### **REVIEW SUMMARY**

### BIOENERGY

# **Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes**

G. Philip Robertson,\* Stephen K. Hamilton, Bradford L. Barham, Bruce E. Dale, R. Cesar Izaurralde, Randall D. Jackson, Douglas A. Landis, Scott M. Swinton, Kurt D. Thelen, James M. Tiedje

BACKGROUND: Cellulosic biofuels offer environmental benefits not available from grainbased biofuels and are a cornerstone of efforts to meet transportation fuel needs in a future low-carbon economy, even with electrified vehicles and other advances. Bioenergy with carbon capture and storage (BECCS) is also key to almost all Intergovernmental Panel on Climate Change mitigation scenarios that constrain end-of-century atmospheric CO<sub>2</sub> to 450 parts per million. Some cellulosic feedstocks can come from industrial and agricultural by-products or from winter cover crops, but a substantial fraction must come from cellulosic biomass crops-perennial grasses and short-rotation trees planted for this purpose. Land requirements, however, are substantial and raise crucial questions about the environmental sustainability of a future bioenergy economy. First, if planted on existing croplands, will biofuel crops increase food prices or lead to the establishment of new cropland elsewhere, with concomitant climate harm? Second, will planting biofuel crops diminish biodiversity, especially if non-native or invasive species are cultivated on land with existing conservation value? Third, might perennial biofuel crops use more water than the vegetation they replace, leading to lower water tables and reduced surface water flows? And finally, if crops are fertilized, how much additional reactive nitrogen might be added to a biosphere already overburdened?

**ADVANCES:** Recent empirical findings have shed considerable light on these questions.



**Switchgrass (Panicum virgatum) at daybreak in the U.S. Midwest.** Switchgrass is one of several promising cellulosic biofuel species that are native and can provide high yields and greenhouse gas mitigation as well as other ecosystem services associated with nitrogen and water conservation and insect and wildlife biodiversity, especially when grown in species mixtures.

Broad generalizations are difficult, but we know now, for example, that planting perennial cellulosic biofuel crops on marginal lands—that is, land not currently used for food production because of low fertility, environmental sensitivity, or other reasons—can potentially avoid food-fuel conflict and indirect land-use change effects while providing substantial climate benefits. The direct carbon costs of establishing

### ON OUR WEBSITE

### Read the full article at http://dx.doi. org/10.1126/ science.aal2324

crops on such lands can be minimized by avoiding tillage and by avoiding land with large existing carbon stocks, such as forests and wetlands. Diverse plantings provide multiple eco-

system services including wildlife conservation, pollination, and pest protection that can benefit neighboring crops; relatively little plant diversity can provide disproportionately large benefits. Biofuel crops can be planted that require little if any nitrogen fertilizer, thus avoiding its environmental impact. And although different crops have different water-use efficiencies, most crops examined appear to evapotranspire about the same proportion of growing season rainfall, suggesting little impact on landscape water balances in humid temperate regions.

It is also clear that there is no best crop for all locations even within a single region, and that all choices involve trade-offs. For example, highly productive non-native species can maximize climate benefits but harm biodiversity. Balancing trade-offs entails societal choices.

**OUTLOOK:** Many questions about cellulosic biofuel sustainability remain. Still needed is an integrated understanding of the entire field-to-product enterprise sufficient to leverage synergies and to avoid trade-offs that can diminish environmental benefits. More specifically, and of particular importance, is the need for knowledge to facilitate the successful cultivation of highly productive native species on marginal lands, where plant growth is often limited by abiotic stressors. Harnessing the plant microbiome to help ameliorate environmental stress is a major untapped frontier, as is the potential for microbiome-assisted soil carbon gain. The promise of cellulosic biofuels for helping to create a more sustainable energy future is bright, but additional effort is required, including policies and incentives to motivate farmers to grow appropriate crops in appropriate places in sustainable ways. We must be careful to facilitate genuine climate mitigation that enhances rather than diminishes other ecosystem services. The planet deserves no less.

The list of author affiliations is available in the full article online.

\*Corresponding author. Email: robert30@msu.edu Cite this article as G. P. Robertson *et al.*, *Science* **356**, eaal2324 (2017). DOI: 10.1126/science.aal2324

### REVIEW

### BIOENERGY

# **Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes**

G. Philip Robertson,<sup>1,2,3</sup>\* Stephen K. Hamilton,<sup>1,3,4</sup> Bradford L. Barham,<sup>5,6</sup> Bruce E. Dale,<sup>3,7</sup> R. Cesar Izaurralde,<sup>3,8,9</sup> Randall D. Jackson,<sup>6,10</sup> Douglas A. Landis,<sup>3,11</sup> Scott M. Swinton,<sup>3,12</sup> Kurt D. Thelen,<sup>2,3</sup> James M. Tiedje<sup>2,3,13</sup>

Cellulosic crops are projected to provide a large fraction of transportation energy needs by mid-century. However, the anticipated land requirements are substantial, which creates a potential for environmental harm if trade-offs are not sufficiently well understood to create appropriately prescriptive policy. Recent empirical findings show that cellulosic bioenergy concerns related to climate mitigation, biodiversity, reactive nitrogen loss, and crop water use can be addressed with appropriate crop, placement, and management choices. In particular, growing native perennial species on marginal lands not currently farmed provides substantial potential for climate mitigation and other benefits.

urpose-grown cellulosic crops are key to a projected future in which biomass-derived fuels displace a substantial fraction of the petroleum used for transportation fuels (1). Projections of future U.S. biomass needs to meet greenhouse gas (GHG) reduction targets of 80% relative to 2005 petroleum use (2)-even with vehicle electrification and other advances (3)suggest that at least 55 to 70% of the petroleum displacement, requiring ~10<sup>9</sup> Mg of biomass, must come from cellulosic biofuel crops such as grasses and short-rotation trees (4, 5). Global projections make a similar case (6), and bioenergy crops combined with CO<sub>2</sub> capture and storage (BECCS) are a feature of almost all Intergovernmental Panel on Climate Change mitigation scenarios that constrain atmospheric CO<sub>2</sub> to 450 parts per million by 2100 (7).

The substantial amount of land required to meet biofuel targets for liquid transportation fuel

has raised numerous environmental concerns (8, 9). Growing biofuel crops on land that might otherwise produce food could exacerbate global food insecurity and might lead to further land conversion elsewhere for agriculture [so-called indirect land-use change (ILUC) effects]. Biodiversity may be diminished as new land is cleared for growing displaced food crops, or as monocultures of new, perhaps non-native or invasive biofuel crops are planted. Greater water use by perennial biofuel crops might reduce groundwater recharge and subsequent subsurface flows to surface waters. More agricultural pollutants, in particular reactive nitrogen (N), may be added to groundwater, surface waters, and the atmosphere as a result of greater fertilizer use. Indeed, even the overall climate benefit of cellulosic biofuels-a primary impetus for developing the industry-has been questioned in light of the carbon (C) costs of crop establishment (10), ILUC effects (11), and the potential loss of C sequestration by existing vegetation replaced by biofuel crops ("foregone sequestration") (12).

Here, we synthesize recent empirical research that targets these concerns to identify potential solutions for managing the land use-related tradeoffs of cellulosic biofuels. We identify existing knowledge gaps but also conclude that current knowledge is sufficient to inform policies that will ensure environmental benefits. Policy is needed because many of these benefits are conditional, and the stakes are high because of the amount of land involved: In the United States alone, projected biomass needs require 33 to 40 Mha of productive land (4) or >50 Mha of marginal land (13), whereas total U.S. crop production currently uses 124 Mha (14). But with the proper safeguards, the likelihood of environmental payoff appears high. We organize our conclusions to articulate seven emerging principles that are relevant globally to the sustainability of cellulosic biofuel crop production.

#### Climate benefits are real but contingent

The climate benefits of cellulosic biofuels derive from two sources: avoided petroleum use (the fossil fuel offset) and GHG mitigation during biofuel production, principally by soil C accumulation and avoided GHG emissions (13). Changes in crop reflectance (albedo) might also affect climate, depending on prior land cover (15). Counting against a crop's fossil fuel offsets are the fossil energy costs embedded in agronomic inputs and farming activities and in the fuel used for biomass transport and refinery operations, minus the additional energy value of burned waste and agricultural coproducts such as distillers grains. If established on otherwise productive cropland, ILUC further discounts-perhaps wholly (16)-a cellulosic biofuel's fossil fuel offset. Counting against a crop's GHG mitigation are increased GHG emissions during and after crop establishment.

