

18. A. Trumpp *et al.*, *Nature* **414**, 768 (2001).
19. M. N. Chamorro *et al.*, *EMBO J.* **24**, 73 (2005).
20. E. H. Jho *et al.*, *Mol. Cell. Biol.* **22**, 1172 (2002).
21. H. Lickert *et al.*, *Development* **132**, 2599 (2005).
22. M. Morkel *et al.*, *Development* **130**, 6283 (2003).
23. U. de Lichtenberg, L. J. Jensen, S. Brunak, P. Bork, *Science* **307**, 724 (2005).
24. We thank G. Glasko, J. Pace, and B. Brede for their help; R. Kopan, E. Furlong, J. Gerton, C. Seidel, B. Cheyette, and

members of the Pourquié lab for comments; and S. Esteban for artwork. J.C. research supported by NSF grant DMS-0426148. This work was supported by Stowers Institute for Medical Research and Defense Advanced Research Projects Agency (DARPA) grant 00001112 to O.P. O.P. is a Howard Hughes Medical Investigator.

#### Supporting Online Material

[www.sciencemag.org/cgi/content/full/1133141/DC1](http://www.sciencemag.org/cgi/content/full/1133141/DC1)

#### Materials and Methods

Figs. S1 to S4  
Tables S1 to S5  
References

28 July 2006; accepted 2 November 2006

Published online 9 November 2006;

10.1126/science.1133141

Include this information when citing this paper.

# Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass

David Tilman,<sup>1\*</sup> Jason Hill,<sup>1,2</sup> Clarence Lehman<sup>1</sup>

Biofuels derived from low-input high-diversity (LIHD) mixtures of native grassland perennials can provide more usable energy, greater greenhouse gas reductions, and less agricultural pollution per hectare than can corn grain ethanol or soybean biodiesel. High-diversity grasslands had increasingly higher bioenergy yields that were 238% greater than monoculture yields after a decade. LIHD biofuels are carbon negative because net ecosystem carbon dioxide sequestration (4.4 megagram hectare<sup>-1</sup> year<sup>-1</sup> of carbon dioxide in soil and roots) exceeds fossil carbon dioxide release during biofuel production (0.32 megagram hectare<sup>-1</sup> year<sup>-1</sup>). Moreover, LIHD biofuels can be produced on agriculturally degraded lands and thus need to neither displace food production nor cause loss of biodiversity via habitat destruction.

Globally escalating demands for both food (1) and energy (2) have raised concerns about the potential for food-based biofuels to be sustainable, abundant, and environmentally beneficial energy sources. Current biofuel production competes for fertile land with food production, increases pollution from fertilizers and pesticides, and threatens biodiversity when natural lands are converted to biofuel production. The two major classes of biomass for biofuel production recognized to date are monoculture crops grown on fertile soils (such as corn, soybeans, oilseed rape, switchgrass, sugarcane, willow, and hybrid poplar) (3–6) and waste biomass (such as straw, corn stover, and waste wood) (7–9). Here, we show the potential for a third major source of biofuel biomass, high-diversity mixtures of plants grown with low inputs on agriculturally degraded land, to address such concerns.

We performed an experiment on agriculturally degraded and abandoned nitrogen-poor sandy soil. We determined bioenergy production and ecosystem carbon sequestration in 152 plots, planted in 1994, containing various combinations of 1, 2, 4, 8, or 16 perennial herbaceous grassland species (table S1) (10). Species composition of each plot was determined by random draw from a pool of species. Plots were unfertilized, irrigated only during

establishment, and otherwise grown with low inputs (10). The 16-species plots are the highest diversity, or the LIHD (low-input, high-diversity), treatment. All plots were burned in early spring to remove aboveground biomass before growth began. Soil samples, collected before planting in 1994 and again in 2004, determined carbon sequestration in soil. Plots were sampled annually from 1996 to 2005 for aboveground biomass production.

Annual production of aboveground bioenergy (i.e., biomass yield multiplied by energy released upon combustion) (10) was an approximate log function of planted species number (Fig. 1A). On average for the last 3 years of the experiment (2003–2005), 2-, 4-, 8-, and 16-species plots produced 84%, 100%, 157%, and 238% more bioenergy, respectively, than did plots planted with single species. In a repeated measures multivariate analysis of variance, annual bioenergy production was positively dependent on the number of planted species ( $F_{1, 155} = 68.4$ ,  $P < 0.0001$ ), on time ( $F_{9, 147} = 8.81$ ,  $P < 0.0001$ ), and on a positive time-by-species number interaction ( $F_{9, 147} = 11.3$ ,  $P < 0.0001$ ). The interaction occurred because bioenergy production increased more through time in LIHD treatments than in monocultures and low-diversity treatments, as shown by the ratio of bioenergy in LIHD (16 species) plots to those in 8-, 4-, 2-, and 1-species plots (Fig. 1B).

