (Fitt 2010). In addition, we suggest that exploring the benefits of species diversification in biomass cultivation systems, and examining the possible use of crop rotation in space and time (Ratnadass *et al.* 2012), are important biofuels research needs. The deliberate cultivation of carefully assembled or naturally assembled, mixed-species feedstock assemblages (polycultures) may help to reduce or eliminate pathogen accumulation and crop declines, whether the feedstocks are terrestrial vascular plants or algae (see Figure 3b).

Investigations into the beneficial effects of biofuel crop diversity on pathogens and their dynamics through time will be essential to the future design and development of cost-effective, high-yield bioenergy systems. Furthermore, the implementation of evolution- and ecology-based approaches will likely help to promote the sustainability of low-cost commercial-scale biofuels production by suppressing disease outbreaks, and by reducing pathogen prevalence, transmission, and evolution in terrestrial and aquatic biofuel crops without the use of expensive and potentially ineffective chemical pest-management strategies. In particular, the development of novel methods and tools to achieve long-lasting (durable) resistance (Mundt 2014) will be key to the sustainable management of pathogens and other pests in industrial-scale biofuel production systems.

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