Attributional life cycle analyses (ALCAs), although imperfect (17), tally disparate benefits and costs to evaluate the net energy balance and climate impact of biofuel crops relative to petroleum, assuming 100% substitution and inelastic supply and demand (18). Early ALCAs revealed corn grain ethanol's low energy return on investment, estimating GHG savings of only ~18% relative to petroleum (19), and noted cellulosic ethanol's more favorable prospects, with potential GHG savings approaching 90% (19). Later ALCAs for cellulosic crops [reviewed in (20)] have largely agreed with these earlier studies, but all rely on some combination of national averages, statistical extrapolations, and simulation models for estimates of yields, soil C storage, and GHG emissions rather than whole-system measurements of individual systems, wherein opposing trends cannot be obscured by average values. Extrapolations can be a particular problem for soil C storage and nitrous oxide  $(N_2O)$  emissions, which are highly variable. are difficult to model, and can dominate GHG balances (21). Fargione et al. (10), for example, inferred that after biofuel crop establishment on USDA Conservation Reserve Program (CRP) land, soil C loss alone creates a C debt of ~130 Mg  $CO_2$  ha<sup>-1</sup>, requiring >90 years of corn grain ethanol production to repay (10). Carbon debt is created when crop establishment releases CO2eq (CO2 equivalent) to the atmosphere.

In contrast to grain ethanol crops, perennial vegetation on former cropland tends to sequester soil C (22) and emit little N<sub>2</sub>O (23), providing potential climate benefits. Gelfand *et al.* (24), in the only system-level empirical study to date, showed that for successional herbaceous vegetation with long-term productivity equivalent to farm-grown switchgrass (*Panicum virgatum*), the climate benefit of annual soil C gain alone was as high as the fossil fuel offset provided by grain crops. And although N<sub>2</sub>O emissions increased with N fertilization, their climate detriment was less than the additional fossil fuel offset provided by increased yield. In total, the fertilized post-establishment

<sup>&</sup>lt;sup>1</sup>W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, USA. <sup>2</sup>Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI 48824, USA. <sup>3</sup>Great Lakes Bioenergy Research Center, Michigan State University, East Lansing, MI 48824, USA. <sup>4</sup>Department of Integrative Biology, Michigan State University, East Lansing, MI 48824, USA. <sup>5</sup>Department of Agricultural and Applied Economics, University of Wisconsin, Madison, WI 53706, USA. <sup>6</sup>Great Lakes Bioenergy Research Center, University of Wisconsin, Madison, WI 53706, USA. <sup>7</sup>Department of Chemical Engineering and Materials Science. Michigan State University, East Lansing, MI 48824, USA. <sup>8</sup>Department of Geographical Sciences, University of Maryland, College Park, MD 20742, USA. 9Texas AgriLife Research, Texas A&M University, Temple, TX 76502, USA. <sup>10</sup>Department of Agronomy, University of Wisconsin, Madison, WI 53706, USA. <sup>11</sup>Department of Entomology, Michigan State University, East Lansing, MI 48824, USA. <sup>12</sup>Department of Agricultural, Food, and Resource Economics, Michigan State University, East Lansing, MI 48824, USA. <sup>13</sup>Center for Microbial Ecology, Michigan State University, East Lansing, MI 48824, USA. \*Corresponding author. Email: robert30@msu.edu



Fig. 1. First-year carbon debt created by greenhouse gas (GHG) fluxes upon establishment of a bioenergy crop on a USDA Conservation Reserve Program (CRP) grass-

**land.** Results are from a site in southwest Michigan on cropland that had been enrolled in CRP for 22 years. (**A**) Components of debt for converted and reference (unconverted) sites.  $CO_2$  flux represents net C loss from soil organic matter (left bar) and net C gain from soil C sequestration (right bar). (**B**) Net C debt for converted sites including foregone C sequestration (left bar) and net C mitigation (negative emissions) for an unconverted reference site (right bar). Standard error bars represent n = 3replicates. [Redrawn from (25)]

cellulosic system directly mitigated 9.5 Mg  $\rm CO_2 eq$   $\rm ha^{-1}\, year^{-1}.$ 

Prior land use, however, substantially affects the net climate benefit. A preexisting uncropped ecosystem will likely have considerable C stores below and perhaps above ground, and its soils may be accumulating C. A net climate benefit from conversion to biofuel production requires C accumulation rates greater than those preexisting even after any C debt incurred during establishment is repaid. Gelfand et al. (25) showed empirically for herbaceous vegetation that both factors are tractable. Conversion of CRP grasslands to no-till soybeans to facilitate the subsequent planting of perennial biofuel crops (a so-called breakout year) created 10.6 Mg CO<sub>2</sub>eq ha<sup>-1</sup> of C debt, including 2.5 Mg CO<sub>2</sub>eq ha<sup>-1</sup> of future foregone C sequestration (Fig. 1). Calculations based on the productivity of nearby farms suggest that payback of the C debt would take 40 years for no-till corn but only ~1 year for a new cellulosic crop. However,



Fig. 2. Yields of alternative perennial cellulosic crops on moderately fertile alfisol and highly fertile mollisol soils in the upper U.S. Midwest. Values are harvested dry mass (DM) over the first 6 years of production, including establishment years. Standard error bars represent six replicate blocks; letters indicate significant differences within a location at  $\alpha$  = 0.10. [Redrawn from (32)]

conversion technology also matters: In a companion experiment, a single tillage event oxidized ~8 years of prior soil C accumulation and increased annual N<sub>2</sub>O emissions by a factor of 3 (26), together increasing C debt by a factor of 4. Conversely, if CRP grasses had been harvested directly with no establishment costs (10), no C debt would have been generated.

Forest conversion magnifies C debt to an even greater degree than tillage because of the large aboveground C stores in wood. Repaying this debt can take a century or more (27), especially considering future foregone sequestration: In the United States, for example, most forests are aggrading and thus actively accumulating biomass C, such that future biofuel crop production must both exceed this rate and repay the C debt to provide any near-term climate benefit (28). The bar is even higher for mature subtropical and tropical forests with their greater C stores and vulnerability to ILUC effects (29).

The climate lessons here are clear: Avoiding ILUC effects while not incurring a large C debt requires the establishment of perennial cellulosic crops on nonforested lands not already used for food production, with practices that minimize or avoid episodic soil C oxidation and  $N_2O$  release. Carbon debt can be avoided entirely by harvesting existing grassland vegetation, such as that on CRP lands, but this creates a climate opportunity cost if the existing vegetation yields less bioenergy than a more productive crop.

### Crop choice is key

The choice of crop to be grown is fundamental to the biofuel cost-benefit equation. We now know that there are no "silver bullet" crops that thrive under most growing conditions even within a given region, nor is there a single crop for any given location that provides a full suite of ecosystem services including high yield. Rather, for any given setting, a number of potential crops can provide some combination of productivity and environmental benefits, with different trade-offs. What do they have in common? Perenniality is the most desirable bioenergy crop trait: With two possible exceptions, the C and GHG costs of annual cropping systems severely detract from their potential climate benefits (10, 24), whereas yields of perennial biomass crops such as switchgrass, giant miscanthus (*Miscanthus* × *giganteus*), and hybrid poplar trees (*Populus* spp.) rival those of annual crops without the climate penalty of annual cultivation and high N fertilizer rates.

Thus, the energy return on investment of perennial crops can be substantial. Schmer et al. (30), for example, found on-farm switchgrass yields across three Great Plains states sufficient to provide annual biomass yields of 5.2 to 11.1 Mg ha  $^{-1}\!,$ for an average net energy return of 60 GJ ha<sup>-1</sup>. In a meta-analysis of small-plot trials from across the U.S. Midwest, Heaton et al. (31) found average annual miscanthus yields of 20 Mg ha<sup>-1</sup>. And in a direct multiyear comparison that spanned both favorable and drought years in the upper Midwest, Sanford et al. (32) found that after 5 years, miscanthus yields were similar to or greater than corn stover yields, and generally higher than those of switchgrass and poplar, depending on location (Fig. 2).

The promise of feedstock-agnostic refining (33)opens opportunities to use diverse species mixes, and early small-plot evidence that diversity benefits productivity (34) provides an expectation for both high yields and biodiversity benefits. Subsequent larger-scale experiments have shown mixed results. In Oklahoma (35), a 5-year comparison showed no consistent differences among single versus polyculture plantings of grasses, whereas in Minnesota (36), four- and eight-species grass and grass/legume mixtures at some locations outperformed monoculture switchgrass. At two upper Midwest locations (32), aboveground net primary productivity (but not yield) over 6 years was similar among switchgrass (7.5 Mg ha<sup>-1</sup> year<sup>-1</sup>) and three polyculture systems-a four-species native grass mixture, an early successional community, and restored prairie (6.7 to 7.0 Mg  $ha^{-1}$  year<sup>-1</sup>)at one site, consistent with whole-field regional comparisons of switchgrass versus restored prairie



Fig. 3. Biodiversity differences among maize (corn), switchgrass, and restored prairie plantings across matched sites in the upper U.S. Midwest. (A to E) Species richness of key taxa. (F to J) Associated differences in ecosystem services. Standard error bars represent 6 to 10 replicate sites per habitat (115 fields total). [Redrawn from (53)]

(*37*), whereas at a more fertile site, monoculture switchgrass productivity was at least 25% higher than that of the more diverse systems. Thus, there appears to be no strong productivity advantage to polycultures of native species at most tested sites to date, but nor do there appear to be consistent penalties. However, many years may be required to fully realize any productivity benefits resulting from diversity. Tilman *et al.* (*34*) documented increased productivity after 10 years, and Gelfand *et al.* (*24*) recorded a 50% jump in the productivity of their mixed-species successional community after an initial 10-year establishment period because of the delayed dominance of high-productivity species (*37*).