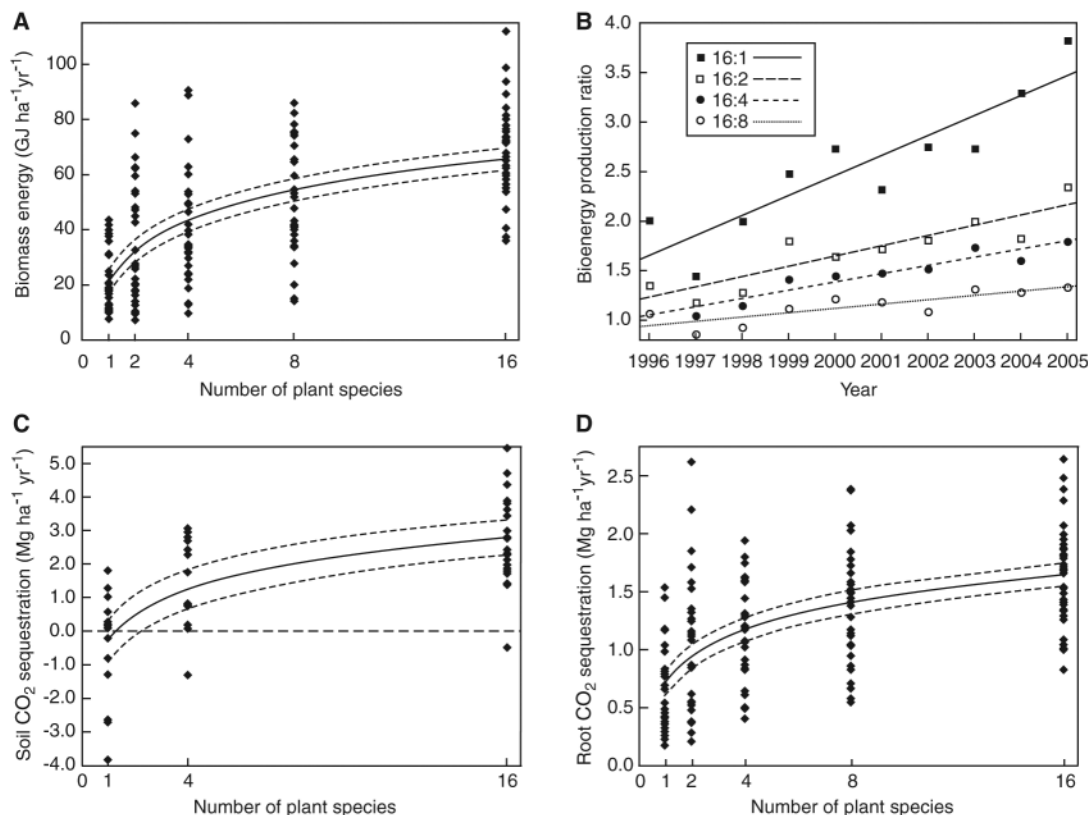
The gross bioenergy yield from LIHD plots was 68.1 GJ ha<sup>-1</sup> year<sup>-1</sup>. Fossil energy needed for biomass production, harvest, and transport to a biofuel production facility was estimated at 4.0 GJ ha<sup>-1</sup> year<sup>-1</sup> (table S2).

Different biofuel production methods capture different proportions of bioenergy in deliverable, usable forms (Fig. 2) (10). Cocombustion of degraded land LIHD biomass with coal in existing coal-fired electric generation facilities would provide a net gain of about 18.1 GJ ha<sup>-1</sup> as electricity (11). Converting LIHD biomass into cellulosic ethanol and electricity is estimated to net 17.8 GJ ha<sup>-1</sup> (12). Conversion into gasoline and diesel synfuels and electricity via integrated gasification and combined cycle technology with Fischer-Tropsch hydrocarbon synthesis (IGCC-FT) is estimated to net 28.4 GJ ha<sup>-1</sup> (10, 13). In contrast, net energy gains from corn and soybeans from fertile agricultural soils are 18.8 GJ ha<sup>-1</sup> for corn grain ethanol and 14.4 GJ ha<sup>-1</sup> for soybean biodiesel (14). Thus, LIHD biomass converted via IGCC-FT yields 51% more usable energy per hectare from degraded infertile land than does corn grain ethanol from fertile soils. This higher net energy gain results from (i) low-energy inputs in LIHD biomass production because the crop is perennial and is neither cultivated, treated with herbicides, nor irrigated once established and likely requires only phosphorus replacement fertilization because nitrogen is provided by legumes; (ii) the more than 200% higher bioenergy yield associated with high crop biodiversity; and (iii) the use of all aboveground biomass, rather than just seed, for energy. LIHD biofuels also provide much greater net energy outputs per unit of fossil fuel input than do current biofuels [net energy balance (NEB) ratios of Fig. 2]. Fertile lands yield about 50% more LIHD biomass (and bioenergy) than our degraded soils (15, 16).