Two exceptions to the disadvantage of annual biofuel crops prove instructive. The first is the potential to harvest annual cover crops that would not otherwise be planted. Annual grasses such as winter rye (*Secale cereale*) can be grown during parts of the year not used by annual crops (*38*), thereby avoiding ILUC effects and the GHG costs of N fertilizer while facilitating soil C storage (*39*). The second is the potential for an annual crop such as energy sorghum (*Sorghum bicolor*), with its seasonal drought tolerance and low N needs (*40*), to fill a niche in semi-arid regions that are becoming more marginal as a result of aquifer depletion and more variable precipitation.

### Biodiversity benefits can extend to nearby cropland

The conversion of natural vegetation to annual cropland has immediate negative consequences for biodiversity, and the expansion of U.S. corn production after 2000 to supply grain for ethanol production (41) harmed wildlife (42) and attenuated benefits provided by insects (43). Had this expansion instead motivated the planting of

perennial cellulosic crops, the biodiversity consequences would likely have been far less severe (9) or even positive (44), but this would depend on a number of factors, chief among them prior land use and crop choice.

Recent field studies have improved our understanding of biodiversity and ecosystem function in bioenergy cropping systems. Zangerl et al. (45), for example, contrasted arthropod detritivore communities in native prairie, switchgrass, and miscanthus systems and found surprisingly few differences in detritivore community structure or function. Lepidopteran alpha (within-field) diversity. in contrast, was greatest in native prairie (2.9 species per trap night, on average), intermediate in switchgrass (2.4 species), and lower in miscanthus and corn (1.8 species) (46). Gardiner et al. (47) quantified insect pollinator and predator communities in fields of corn, switchgrass, and restored prairie in Michigan and Wisconsin; they found that although the numbers of bee species were similar, individual species were more abundant in switchgrass and prairie than in corn by a factor of 3 to 4. Most arthropod predator groups were also more abundant in the perennial grasslands (47). The pest suppression potential of predators increased 20% as the number of flowering plant species increased from 0 to 15 within fields, but leveled off thereafter; this finding suggests that even limited plant diversity can support key ecosystem functions such as pest suppression (48).

The benefits of arthropod diversity in perennial habitats also extend to nearby annual croplands. Both pollination (49) and pest suppression (48) in annual crops increase by up to 24% with an increasing abundance of perennial habitats in the surrounding landscape, increasing yields by as much as 22% (50). Indeed, farmers in parts of the Midwest with more noncrop habitat nearby used 14% less insecticides than those in landscapes with a high proportion of annual cropland (*51*). This suggests that increasing perenniality at the landscape scale with bioenergy crops could lower pest control costs on nearby annual cropland and thereby reduce nontarget pesticide impacts and environmental escape.

Other taxa also respond to greater perenniality. Both methanotrophic bacterial richness and methane consumption can increase upon establishment of diverse perennial vegetation on former cropland (52). Perennial grasslands also contain 6 to 19% more arthropod prey for birds and provide migratory as well as spring nesting habitats (44). Werling et al. (53) documented increased species richness (from 17 to 74%) for multiple taxa in switchgrass and restored prairie relative to corn (Fig. 3), leading to increased methane consumption, crop pest suppression, pollination, and grassland bird conservation. Benefits appeared to result mostly from perenniality per se; that is, often as much benefit was delivered by low-diversity switchgrass as by high-diversity prairie (Fig. 3). Spatial modeling suggests that, depending on landscape configuration, replacing corn production on marginal soils with switchgrass would increase bird species richness (54) and pest suppression (55) by as much as 2 times, and would increase bee diversity and abundance by as much as 1.5 and 6 times, respectively (56).

Overall, the biodiversity and conservation benefits of adding perennial grasslands to agricultural landscapes are compelling. If strategically located and managed, grasslands could enhance a wide variety of wildlife while producing bioenergy and other conservation benefits (42). For example, placing perennial grasslands in riparian zones can reduce expected phosphorus exports by 29% and N<sub>2</sub>O emissions by 84% while increasing soil C



Fig. 4. Yield and nitrogen loss responses to increasing rates of nitrogen fertilizer during switchgrass crop establishment. (A) Switchgrass yields, (B) N<sub>2</sub>O emissions, and (C) nitrate leaching for the first three harvest years following an initial establishment year at an upper U.S. Midwest site. Standard error bars and shadings are based on n = 4 replicate blocks. [From (63)]

sequestration by 30% and bird and pollinator abundance by 11% (*57*). Similarly, adding prairie strips to as little as 10% of corn and soybean fields in Iowa can drastically reduce sediment, total phosphorus, and N exports (by 95%, 90%, and 85%, respectively) while increasing biodiversity (*58*).

### Reactive N loss can be minimized by parsimonious fertilizer use

Cropland expansion and intensification to produce more grain-based biofuel in the United States has also led to greater N fertilizer use, with attendant environmental costs. Projections of both nitrate loss to surface waters (59) and N<sub>2</sub>O emissions to the atmosphere (21) assign a high reactive N cost to grain-based biofuel expansion that could last for decades (60). Cellulosic crops, in contrast, often appear to require little if any N fertilizer [e.g., (61-63)] and, when used, tend to require fertilizer N only at rates close to harvest N removal (64). This high efficiency of ecosystem N use suggests a correspondingly low reactive N loss.

Is this borne out by measurements? Long-term nitrate loss from the root zone of successional herbaceous vegetation as productive as on-farm switchgrass was <1 kg N ha<sup>-1</sup> year<sup>-1</sup>, far lower than fertilized annual crops (40 to 60 kg N  $ha^{-1}$ year<sup>-1</sup>) and lower even than adjacent mature forest (65). Leaching from hybrid poplar was lower still. Ruan et al. (63) measured nitrate leaching from unfertilized switchgrass at 2.6 kg N ha year<sup>-1</sup> over the first three harvest years, and leaching after fertilizing at crop N-removal rates was little different. Duran et al. (66) likewise found consistently low extractable nitrate below the rooting zone of post-establishment switchgrass in Wisconsin and even less under mixed-species grasses, and Smith et al. (67) found that N losses from corn in Illinois were markedly reduced when replaced by switchgrass and even more so by miscanthus and restored prairie. Similar conclusions come from studies of perennial grasslegume and willow (Salix sp.) stands in Denmark (68) as well as switchgrass and miscanthus in France (69). On the other hand, substantial nitrate can be lost from even moderately overfertilized grasses (63) and upon initial conversion of noncropped land if tilled (70).

Soil N<sub>2</sub>O emissions from established perennial vegetation are also substantially lower than from annual crops (23). A 3-year comparison of eight different cropping systems (71) showed fluxes from annual crops 2.5 times those from perennial crops, although even modest N fertilization doubled fluxes from perennial systems. That small N fertilizer additions result in disproportionately higher N<sub>2</sub>O fluxes is consistent with emerging findings that N<sub>2</sub>O fluxes in annual crops respond exponentially to added N (72); a similar nonlinear relationship appears to hold for switchgrass (63) (Fig. 4), underscoring the importance of careful fertilizer management. Nitrate leaching appears to show a similar nonlinear response to N fertilization (63).

Efficient N use by perennial crops stems from four traits: (i) Perenniality allows early spring and late fall plant growth with associated N uptake; these are periods when inorganic N is otherwise subject to leaching. Wintertime plants can also trap snow in northern regions (73), protecting soil from freeze-thaw cycles that liberate inorganic N and stimulate  $N_2O$  production (74). (ii) Relatively little N is removed in harvested biomass; unlike annual grain crops that are bred for protein-rich seeds, most cellulosic crop biomass is harvested as lower-N vegetative tissue or wood. (iii) If harvest is properly timed to post-senescence, much of the N in vegetative tissues will have been translocated belowground (75). (iv) Without annual tillage, perennial crops accumulate N in soil organic matter (22).

N-conservative crops are thus a key part of cellulosic biofuel's environmental promise, but their propensity to retain N and avoid further polluting the atmosphere, groundwater, and surface waters with N can be easily undermined with even moderately excessive fertilizer use.

## Water-use efficiency varies greatly, but for rainfed crops, total water use does not

Evapotranspiration (ET), the sum of water lost by evaporation and transpiration, is a major component of the water balance in terrestrial landscapes (76). If a biofuel crop evapotranspires more water than the vegetation it replaces, then converting large portions of landscapes to bioenergy production could divert more precipitation back to the atmosphere, reducing groundwater recharge and lowering surface water levels.