Annual carbon storage in soil was a log function of plant species number (Fig. 1C). For 1994–2004, there was no significant net sequestration of atmospheric CO<sub>2</sub> in monoculture plots [mean net release of CO<sub>2</sub> of 0.48 ± 0.44 Mg ha<sup>-1</sup> year<sup>-1</sup> (mean ± SE)], but, in LIHD plots, there was significant soil sequestration of CO<sub>2</sub> (2.7 ± 0.29 Mg ha<sup>-1</sup> year<sup>-1</sup>). Soil carbon storage occurred even though all aboveground biomass-based organic matter was removed annually via burning. Periodic resampling of soils in a series of prairie-like agriculturally degraded fields found C storage rates similar to those of the LIHD treatment and suggested that this rate could be maintained for a century (17). The observed annual rate of change in soil C at a particular soil depth declined with depth ( $P = 0.035$ ), suggesting that an additional 5% more

<sup>1</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA. <sup>2</sup>Department of Applied Economics, University of Minnesota, St. Paul, MN 55108, USA.

\*To whom correspondence should be addressed. E-mail: [tilman@umn.edu](mailto:tilman@umn.edu)

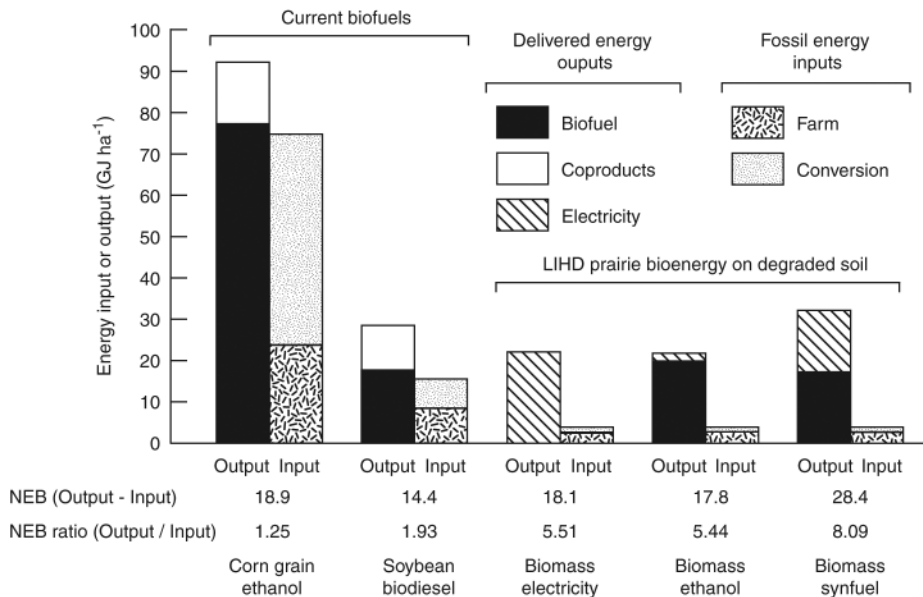


**Fig. 1.** Effects of plant diversity on biomass energy yield and CO<sub>2</sub> sequestration for low-input perennial grasslands. **(A)** Gross energy content of harvested aboveground biomass (2003–2005 plot averages) increases with plant species number. **(B)** Ratio of mean biomass energy production of 16-species (LIHD) treatment to means of each lower diversity treatment. Diverse plots became increasingly more productive over time. **(C)** Annual net increase in soil organic carbon (expressed as mass of CO<sub>2</sub> sequestered in upper 60 cm of soil) increases with plant diversity as does **(D)** annual net sequestration of atmospheric carbon (as mass of CO<sub>2</sub>) in roots of perennial plant species. Solid curved lines are log fits; dashed curved lines give 95% confidence intervals for these fits.

C may be stored in soils deeper than we measured (below 60 cm depth).