Empirical evidence comparing ET rates of perennial biomass crops to annual grain crops is scant, but results from sites with high water tables that require subsurface drainage [e.g., (77-79)] as well as modeling studies based on data from those sites (80-82) suggest that planting perennial grasses on lands now used for annual crops could increase ET by at least 25% for switchgrass and >50% for miscanthus. The higher leaf area index and longer growing season of perennial grasses were implicated as the major reasons for the higher ET. However, more recent evidence from experiments on a well-drained upper Midwest site (83) suggests that projections of higher ET for perennial biomass crops may not apply where soil water limits crop growth.

Three lines of evidence support this assertion: (i) Continuous observations of soil water profiles under switchgrass, miscanthus, native grasses, restored prairie, and hybrid poplar indicated similar ET rates in both ample-water years and a drought year, and those rates were no different from that of corn. In this humid temperate setting, all crops used all available soil water. (ii) These plot-scale results are corroborated by field-scale observations nearby based on eddy covariance measures of energy and water vapor fluxes. Switchgrass, restored prairie, and corn also evapotranspired similar amounts during years of normal water availability as well as during the 2012 drought year (84). (iii) A water balance for a 95-km<sup>2</sup> watershed nearby showed remarkably stable ET over 50 years of changing land use (27% abandoned from row crops) and climate warming (1.14°C), both of which might be expected to increase ET (85). Together, these findings suggest that in humid temperate climates, conversion of annual crops to perennial crops-or of unmanaged herbaceous vegetation to cellulosic crops-may have little impact on terrestrial water balances.

## The plant microbiome may be key for productivity in challenging environments

Plants, like all higher organisms, evolved in concert with microorganisms, in many cases forming beneficial associations, only some of which are known. A supportive soil microbiome is likely to be important for low-input biofuel production everywhere, but especially on marginal lands. The development of metagenomics has allowed the plant rhizosphere—that portion of the soil under direct root influence—to be interrogated for microbial constituents in ways only newly appreciated. The rhizosphere has long been known as a hotspot of soil microbial activity, and the importance of certain microorganisms to plant functioning is well established. Among the best known are *Rhizobium* symbionts, which capture atmospheric N for plant use, and mycorrhizal fungi that provide plants better access to phosphorus and other soil resources. Yet rhizosphere diversity is far richer than the known symbionts and pathogens, and the functional importance of this diversity has been barely explored (86).

New evidence is beginning to show how the microbiome matters to bioenergy crop vigor. Recently established cropping systems tend to reflect microbial community differences related to soil type and land-use history (87-89), but over time, the distinct influences of specific plant species emerge. In post-establishment corn, switchgrass, and restored prairie communities, both cross-site (87) and within-site (87, 90-92) comparisons reveal striking plant species effects (e.g., Fig. 5). In all cases, corn selected for more copiotrophs (microorganisms that prefer more resource-rich environments) while the perennial crops selected for more oligotrophs (microorganisms that prefer more resource-poor environments). The perennial crops also selected for more N2-fixing genes, arbuscular mycorrhizal fungi, and a higher fungi/bacteria ratio. Rooting depth also contributes to patterns of community change throughout the soil profile, particularly on lower-fertility soils (93).

The importance of functional differences related to these community composition changes awaits further research. However, faster turnover of microbial residues in switchgrass rhizospheres (91), a greater capacity for perennial systems to oxidize methane (52, 53), bacterial growth efficiencies that vary by land use (94), and differences among systems in the occurrence and activity of different denitrifier genes (95) and enzymes (96) suggest the potential for wide-ranging effects on C sequestration, GHG emissions, nutrient cycling, and soil fertility in general. Moreover, strong differences in rhizosphere communities suggest that different microbiomes serve particular purposes.

#### Marginal land availability may ultimately limit the potential biofuel climate benefit

Marginal lands have considerable potential to produce cellulosic feedstocks from successional vegetation or perennial grasses, and their use can forestall food-fuel conflicts, including those resulting from ILUC effects (24, 97–99). Marginal lands denote nonforested lands that are not wetlands, are not used for row crops or livestock, but are sufficiently productive and accessible for bioenergy production. Often these lands were formerly used for agriculture but were abandoned because of low productivity, low crop prices, or high environmental risk (100), and their plant communities tend to be dominated by non-native species



**Fig. 5.** Principal components analysis of rhizosphere metagenomes from three crops in Michigan. Samples were collected from replicate corn, miscanthus, and switchgrass rhizospheres 5 years post-establishment. Ellipses represent one standard deviation of the points (n = 7 shotgun metagenome samples) from the centroid. (**A**) Nitrite reductase (nirK). (**B**) Ribosomal protein L2 (rplB). [Redrawn from (93)]

of questionable conservation value. Some portion of the 30% of U.S. cropland abandoned since 1900 (97) falls into this category, as does some portion of CRP lands. A more expansive view of marginal lands (99, 101) includes current croplands and grasslands of low productivity.

Estimates of marginal lands available for cellulosic feedstock production at global and regional scales vary depending on methodologies and available data. Campbell *et al.* (*98*), for example, used historical land-use data and satellite imagery to estimate that 385 to 471 Mha have been abandoned from agriculture worldwide as a result of low soil productivity. Cai *et al.* (*99*) used global land-use capability and soil databases to conclude that ~1100 Mha of marginal lands not currently grazed are available globally.

In the United States, the area of available marginal lands is also uncertain, ranging from ~70 to 100 Mha. Estimates of abandoned U.S. croplands and pastures, based on county-level historical assessments (97), sum to ~99 Mha excluding those lands now urban and forested. Contemporary satellitebased assessments of marginal lands plus the identification of soils with limited productivity (101) sum to ~74 Mha, mostly in the Great Plains.

Certainly not all of this land will be available for cellulosic feedstock production. Two factors in particular are likely to determine availability: the economic and GHG costs of feedstock transport, and landowner acceptance. Although most LCA analyses assign only modest GHG costs to feedstock transport [e.g., (102)], the costs are nonetheless present and, together with economic costs, rise rapidly with distance from the biorefinery. Gelfand et al. (24) constrained feedstock production on marginal lands of 10 U.S. Midwest states to locations sufficient to provide a biorefinery capable of producing  $9 \times 10^7$  liters of ethanol annually with adequate biomass from within a collection radius of 80 km. About 11 Mha or 58% of the available marginal land in this region met this criterion, which would be relaxed with higher crop productivity, more aggregated land parcels, or more distributed collection depots (*103*). Nonetheless, they estimated that dedicating this portion of the available land base to growing unimproved cellulosic biomass crops could satisfy ~25% of the 2022 U.S. production mandate established by the 2007 Energy Independence and Security Act.

### Farmer acceptance is critical and needs incentives

Grower and landowner acceptance of perennial cellulosic crops in the future is difficult to predict in the absence of a biomass energy market, the uncertainty of future petroleum prices, and potential fossil C taxation, but economic research defines at least four necessary conditions.

First, and perhaps most obviously, direct farming costs must be met. Production, harvest, transport, and storage costs are predictable recurring costs: establishment costs are ideally nonrecurring but are less predictable. In one experimental planting in the upper Midwest, for example, first-year switchgrass and restored prairie plantings were washed away by heavy rains at one location, and miscanthus rhizomes failed to survive their initial hard winter at the other (32). In both cases, establishment costs almost doubled, initial harvests were delayed by a year, and profitability was delayed by several years or longer (104). Such establishment risks, although not unusual (105), are not typically considered in minimum biomass selling price projections.

Second, payment for biomass must equal or exceed the opportunity cost of foregone profit if the prior land use had been maintained. On arable cropland, comparative break-even budgeting of side-by-side crops (104) shows that yields of perennial bioenergy crops would have to increase by a factor of 4 to 16 to exceed the profits of continuous corn at biomass prices of \$50 Mg<sup>-1</sup> and grain prices of \$159 Mg<sup>-1</sup> (\$4 bu<sup>-1</sup>). Where corn stover on the same land would otherwise outproduce perennial biomass—for example, during



**Fig. 6. Regional supply chain modeling reveals unexpected benefits of large-scale biofuel crop production. (A)** Global warming intensity (GWI) for cellulosic biomass priced at US\$40 Mg<sup>-1</sup> that produces 19 billion liters per year (bly) at US\$0.58 liter<sup>-1</sup>. (**B**) A biomass price of US\$80 Mg<sup>-1</sup> that produces 176 bly at US\$0.65 liter<sup>-1</sup>. [Redrawn from (113)]

the perennial crop establishment phase and perhaps indefinitely on fertile soils (32)—there is no price at which perennial bioenergy crops could compete (104). Regional bioeconomic modeling (106) reinforces these findings, insofar as the provision of crop residue—corn stover and wheat straw—as a source of cellulosic biomass incurs only the marginal costs of harvest, transport, and storage because production costs are covered by grain sales. The perennial cellulosic crop, switchgrass in this case, is provided only at a much higher relative biomass price and only where switchgrass yields exceed crop residue yields. If cover crops were planted and harvested (38), the disparity would be still greater.