In 2004, after 10 years of growth, atmospheric CO<sub>2</sub> sequestration in roots was a log function of plant species numbers (Fig. 1D). On an annual basis, 0.62 Mg ha<sup>-1</sup> year<sup>-1</sup> of atmospheric CO<sub>2</sub> was sequestered in roots of species grown in monocultures, and 160% more CO<sub>2</sub> (1.7 Mg ha<sup>-1</sup> year<sup>-1</sup>) was captured in roots of 16-species plots. Multiple regression showed that root CO<sub>2</sub> sequestration (Mg ha<sup>-1</sup> of CO<sub>2</sub>) increased as a log function of plant species number (*S*), as a log function of time (*Year*), and their interaction { $C_{\text{root}} = -1.47 + 6.16\log_{10}(S) + 9.64\log_{10}(\text{Year}) + 9.60[\log_{10}(S) - 0.613][\log_{10}(\text{Year}) - 0.782]$  where *Year* = 3 for 1997, the first time roots were sampled; overall  $F_{3, 1260} = 191, P < 0.0001$ ; for  $\log_{10}(S)$ ,  $F_{1, 1260} = 398, P < 0.0001$ ; for *Year*,  $F_{1, 1260} = 148, P = 0.0001$ ; for  $S \times \text{Year}$ ,  $F_{1, 1260} = 27.3, P = 0.0001$ }. This regression suggests that most root carbon storage occurred in the first decade of growth; during the second decade, roots of 16-species plots are projected to store just 22% of C stored during the first decade. Measurements at greater depths in 10 LIHD plots suggest that 43% more C may be stored in roots between 30 and 100 cm.

LIHD plots had a total CO<sub>2</sub> sequestration rate of 4.4 Mg ha<sup>-1</sup> year<sup>-1</sup> in soil and roots during the decade of observation. Trends suggest that this rate might decline to about 3.3 Mg ha<sup>-1</sup> year<sup>-1</sup> during the second decade because of slower root mass accumulation. In



**Fig. 2.** NEB for two food-based biofuels (current biofuels) grown on fertile soils and for LIHD biofuels from agriculturally degraded soil. NEB is the sum of all energy outputs (including coproducts) minus the sum of fossil energy inputs. NEB ratio is the sum of energy outputs divided by the sum of fossil energy inputs. Estimates for corn grain ethanol and soybean biodiesel are from (14).

contrast, the annual rate of CO<sub>2</sub> sequestration for monocultures was 0.14 Mg ha<sup>-1</sup> year<sup>-1</sup> for the first decade and projected to be indistinguishable from zero for subsequent decades.

Across their full life cycles, biofuels can be carbon neutral [no net effect on atmospheric

CO<sub>2</sub> and other greenhouse gases (GHG)], carbon negative (net reduction in GHG), or carbon sources (net increase in GHG), depending on both how much CO<sub>2</sub> and other greenhouse gases, expressed as CO<sub>2</sub> equivalents, are removed from or released into the atmosphere

during crop growth and how much fossil CO<sub>2</sub> is released in biofuel production. Both corn ethanol and soybean biodiesel are net carbon sources but do have 12% and 41% lower net GHG emissions, respectively, than combustion of the gasoline and diesel they displace (14). In contrast, LIHD biofuels are carbon negative, leading to net sequestration of atmospheric CO<sub>2</sub> across the full life cycle of biofuel production and combustion (table S3). LIHD biomass removed and sequestered more atmospheric CO<sub>2</sub> than was released from fossil fuel combustion during agriculture, transportation, and processing (0.32 Mg ha<sup>-1</sup> year<sup>-1</sup> of CO<sub>2</sub>), with net life cycle sequestration of 4.1 Mg ha<sup>-1</sup> year<sup>-1</sup> of CO<sub>2</sub> for the first decade and an estimated 2.7 to 3 Mg ha<sup>-1</sup> year<sup>-1</sup> for subsequent decades. GHG reductions from use of LIHD biofuels in lieu of gasoline and diesel fuel are from 6 to 16 times greater than those from use of corn grain ethanol and soybean biodiesel in lieu of fossil fuels (Fig. 3A).

LIHD biofuel production should be sustainable with low inputs of agrichemicals, as in our study. Legumes in LIHD plots can supply nitrogen (18). In our experiment, total soil nitrogen of LIHD plots increased 24.5% ( $P < 0.001$ ) from 1994–2004, but monoculture total soil nitrogen was unchanged ( $P = 0.83$ ). However, some amount of N fertilization may be useful in dry habitats that lack efficient N-fixing species. Application of P or other nutrients may be needed if initially limiting or to replace nutrient exports (Fig. 3B). Production may be sustainable with low pesticide use, because plant disease incidence and invasion by exotic species are low in high-diversity plant mixtures (Fig. 3C) (19).