An additional opportunity cost is the grower's inability to rotate out of a perennial cellulosic crop rapidly as market conditions change. Sunk costs associated with crop establishment require long rotations and also include the future costs of seed bed restoration if woody crops such as poplar, or rhizomatous crops such as miscanthus, impede the subsequent planting of different crops. A third cost is income risk, which is currently high with most perennial bioenergy crops (104). Risk simulation using real options analysis (107) suggests that net returns from a new perennial biomass crop must exceed those from the existing crop by a factor of 2 to motivate farmers to switch crops.

All told, at current biomass prices there seems little economic case for growing dedicated cellu-

losic crops on productive cropland. And that case is likely to get weaker in a future with greater food demand.

On the other hand, although the economic case for growing perennial cellulosic crops on marginal lands avoids opportunity costs and income risk, it faces the different hurdle of amenity cost. Surveys of Michigan and Wisconsin landowners (*108–110*) revealed a reluctance to convert marginal land to perennial cellulosic crops because of the loss of recreational value (e.g., hiking, hunting, birdwatching) from what is typically early successional vegetation. To overcome this hurdle requires either higher payments for biomass or perennial cellulosic crops that can provide similar recreational value, often related to biodiversity.

#### **Emerging principles**

Seven bioenergy sustainability principles emerge from or are strengthened by these findings: (i) Perennial vegetation, whether herbaceous grasses and dicots or short-rotation trees, offers environmental outcomes superior to those of annual crops -high net energy return on investment, greater soil C and N retention, and improved insect and wildlife habitat-with no observable impact on landscape water balances in humid temperate climates. (ii) Polycultures appear thus far to offer little productivity advantage over monocultures, but neither do they harm productivity so long as they are dominated by high-productivity species. (iii) Biodiverse plantings provide ecosystem services such as pollination, pest protection, and wildlife conservation that often benefit other cropping systems in the landscape, and relatively little plant diversity can provide disproportionately large benefits. (iv) C debt generated by stand establishment can be minimized by avoiding tillage and by avoiding lands with large C stores either above ground (such as forests) or below ground (such as wetlands). (v) N fertilization can substantially discount the climate and water quality benefits of bioenergy crops if applied in excess of plant need; some highproductivity perennial crops require little if any supplemental N. (vi) Food-fuel economic conflicts and C debt generated by ILUC can be avoided by establishing bioenergy crops on marginal lands not used for food production, and also by producing biomass from cover crops in annual cropping systems. (vii) Economic appeal, relative to alternative land uses, is a sine qua non for landowners to be willing to convert their lands to bioenergy crop production.

A further, overarching principle is that there is no best crop for all locations. Rather, one must consider trade-offs with respect to desired outcomes. In the United States, maximizing productivity with an exotic species such as miscanthus, for example, provides substantial climate mitigation but with an accompanying risk of introducing a potentially pernicious invasive (*111*). Thus, miscanthus and other exotics represent a biodiversity trade-off if not an outright threat. Switchgrass and other prairie grasses, on the other hand, are native to large parts of North America and thus have biodiversity benefits not furnished by non-native species. However, even switchgrass currently produces substantially less biomass than miscanthus (*31*). Restored prairies have still further biodiversity benefits but comparably high productivity is less assured, especially as improved varieties of switchgrass are developed. Thus, as is true for annual grain crops (*112*), farming bioenergy crops for multiple ecosystem services entails trade-offs. Ultimately, the weight provided to any one service will be determined by society and its collective decision to favor one crop over another by incentives, regulation, and profitability.

Modeling can help to identify alternative outcomes and environmental trade-offs for different management choices, landscapes, and price scenarios. Spatially explicit bioeconomic modeling with price feedbacks of multicounty regions in Michigan and Wisconsin (106), for example, predicts that on cropland, farmers would require moderate biomass prices (\$50 Mg<sup>-1</sup>) to switch from alfalfa and hay to residue-producing grain crops. Feedstock prices nearly twice as high would be needed to trigger large-scale switchgrass production, providing direct climate and water quality benefits but at the unintended cost of less food production and potentially stimulating ILUC with its GHG and other costs.

A national-scale modeling analysis (113) illustrates a plausible if nonintuitive scenario for high biomass prices. Doubling the biomass supply price from  $40 \text{ Mg}^{-1}$  to  $80 \text{ Mg}^{-1}$  stimulated far higher potential farmer participation, with nine times as much biomass produced, enabling more and larger biorefineries. With lower transportation costs and economies of scale within refineries, the average minimum ethanol selling price increased only 12%, from  $0.58 \text{ liter}^{-1}$  to  $0.65 \text{ liter}^{-1}$ . Simulated GHG savings, assuming all biomass was produced on marginal or cover-cropped lands, increased by almost a factor of 10 (Fig. 6). Thus, in the absence of systems modeling of the entire field-to-product enterprise, it is difficult to predict likely outcomes and trade-offs.

### **Future research needs**

A successful, sustainable cellulosic bioenergy enterprise requires integration across the entire value chain from field to product, and overall success requires an understanding of the system sufficient to identify key factors that affect environmental sustainability and their potential management. Desirable environmental attributes include climate mitigation, biodiversity conservation, and clean water. We now have enough empirical evidence to know that these aspirations are, with conditions, tractable. We do not yet know with sufficient confidence the sustainability responses of alternative systems to different management decisions and environmental variability.

Six research priorities will better define and realize the environmental promise of cellulosic biofuels:

1) Improved understanding of how to integrate biofuel cropping systems into agricultural landscapes is needed to produce diversified cropping systems that deliver multiple ecosystem services and greater resilience to environmental stress. In particular, better understanding the genetic variability of desirable plant species is needed to create varieties that can tolerate the abiotic and biotic stresses present everywhere but magnified on marginal lands.

2) Understanding the microbiome goes hand in hand with the first goal: The functional diversity represented within the microbial rhizosphere is largely unknown but likely important for plant nutrient acquisition, drought stress, and disease tolerance. Harnessing the microbiome to fix atmospheric  $N_2$ , for example, seems an important, achievable goal.

3) Understanding the processes that regulate soil C accumulation and persistence would help to enhance soil C accrual. Reducing  $N_2O$  emissions to nil or even reversing them by promoting rhizosphere  $N_2O$  consumption would likewise provide huge climate synergies. These ambitious goals require a better understanding of microbial interactions with the soil environment as influenced by plants and environmental variability at different scales.

4) A better understanding of how cellulosic crops provide biodiversity services would help to resolve a number of questions: What level of alpha diversity is optimal for protecting long-term productivity in low-input environments subjected to chronic and episodic stress? What level of gamma (landscape-level) diversity is optimal for providing conservation, pest protection, disease suppression, and other services to other crops and habitats in the landscape? What regulates the maintenance of alpha diversity in managed ecosystems?

5) At the landscape and regional scale, it is crucially important to explore the entire field-toproduct enterprise through a combination of ecosystem, technoeconomic, and life cycle assessment modeling that is sufficiently integrated to provide overall sustainability metrics sensitive to management and environmental variability. We cannot perform empirical research at this scale and thus must rely on modeling both to integrate across the value chain and to extend knowledge to environments not explicitly observed.

6) We need to understand the most effective ways to incentivize sustainability in a world that is primarily driven by economic profit. If a primary goal of developing a bioenergy capacity is to mitigate atmospheric GHG loading, then we will need knowledge sufficient to inform policy incentives that can motivate farmers and landowners to grow the most appropriate crops in the most appropriate places. We must be careful to provide real climate mitigation that also promotes the delivery of other valuable ecosystem services. The planet deserves no less.

#### **REFERENCES AND NOTES**

- S. Chu, A. Majumdar, Opportunities and challenges for a sustainable energy future. *Nature* 488, 294–303 (2012). doi: 10.1038/nature11475; pmid: 22895334
- National Research Council, Liquid Transportation Fuels from Coal and Biomass: Technological Status, Costs, and Environmental Impacts (National Academies Press, 2009).
- P. J. Meier et al., Potential for electrified vehicles to contribute to U.S. petroleum and climate goals and implications for advanced biofuels. Environ. Sci. Technol.

**49**, 8277–8286 (2015). doi: 10.1021/acs.est.5b01691; pmid: 26086692

- U.S. Department of Energy, 2016 Billion-Ton Report: Advancing Domestic Resources for a Thriving Bioeconomy, Volume 1: Economic Availability of Feedstocks (Oak Ridge National Laboratory, 2016).
- In the BT2016 analysis (4), energy crops contribute 547 Mt, or 55% of a total cellulosic biomass of 1001 Mt, assuming 1% yield growth and a biomass price of US\$80/ton; this requires 33 Mha of existing crop and pasture land. A highproductivity scenario (3% yield growth) projects 853 Mt (64% of a total 1333 Mt), requiring 40 Mha.
- S. Nakada, D. Sayfin, D. Gielen, Global Bioenergy Supply and Demand Projections: A Working Paper for REmap 2030 (International Renewable Energy Agency, 2014).
- Intergovernmental Panel on Climate Change, Climate Change 2014: Mitigation of Climate Change, Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge Univ. Press, 2014).
- G. P. Robertson *et al.*, Sustainable biofuels redux. *Science* 322, 49–50 (2008). doi: 10.1126/science.1161525; pmid: 18832631
- D. Tilman et al., Beneficial biofuels—the food, energy, and environment trilemma. Science 325, 270–271 (2009). doi: 10.1126/science.1177970; pmid: 19608900
- J. Fargione, J. Hill, D. Tilman, S. Polasky, P. Hawthorne, Land clearing and the biofuel carbon debt. *Science* **319**, 1235–1238 (2008). doi: 10.1126/science.1152747; pmid: 18258862
- T. Searchinger et al., Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change. Science 319, 1238–1240 (2008). doi: 10.1126/ science.1151861; pmid: 18258860
- C. B. Field, J. E. Campbell, D. B. Lobell, Biomass energy: The scale of the potential resource. *Trends Ecol. Evol.* 23, 65–72 (2008). doi: 10.1016/j.tree.2007.12.001; pmid: 18215439
- G. P. Robertson, S. K. Hamilton, S. J. Del Grosso, W. J. Parton, The biogeochemistry of bioenergy landscapes: Carbon, nitrogen, and water considerations. *Ecol. Appl.* 21, 1055–1067 (2011). doi: 10.1890/09-0456.1; pmid: 21774413
- National Agricultural Statistics Service, Crop Production 2015 Summary (January 2016) (U.S. Department of Agriculture, 2016).
- M. Georgescu, D. B. Lobell, C. B. Field, Direct climate effects of perennial bioenergy crops in the United States. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 4307–4312 (2011). doi: 10.1073/pnas.1008779108; pmid: 21368189
- R. J. Plevin, D. M. Kammen, in *Encyclopedia of Biodiversity*, S. A. Levin, Ed. (Academic Press, ed. 2, 2013), pp. 293–297.
- R. J. Plevin, M. A. Delucchi, F. Creutzig, Using attributional life cycle assessment to estimate climate-change mitigation benefits misleads policy makers. *J. Ind. Ecol.* 18, 73–83 (2014). doi: 10.1111/jiec.12074
- J. Hill, in *Encyclopedia of Biodiversity*, S. A. Levin, Ed. (Academic Press, ed. 2, 2013), pp. 627–630.
- A. E. Farrell *et al.*, Ethanol can contribute to energy and environmental goals. *Science* **311**, 506–508 (2006). doi: 10.1126/science.1121416; pmid: 16439656
- M. Morales, J. Quintero, R. Conejeros, G. Aroca, Life cycle assessment of lignocellulosic bioethanol: Environmental impacts and energy balance. *Renew. Sustain. Energy Rev.* 42, 1349–1361 (2015). doi: 10.1016/j.rser.2014.10.097
- P. J. Crutzen, A. R. Mosier, K. A. Smith, W. Winiwarter, N<sub>2</sub>O release from agro-biofuel production negates global warming reduction by replacing fossil fuels. *Atmos. Chem. Phys.* 8, 389–395 (2008). doi: 10.5194/acp-8-389-2008
- T. O. West, W. M. Post, Soil organic carbon sequestration rates by tillage and crop rotation: A global data analysis. *Soil Sci. Soc. Am. J.* 66, 1930–1946 (2002). doi: 10.2136/ sssaj2002.1930
- G. P. Robertson, E. A. Paul, R. R. Harwood, Greenhouse gases in intensive agriculture: Contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289, 1922–1925 (2000). doi: 10.1126/science.289.5486.1922; pmid: 10988070
- I. Gelfand et al., Sustainable bioenergy production from marginal lands in the US Midwest. Nature 493, 514–517 (2013). doi: 10.1038/nature11811; pmid: 23334409
- I. Gelfand et al., Carbon debt of Conservation Reserve Program (ORP) grasslands converted to bioenergy production. Proc. Natl. Acad. Sci. U.S.A. 108, 13864–13869 (2011). doi: 10.1073/pnas.1017277108; pmid: 21825117

- L. Ruan, G. P. Robertson, Initial nitrous oxide, carbon dioxide, and methane costs of converting conservation reserve program grassland to row crops under no-till vs. conventional tillage. *Glob. Change Biol.* **19**, 2478–2489 (2013). doi: 10.1111/gcb.12216; pmid: 23553929
- E.-D. Schulze, C. Körner, B. E. Law, H. Haberl, S. Luyssaert, Large-scale bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse gas neutral. *Glob. Change Biol. Bioenergy* 4, 611–616 (2012). doi: 10.1111/ j.1757-1707.2012.01169.x
- S. D. Peckham, S. T. Gower, Simulated long-term effects of harvest and biomass residue removal on soil carbon and nitrogen content and productivity for two Upper Great Lakes forest ecosystems. *Glob. Change Biol. Bioenergy* 3, 135–147 (2011). doi: 10.1111/j.1757-1707.2010.01067.x
- J. M. Melillo et al., Indirect emissions from biofuels: How important? Science 326, 1397–1399 (2009). doi: 10.1126/ science.1180251; pmid: 19933101
- M. R. Schmer, K. P. Vogel, R. B. Mitchell, R. K. Perrin, Net energy of cellulosic ethanol from switchgrass. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 464–469 (2008). doi: 10.1073/pnas.0704767105; pmid: 18180449
- E. Heaton, T. Voigt, S. P. Long, A quantitative review comparing the yields of two candidate C4 perennial biomass crops in relation to nitrogen, temperature and water. *Biomass Bioenergy* 27, 21–30 (2004). doi: 10.1016/ j.biombioe.2003.10.005
- G. R. Sanford *et al.*, Comparative productivity of alternative cellulosic bioenergy cropping systems in the North Central USA. *Agric. Ecosyst. Environ.* **216**, 344–355 (2016). doi: 10.1016/j.agee.2015.10.018
- J. S. Luterbacher *et al.*, Nonenzymatic sugar production from biomass using biomass-derived γ-valerolactone. *Science* 343, 277–280 (2014). doi: 10.1126/science.1246748; pmid: 24436415
- D. Tilman, J. Hill, C. Lehman, Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314, 1598–1600 (2006). doi: 10.1126/science.1133306; pmid: 17158327
- A. P. Griffith, F. M. Epplin, S. D. Fuhlendorf, R. Gillen, A comparison of perennial polycultures and monocultures for producing biomass for biorefinery feedstock. *Agron. J.* 103, 617–627 (2011). doi: 10.2134/agronj2010.0336
- J. M. Jungers et al., Long-term biomass yield and species composition in native perennial bioenergy cropping systems. *Agron. J.* 107, 1627–1640 (2015). doi: 10.2134/agronj15.0014
- T. L. Dickson, K. L. Gross, Can the results of biodiversityecosystem productivity studies be translated to bioenergy production? *PLOS ONE* **10**, e0135253 (2015). doi: 10.1371/ journal.pone.0135253; pmid: 26359662
- G. W. Feyereisen, G. G. T. Camargo, R. E. Baxter, J. M. Baker, T. L. Richard, Cellulosic biofuel potential of a winter rye double crop across the U.S. Corn-Soybean Belt. Agron. J. 105, 631–642 (2013). doi: 10.2134/agronj2012.0282
- S. P. Syswerda, A. T. Corbin, D. L. Mokma, A. N. Kravchenko, G. P. Robertson, Agricultural management and soil carbon storage in surface vs. deep layers. *Soil Sci. Soc. Am. J.* 75, 92–101 (2011). doi: 10.2136/sssaj2009.0414
- P. Y. Oikawa, G. D. Jenerette, D. A. Grantz, Offsetting high water demands with high productivity: Sorghum as a biofuel crop in a high irradiance arid ecosystem. *Glob. Change Biol. Bioenergy* 7, 974–983 (2015). doi: 10.1111/ gcbb.12190
- T. J. Lark, J. M. Salmon, H. K. Gibbs, Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environ. Res. Lett.* **10**, 044003 (2015). doi: 10.1088/ 1748-9326/10/4/044003
- J. E. Fargione *et al.*, Bioenergy and wildlife: Threats and opportunities for grassland conservation. *Bioscience* 59, 767–777 (2009). doi: 10.1525/bio.2009.59.9.8
- D. A. Landis, M. M. Gardiner, W. van der Werf, S. M. Swinton, Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Natl. Acad. Sci.* U.S.A. 105, 20552–20557 (2008). doi: 10.1073/ pnas.0804951106; pmid: 19075234
- B. A. Robertson, P. J. Doran, L. R. Loomis, J. R. Robertson, D. W. Schemske, Perrennial biomass feedstocks enhance avian diversity. *Glob. Change Biol. Bioenergy* 3, 235–246 (2011). doi: 10.1111/j.1757-1707.2010.01080.x
- A. R. Zangerl et al., Role of arthropod communities in bioenergy crop litter decomposition. *Insect Sci.* 20, 671–678 (2013). doi: 10.1111/j.1744-7917.2012.01532.x; pmid: 23956135