Switchgrass (*Panicum virgatum*), which is being developed as a perennial bioenergy crop,

was included in our experiment. Switchgrass monocultures can be highly productive on fertile soils, especially with application of pesticides and fertilizer (20, 21). However, on our infertile soils, switchgrass monoculture bioenergy [23.0 ± 2.4 GJ ha<sup>-1</sup> year<sup>-1</sup> (mean ± SE)] was indistinguishable from mean bioenergy of monocultures of all other species (22.7 ± 2.7 GJ ha<sup>-1</sup> year<sup>-1</sup>) and yielded just a third of the energy of LIHD plots (10).

How much energy might LIHD biomass potentially provide? For a rough global estimate, consider that about 5 × 10<sup>8</sup> ha of agriculturally abandoned and degraded land producing biomass at 90 GJ ha<sup>-1</sup> year<sup>-1</sup> (22) could provide, via IGCC-FT, about 13% of global petroleum consumption for transportation and 19% of global electricity consumption (2). Without accounting for ecosystem CO<sub>2</sub> sequestration, this could eliminate 15% of current global CO<sub>2</sub> emissions, providing one of seven CO<sub>2</sub> reduction “wedges” needed to stabilize global CO<sub>2</sub> (23). GHG benefits would be larger if LIHD biofuels were, in general, carbon negative, as might be expected if late-successional native plant species were used in LIHD biomass production on degraded soils [e.g., (17)].

The doubling of global demand for food and energy predicted for the coming 50 years (1, 2) and the accelerating use of food crops for biofuels have raised concerns about biodiversity loss if extant native ecosystems are converted to meet demand for both food and biofuels. There are also concerns about environmental impacts of agrichemical pollution from biofuel production and about climate change from fossil fuel combustion (14, 24–26). Because LIHD biomass can be produced on abandoned agricultural lands, LIHD biofuels

need neither compete for fertile soils with food production nor encourage ecosystem destruction. LIHD biomass can produce carbon-negative biofuels and can reduce agrichemical use compared with food-based biofuels. Moreover, LIHD ecosystem management may provide other ecosystem services, including stable production of energy, renewal of soil fertility, cleaner ground and surface waters, wildlife habitat, and recreation (18, 19, 24, 27, 28). We suggest that the potential for biofuel production and carbon sequestration via low inputs and high plant diversity be explored more widely.

## References and Notes

- N. Fedoroff, J. Cohen, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5903 (1999).
- International Energy Outlook* (DOE/EIA-0484, Energy Information Administration, U.S. Department of Energy, Washington, DC, 2006).
- A. E. Farrell *et al.*, *Science* **311**, 506 (2006).
- J. Outlaw, K. Collins, J. Duffield, Eds., *Agriculture as a Producer and Consumer of Energy* (CABI, Wallingford, UK, 2005).
- G. Keoleian, T. Volk, *Crit. Rev. Plant Sci.* **24**, 385 (2005).
- I. Lewandowski, J. Scurlock, E. Lindvall, M. Christou, *Biomass Bioenergy* **25**, 335 (2003).
- P. Gallagher *et al.*, *Environ. Resour. Econ.* **24**, 335 (2003).
- Y. Zhang, M. Dubé, D. McLean, M. Kates, *Bioresource Technol.* **89**, 1 (2003).
- S. Kim, B. Dale, *Biomass Bioenergy* **26**, 361 (2004).
- Materials and methods are available as supporting material on Science Online.
- M. Mann, P. Spath, *Clean Prod. Process.* **3**, 81 (2001).
- J. Sheehan *et al.*, *J. Ind. Ecol.* **7**, 117 (2003).
- C. Hamelinck, A. Faaij, H. den Uil, H. Boerrigter, *Energy* **29**, 1743 (2004).
- J. Hill, E. Nelson, D. Tilman, S. Polasky, D. Tiffany, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 11206 (2006).
- P. Camill *et al.*, *Ecol. Appl.* **14**, 1680 (2004).
- C. Owensby, J. Ham, A. Knapp, L. Auen, *Global Change Biol.* **5**, 497 (1999).
- J. Knops, D. Tilman, *Ecology* **81**, 88 (2000).
- D. Tilman *et al.*, *Science* **294**, 843 (2001).
- J. Knops *et al.*, *Ecol. Lett.* **2**, 286 (1999).
- D. Parrish, J. Fike, *Crit. Rev. Plant Sci.* **24**, 423 (2005).
- K. Vogel, J. Brejda, D. Walters, D. Buxton, *Agron. J.* **94**, 413 (2002).
- M. Hoogwijk *et al.*, *Biomass Bioenergy* **25**, 119 (2003).
- S. Pacala, R. Socolow, *Science* **305**, 968 (2004).
- P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, *Science* **277**, 494 (1997).
- D. Tilman *et al.*, *Science* **292**, 281 (2001).
- G. Berndes, *Global Environ. Change* **12**, 253 (2002).
- J. A. Foley *et al.*, *Science* **309**, 570 (2005).
- D. Hooper *et al.*, *Ecol. Monogr.* **75**, 3 (2005).
- Agricultural Chemical Usage 2004 and 2005 Field Crops Summaries* (National Agricultural Statistics Service, U.S. Department of Agriculture, Washington, DC, 2006).
- Supported by grants from the University of Minnesota's Initiative for Renewable Energy and the Environment, the NSF (grant DEB 0080382), and the Bush Foundation. We thank S. Polasky, J. Fargione, E. Nelson, P. Spath, E. Larson, and R. Williams for comments.

## Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5805/1598/DC1

Materials and Methods

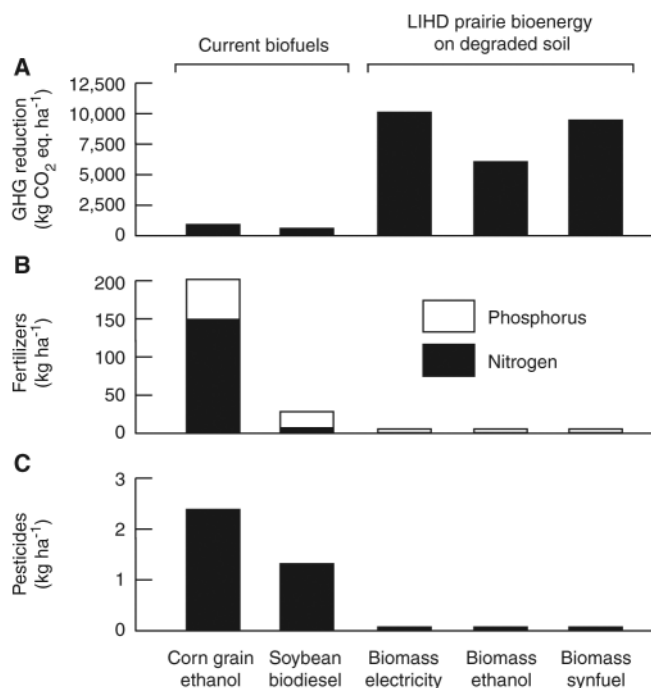
Tables S1 to S3

References

1 August 2006; accepted 24 October 2006  
10.1126/science.1133306

**Fig. 3.** Environmental effects of bioenergy sources.

(A) GHG reduction for complete life cycles from biofuel production through combustion, representing reduction relative to emissions from combustion of fossil fuels for which a biofuel substitutes. (B) Fertilizer and (C) pesticide application rates are U.S. averages for corn and soybeans (29). For LIHD biomass, application rates are based on analyses of table S2 (10).



## Materials and Methods

**Experimental Design:** We controlled the number of plant species in 168 plots, each 9 m x 9 m, in a 7 ha field at Cedar Creek Natural History Area, Minnesota, USA. Plots were randomly chosen for seeding with 1, 2, 4, 8, or 16 perennial grassland/savanna species. Composition of each plot was randomly chosen from a set of 18 perennials: four C<sub>4</sub> grasses, four C<sub>3</sub> grasses, three herbaceous and one woody/shrubby legume, four non-legume herbaceous forbs, and two savanna oak species (Table S1). Plots received 10 g m<sup>-2</sup> of seed in May 1994 and 5 g m<sup>-2</sup> in May 1995, with seed mass divided equally among species. Treatments were maintained by weeding 3 or 4 times annually, with low-diversity treatments having much more weedy biomass removed than high-diversity treatments (*S1*). Plots received low inputs (i.e., no fertilization, irrigation only during initial establishment, and herbicide only to prepare area for initial planting). Plots were burned annually in spring before growth began. Additional experimental design details have been published previously (*S2*). Plots were sampled annually in early August for aboveground living plant biomass by clipping, drying, and weighing four parallel and evenly spaced 0.1 x 3.0 m vegetation strips per plot from 1996–1999 and four 0.1 x 6.0 m strips per plot from 2000–2005. Different locations were clipped each year. For most plots, including the LIHD plots, burning effectively removed all aboveground biomass; however, fire did not carry through woody monocultures nor through low-diversity woody-dominated plots. In contrast, annual burning removed aboveground woody biomass, and essentially removed woody species, from multispecies plots, making aboveground biomass a good measure of annual production of these herbaceous plots. Because this paper focuses on yearly biomass and energy production by herbaceous perennial species, and because woody biomass accumulated over many years in plots through which fire did not carry and is thus not a measure of annual production, monocultures of woody species and low-diversity plots dominated by woody species are not included in analyses, leaving 152 plots with data on annual herbaceous biomass and energy production (30, 28, 29, 30 and 35 replicates, respectively, of 1-, 2-, 4-, 8-, and 16-species treatments).

Two plots were planted in 1994 as switchgrass (*Panicum virgatum*) monocultures, in which only one became well-established, despite re-seeding switchgrass in both plots in 1995. Two additional plots originally planted to contain two species (switchgrass and a second species) effectively became switchgrass monocultures by the last five years of the study because the other species comprised less than 2% of total plot biomass. We used 2003–2005 average harvested biomass for these three plots to estimate monoculture bioenergy production by switchgrass.

We measured organic carbon in the soil in 50 plots that were a randomly chosen subset of 1-, 4-, and 16-species plots. Soils were sampled at 3 depths (0-20 cm; 20-40 cm; 40-60 cm) for each of four sites per plot both before plots were planted in 1994 and again in 2004. Soils were sieved to remove roots. Soil sequestration or release of carbon was determined as the change ( $\Delta C$ ), at each soil depth, in the soil organic C of each plot from 1994–2004. These  $\Delta C$  values were then summed over the three soil depths and divided by the lapsed time to give the annual net rate of carbon storage or release. Root mass was sampled in all 152 plots using twelve soil cores per plot (5 cm diameter by 30 cm deep), collected in mid-August just after biomass sampling. Soil cores were placed on a fine mesh screen and a gentle spray of water was used to rinse soil from roots. Roots were dried, any residual soil on dried samples was removed, then roots were weighed to obtain root mass per area. An additional subset of 10 plots planted to 16 species was sampled for roots from 0-30 cm depth, 30-60 cm depth, and 60-100 cm depth to estimate root

mass below 30 cm in high diversity plots. Based on numerous measurements, we estimate C content of root biomass as 40% C by mass.

**Net Energy Balance of Prairie Biomass:** Energy inputs for growing, harvesting, and transporting prairie biomass are estimated assuming standard agricultural practices on a 240 ha farm (Table S2). We divide over 30 years one-time energy inputs for establishing prairie, including fossil fuel energy use for initial spraying, planting, and mowing, and the energy required to produce the farm machinery used on the farm, the herbicides applied to prepare the seed bed, and the seed planted to give the prairie. We estimate annual energy inputs, including fossil fuel use for mowing, baling, and fertilizing, fossil fuel use for transporting hay bales from fields to their point of end use, and energy for sustaining the farm households. We estimate total energy inputs in prairie biomass production at  $4.01 \text{ GJ ha}^{-1} \text{ yr}^{-1}$  for a biomass yield of  $3,682 \text{ kg ha}^{-1} \text{ yr}^{-1}$ , which has been demonstrated on highly-degraded Cedar Creek soils. Harvesting prairie biomass in mid-September might both yield greater biomass and decrease ecosystem loss of N, P, and other nutrients. For an estimated fertile prairie yield of  $6,000 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (S3, S4), total energy inputs are  $4.64 \text{ GJ ha}^{-1} \text{ yr}^{-1}$ . With  $18.5 \text{ MJ kg}^{-1}$  released upon combustion (S5), the gross prairie energy output is 68.1 and  $111.0 \text{ GJ ha}^{-1} \text{ yr}^{-1}$  for degraded and fertile prairie, respectively.

**Biomass Conversion to Usable Energy:** We model three scenarios for utilizing prairie biomass for bioenergy. Biomass can be co-fired with coal in existing facilities at low levels to generate electricity with little loss of efficiency (e.g., a 0.5% decrease in overall efficiency with a 95% coal/5% biomass blend as compared to 100% coal) (S6, S7). Average U.S. coal electricity production efficiency in 2004 was 32.9% (S8); therefore, we assume biomass may be converted to electricity at 32.4% efficiency.

Biomass may also be converted to ethanol via cellulose digestion to sugars followed by fermentation and distillation. This yields ethanol at a rate of  $0.255 \text{ L kg}^{-1}$  of dry biomass, simultaneously generating electricity equal to 9.2% of the energy output of ethanol (S9). This overall efficiency of 32.0% was demonstrated using corn stover and is supported by a similar study that estimated 38% efficiency when converting hybrid poplar to ethanol while noting an efficiency of approximately 34% would be achieved with switchgrass (S10).