- T. Harrison, M. R. Berenbaum, Moth diversity in three biofuel crops and native prairie in Illinois. *Insect Sci.* 20, 407–419 (2013). doi: 10.1111/j.1744-7917.2012.01530.x; pmid: 23955892
- M. M. Gardiner *et al.*, Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *BioEnergy Res.* **3**, 6–19 (2010). doi: 10.1007/s12155-009-9065-7
- B. P. Werling, T. D. Meehan, B. A. Robertson, C. Gratton, D. A. Landis, Biocontrol potential varies with changes in biofuel-crop plant communities and landscape perenniality. *Glob. Change Biol. Bioenergy* 3, 347–359 (2011). doi: 10.1111/ j.1757-1707.2011.01092.x
- A. B. Bennett, R. Isaacs, Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agric. Ecosyst. Environ.* **193**, 1–8 (2014). doi: 10.1016/j.agee.2014.04.016
- H. Liere *et al.*, Trophic cascades in agricultural landscapes: Indirect effects of landscape composition on crop yield. *Ecol. Appl.* 25, 652–661 (2015). doi: 10.1890/14-0570.1; pmid: 26214911
- T. D. Meehan, C. Gratton, A consistent positive association between landscape simplification and insecticide use across the Midwestern US from 1997 through 2012. *Environ. Res. Lett.* **10**, 114001 (2015). doi: 10.1088/1748-9326/10/11/ 114001
- U. Y. Levine, T. K. Teal, G. P. Robertson, T. M. Schmidt, Agriculture's impact on microbial diversity and associated fluxes of carbon dioxide and methane. *ISME J.* 5, 1683–1691 (2011). doi: 10.1038/ismej.2011.40; pmid: 21490688
- B. P. Werling *et al.*, Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 111, 1652–1657 (2014). doi: 10.1073/pnas.1309492111; pmid: 24474791
- T. D. Meehan, A. H. Hurlbert, C. Gratton, Bird communities in future bioenergy landscapes of the Upper Midwest. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 18533–18538 (2010). doi: 10.1073/pnas.1008475107; pmid: 20921398
- T. D. Meehan, B. P. Werling, D. A. Landis, C. Gratton, Pestsuppression potential of midwestern landscapes under contrasting bioenergy scenarios. *PLOS ONE* 7, e41728 (2012). doi: 10.1371/journal.pone.0041728; pmid: 22848582
- A. B. Bennett, T. D. Meehan, C. Gratton, R. Isaacs, Modeling pollinator community response to contrasting bioenergy scenarios. *PLOS ONE* 9, e110676 (2014). doi: 10.1371/ iournal.oone.0110676: pmid: 25365559
- T. D. Meehan et al., Ecosystem-service tradeoffs associated with switching from annual to perennial energy crops in riparian zones of the US Midwest. PLOS ONE 8, e80093 (2013). doi: 10.1371/journal.pone.0080093; pmid: 24223215
- M. Liebman, L. A. Schulte, Enhancing agroecosystem performance and resilience through increased diversification of landscapes and cropping systems. *Elementa* 3, 41 (2015). doi: 10.12952/journal.elementa.000041
- S. D. Donner, C. J. Kucharik, Corn-based ethanol production compromises goal of reducing nitrogen export by the Mississippi River. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 4513–4518 (2008). doi: 10.1073/pnas.0708300105; pmid: 18332435
- S. K. Hamilton, Biogeochemical time lags may delay responses of streams to ecological restoration. *Freshw. Biol.* 57 (suppl. 1), 43–57 (2012). doi: 10.1111/j.1365-2427.2011.02685.x
- D. G. Christian, A. B. Riche, N. E. Yates, The yield and composition of switchgrass and coastal panic grass grown as a biofuel in southern England. *Bioresour. Technol.* 83, 115–124 (2002). doi: 10.1016/S0960-8524(01)00201-2; pmid: 12056486
- W. E. Thomason *et al.*, Switchgrass response to harvest frequency and time and rate of applied nitrogen. *J. Plant Nutr.* **27**, 1199–1226 (2005). doi: 10.1081/ PLN-120038544
- L. Ruan, A. K. Bhardwaj, S. K. Hamilton, G. P. Robertson, Nitrogen fertilization challenges the climate benefit of cellulosic biofuels. *Environ. Res. Lett.* 11, 064007 (2016). doi: 10.1088/1748-9326/11/6/064007
- M. P. Davis, M. B. David, T. B. Voigt, C. A. Mitchell, Effect of nitrogen addition on *Miscanthus × giganteus* yield, nitrogen losses, and soil organic matter across five sites. *Glob. Change Biol. Bioenergy* 7, 1222–1231 (2015). doi: 10.1111/gcbb.12217
- S. P. Syswerda, B. Basso, S. K. Hamilton, J. B. Tausig, G. P. Robertson, Long-term nitrate loss along an agricultural intensity gradient in the Upper Midwest USA.

Agric. Ecosyst. Environ. 149, 10–19 (2012). doi: 10.1016/ j.agee.2011.12.007

- B. E. L. Duran, D. S. Duncan, L. G. Oates, C. J. Kucharik, R. D. Jackson, Nitrogen fertilization effects on productivity and nitrogen loss in three grass-based perennial bioenergy cropping systems. *PLOS ONE* **11**, e0151919 (2016). doi: 10.1371/journal.pone.0151919; pmid: 26991790
- C. M. Smith *et al.*, Reduced nitrogen losses after conversion of row crop agriculture to perennial biofuel crops. *J. Environ. Qual.* 42, 219–228 (2013). doi: 10.2134/ jeq2012.0210; pmid: 23673757
- S. Pugesgaard, K. Schelde, S. U. Larsen, P. E. Lærke, U. Jørgensen, Comparing annual and perennial crops for bioenergy production—influence on nitrate leaching and energy balance. *Glob. Change Biol. Bioenergy* 7, 1136–1149 (2015). doi: 10.1111/gcbb.12215
- F. Ferchaud, B. Mary, Drainage and nitrate leaching assessed during 7 years under perennial and annual bioenergy crops. *BioEnergy Res.* 9, 656–670 (2016). doi: 10.1007/s12155-015-9710-2
- P. Nikièma, D. E. Rothstein, R. O. Miller, Initial greenhouse gas emissions and nitrogen leaching losses associated with converting pastureland to short-rotation woody bioenergy crops in northern Michigan, USA. *Biomass Bioenergy* **39**, 413–426 (2012). doi: 10.1016/ i.biombioe.2012.01.037
- L. G. Oates *et al.*, Nitrous oxide emissions during establishment of eight alternative cellulosic bioenergy cropping systems in the North Central United States. *Glob. Change Biol. Bioenergy* 8, 539–549 (2016). doi: 10.1111/ gcbb.12268
- I. Shcherbak, N. Millar, G. P. Robertson, Global metaanalysis of the nonlinear response of soil nitrous oxide (N<sub>2</sub>O) emissions to fertilizer nitrogen. *Proc. Natl. Acad. Sci. U.S.A.* 111, 9199–9204 (2014). doi: 10.1073/pnas.1322434111; pmid: 24927583
- Z. Qin, Q. Zhuang, M. Chen, Impacts of land use change due to biofuel crops on carbon balance, bioenergy production, and agricultural yield, in the conterminous United States. *Glob. Change Biol. Bioenergy* 4, 277–288 (2012). doi: 10.1111/ j.1757-1707.2011.01129.x
- L. Ruan, G. P. Robertson, Reduced snow cover increases wintertime nitrous oxide (N<sub>2</sub>O) emissions from an agricultural soil in the upper U.S. Midwest. *Ecosystems* 10.1007/s10021-016-0077-9 (2016). doi: 10.1007/ s10021-016-0077-9
- L. C. Jach-Smith, R. D. Jackson, Nitrogen conservation decreases with fertilizer addition in two perennial grass cropping systems for bioenergy. *Agric. Ecosyst. Environ.* 204, 62–71 (2015). doi: 10.1016/j.agee.2015.02.006
- S. Jasechko et al., Terrestrial water fluxes dominated by transpiration. Nature 496, 347–350 (2013). doi: 10.1038/ nature11983; pmid: 23552893
- A. L. Daigh *et al.*, Subsurface drainage flow and soil water dynamics of reconstructed prairies and corn rotations for biofuel production. *Vadose Zone J.* **13**, 10.2136/ vzj2013.10.0177 (2014). doi: 10.2136/vzj2013.10.0177
- G. F. McIsaac, M. B. David, C. A. Mitchell, Miscanthus and switchgrass production in central Illinois: Impacts on hydrology and inorganic nitrogen leaching. *J. Environ. Qual.* 39, 1790–1799 (2010). doi: 10.2134/jeq2009.0497; pmid: 21043284
- G. C. Hickman, A. Vanloocke, F. G. Dohleman, C. J. Bernacchi, A comparison of canopy evapotranspiration for maize and two perennial grasses identified as potential bioenergy crops. *Glob. Change Biol. Bioenergy* 2, 157–168 (2010).
- P. V. V. Le, P. Kumar, D. T. Drewry, Implications for the hydrologic cycle under climate change due to the expansion of bioenergy crops in the Midwestern United States. *Proc. Natl. Acad. Sci. U.S.A.* 108, 15085–15090 (2011). doi: 10.1073/pnas.1107177108; pmid: 21876137
- A. VanLoocke, T. E. Twine, M. Zeri, C. J. Bernacchi, A regional comparison of water use efficiency for miscanthus, switchgrass and maize. *Agric. For. Meteorol.* 164, 82–95 (2012). doi: 10.1016/j.agrformet.2012.05.016
- Q. Zhuang, Z. Qin, M. Chen, Biofuel, land and water: Maize, switchgrass or miscanthus? *Environ. Res. Lett.* 8, 015020 (2013). doi: 10.1088/1748-9326/8/1/015020
- S. K. Hamilton, M. Z. Hussain, A. K. Bhardwaj, B. Basso, G. P. Robertson, Comparative water use by maize, perennial crops, restored prairie, and poplar trees in the US Midwest. *Environ. Res. Lett.* 10, 064015 (2015). doi: 10.1088/ 1748-9326/10/6/064015

- M. Abraha et al., Evapotranspiration of annual and perennial biofuel crops in a variable climate. *Glob. Change Biol. Bioenergy* 7, 1344–1356 (2015). doi: 10.1111/gcbb.12239
- S. K. Hamilton, M. Z. Hussain, C. J. Lowrie, Watershed-scale evapotranspiration changed little over 50 years of agricultural land abandonment in southern Michigan. American Geophysical Union Fall Meeting, San Francisco, 16 December 2015, abstract H3IF-1496.
- R. Mendes, P. Garbeva, J. M. Raaijmakers, The rhizosphere microbiome: Significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *FEMS Microbiol. Rev.* 37, 634–663 (2013). doi: 10.1111/1574-6976.12028; pmid: 23790204
- E. C. Jesus *et al.*, Influence of corn, switchgrass, and prairie cropping systems on soil microbial communities in the upper Midwest of the United States. *Glob. Change Biol. Bioenergy* 8, 481–494 (2016). doi: 10.1111/gcbb.12289
- K. Jangid et al., Land-use history has a stronger impact on soil microbial community composition than aboveground vegetation and soil properties. Soil Biol. Biochem. 43, 2184–2193 (2011). doi: 10.1016/j.soilbio.2011.06.022
- Y. Mao, A. C. Yannarell, S. C. Davis, R. I. Mackie, Impact of different bioenergy crops on N-cycling bacterial and archaeal communities in soil. *Environ. Microbiol.* **15**, 928–942 (2013). doi: 10.1111/j.1462-2920.2012.02844.x; pmid: 22891790
- C. Liang et al., Soil microbial communities under model biofuel cropping systems in southern Wisconsin, USA: Impact of crop species and soil properties. *Appl. Soil Ecol.* 54, 24–31 (2012). doi: 10.1016/j.apsoil.2011.11.015
- C. Liang *et al.*, Switchgrass rhizospheres stimulate microbial biomass but deplete microbial necromass in agricultural soils of the upper Midwest, USA. *Soil Biol. Biochem.* **94**, 173–180 (2016). doi: 10.1016/j.soilbio.2015.11.020
- J. Guo *et al.*, Rhizosphere metagenomics of three biofuel crops. 16th International Symposium on Microbial Ecology, Montreal. 22 August 2016, abstract 135A.
- B. Zhang et al., Soil bacteria community variance with depth under biofuel cropping systems. American Society for Microbiology 115th General Meeting, Las Vegas, 31 May 2015, abstract 295.
- Z. M. Lee, T. M. Schmidt, Bacterial growth efficiency varies in soils under different land management practices. *Soil Biol. Biochem.* 69, 282–290 (2014). doi: 10.1016/ j.soilbio.2013.11.012
- Q. Wang et al., Xander: Employing a novel method for efficient gene-targeted metagenomic assembly. *Microbiome* 3, 32 (2015). doi: 10.1186/s40168-015-0093-6; pmid: 26246894
- M. A. Cavigelli, G. P. Robertson, Role of denitrifier diversity in rates of nitrous oxide consumption in a terrestrial ecosystem. *Soil Biol. Biochem.* **33**, 297–310 (2001). doi: 10.1016/S0038-0717(00)00141-3
- J. E. Campbell, B. L. David, C. G. Robert, Z. Andrew, B. F. Christopher, Seasonal energy storage using bioenergy production from abandoned croplands. *Environ. Res. Lett.* 8, 035012 (2013). doi: 10.1088/1748-9326/8/3/035012
- J. E. Campbell, D. B. Lobell, R. C. Genova, C. B. Field, The global potential of bioenergy on abandoned agriculture lands. *Environ. Sci. Technol.* 42, 5791–5794 (2008). doi: 10.1021/ es800052w; pmid: 18754510
- X. Cai, X. Zhang, D. Wang, Land availability for biofuel production. *Environ. Sci. Technol.* **45**, 334–339 (2011). doi: 10.1021/es103338e; pmid: 21142000
- S. Kang *et al.*, Marginal lands: Concept, assessment and management. *J. Agric. Sci.* 5, 129–139 (2013). doi: 10.5539/ jas.v5n5p129
- V. Bandaru, R. C. Izaurralde, K. Zhao, in Sustainable Biofuels: An Ecological Assessment of the Future Energy, A. K. Bhardwaj, T. Zenone, J. Chen, Eds. (DeGruyter, 2015), pp. 299–317.
- 102. M. Wang, J. Han, J. B. Dunn, H. Cai, A. Elgowainy, Well-towheels energy use and greenhouse gas emissions of ethanol from corn, sugarcane and cellulosic biomass for US use. *Environ. Res. Lett.* **7**, 045905 (2012). doi: 10.1088/1748-9326/7/4/045905
- P. L. Eranki, B. E. Dale, Comparative life cycle assessment of centralized and distributed biomass processing systems combined with mixed feedstock landscapes. *Glob. Change Biol. Bioenergy* 3, 427–438 (2011). doi: 10.1111/ j.1757-1707.2011.01096.x
- T. Skevas, S. M. Swinton, S. Tanner, G. Sanford, K. D. Thelen, Investment risks in bioenergy crops. *Glob. Change Biol. Bioenergy* 8, 1162–1177 (2016). doi: 10.1111/gcbb.12320

- 105. C. J. Kucharik, A. Vanloocke, J. D. Lenters, M. M. Motew, Miscanthus establishment and overwintering in the Midwest USA: A regional modeling study of crop residue management on critical minimum soil temperatures. *PLOS ONE* 8, e68847 (2013). doi: 10.1371/journal.pone.0068847; pmid: 23844244
- 106. A. Egbendewe-Mondzozo et al., Bioenergy supply and environmental impacts on cropland: Insights from multimarket forecasts in a Great Lakes subregional bioeconomic model. Appl. Econ. Perspect. Policy 37, 602–618 (2015). doi: 10.1093/aepp/ppu044
- F. Song, J. Zhao, S. M. Swinton, Switching to perennial energy crops under uncertainty and costly reversibility. *Am. J. Agric. Econ.* 93, 768–783 (2011). doi: 10.1093/ ajae/aar018
- 108. D. F. Mooney, B. L. Barham, C. Lian, Inelastic and fragmented farm supply response to second-generation

bioenergy feedstocks: *Ex ante* survey evidence from Wisconsin. *Appl. Econ. Perspect. Policy* **37**, 287–310 (2014). doi: 10.1093/aepp/ppu033

- 109. S. M. Swinton, S. Tanner, B. L. Barham, D. F. Mooney, T. Skevas, How willing are landowners to supply land for bioenergy crops in the Northern Great Lakes Region? *Glob. Change Biol. Bioenergy* 9, 414–428 (2016). doi: 10.1111/ gcbb.12336
- T. Skevas, N. J. Hayden, S. M. Swinton, F. Lupi, Landowner willingness to supply marginal land for bioenergy production. *Land Use Policy* **50**, 507–517 (2016). doi: 10.1016/ j.landusepol.2015.09.027
- S. E. Pittman et al., Mitigating the potential for invasive spread of the exotic biofuel crop, Miscanthus × giganteus. Biol. Invasions 17, 3247–3261 (2015). doi: 10.1007/ s10530-015-0950-z
- G. P. Robertson *et al.*, Farming for ecosystem services: An ecological approach to production agriculture. *Bioscience* 64, 404–415 (2014). doi: 10.1093/biosci/biu037; pmid: 26955069
- S. Kim, B. E. Dale, All biomass is local: The cost, volume produced, and global warming impact of cellulosic biofuels depend strongly on logistics and local conditions. *Biofuels Bioprod. Biorefin.* 9, 422–434 (2015). doi: 10.1002/bbb.1554

#### ACKNOWLEDGMENTS

Supported by U.S. Department of Energy Office of Science grant DE-FC02-07ER64494, Office of Energy Efficiency and Renewable Energy grant DE-AC05-76RL01830, NSF Long-Term Ecological Research program grant DEB 1027253, and MSU AgBioResearch.

10.1126/science.aal2324