Biomass may also be gasified and converted to both synfuel and electricity simultaneously via high-pressure Fischer-Tropsch liquid synthesis integrated with gas turbine combined cycle electric power generation. There are many proposed variations on this process that provide different estimated efficiencies of energy capture in synfuels and electricity. The process-dependent ranges of overall efficiency from four studies are from 42.4% to 46.2% (S11), from 41.6% to 51.5% (S12), from 32% to 50% (S13), and, for a highly optimized process, 57.3% (S14). Here we use the average efficiency for this process as estimated by these four studies, 47.6%. The relative amounts of liquid fuels and electricity can vary depending upon the specifications and input parameters of the conversion facility; therefore, for illustrative purposes only, we assume that an average of 53% of the net power output is realized in the liquid fuels and 47% is in electricity (S13), and that 62% and 38% of the liquid fuels produced are diesel and gasoline, respectively (S14).

**Greenhouse Gas (GHG) Savings:** We consider the total life cycle GHG savings from producing and using biomass to generate various biofuels and electricity (Table S3). GHG savings results both from displacing fossil fuels and from the net GHG sink on the prairie land itself. To estimate

net GHG savings, we subtract from this amount the total life cycle GHG release from the fossil fuels used to produce prairie biomass and transport it to its point of end use.

***Fertilizer Application:*** Legumes in high-diversity species mixtures may eliminate the need for nitrogen fertilization (e.g., in our experiment, total soil nitrogen increased 24.5% in LIHD plots from 1994–2004). To replace phosphorus, which constitutes 0.2% of the mass of dry biomass (*S15*) annually harvested, we estimate phosphorus fertilizer would be added at a rate of 7.4 kg ha<sup>-1</sup> yr<sup>-1</sup> on degraded prairie and 12.0 kg ha<sup>-1</sup> yr<sup>-1</sup> on fertile prairie.

**Table S1.** The 18 perennial native prairie species planted in this experiment. Species are listed in order of decreasing biomass as measured in 16-species plots from 2002–2005.

Species	Functional type
<i>Lupinus perennis</i>	Legume
<i>Andropogon gerardi</i>	C <sub>4</sub> grass
<i>Schizachyrium scoparium</i>	C <sub>4</sub> grass
<i>Sorghastrum nutans</i>	C <sub>4</sub> grass
<i>Solidago rigida</i>	Forb
<i>Amorpha canescens</i>	Woody legume
<i>Lespedeza capitata</i>	Legume
<i>Poa pratensis</i>	C <sub>3</sub> grass
<i>Petalostemum purpureum</i>	Legume
<i>Monarda fistulosa</i>	Forb
<i>Achillea millefolium</i>	Forb
<i>Panicum virgatum</i>	C <sub>4</sub> grass
<i>Liatris aspera</i>	Forb
<i>Quercus macrocarpa</i>	Woody
<i>Koeleria cristata</i>	C <sub>3</sub> grass
<i>Quercus elipsoidalis</i>	Woody
<i>Elymus canadensis</i>	C <sub>3</sub> grass
<i>Agropyron smithii</i>	C <sub>3</sub> grass

**Table S2.** Estimated annual energy inputs for growing and harvesting prairie biomass.

Energy input	Annual energy use (MJ ha <sup>-1</sup> )	
	Degraded prairie	Fertile prairie
Prairie species seed*	134	103
Fossil fuel for planting and harvesting <sup>†</sup>	543	543
Farm capital and machinery <sup>‡</sup>	188	188
Pesticide/fertilizer production and distribution <sup>§</sup>	103	146
Sustaining farm household <sup>  </sup>	1,864	1,864
Fossil fuel use for transporting biomass <sup>¶</sup>	1,174	1,796
Total	4,006	4,640

\* We assume that producing seed for planting prairies requires twice the energy used to produce prairie biomass, and that two or three hectares can be planted from the seeds harvested from each hectare of degraded or fertile prairie, respectively. We divide this total energy input over an assumed 30 year life of the prairie.

<sup>†</sup> We assume 30.5 L ha<sup>-1</sup> of diesel are used in the first year for spraying, disking, planting, and mowing (S16), and that diesel releases 36.6 MJ L<sup>-1</sup>. We distribute this total energy input over a 30 year life of the prairie. Annual fuel use for mowing, baling, and fertilizing is 13.8 L ha<sup>-1</sup>.

<sup>‡</sup> We estimate the weight of equipment used in production (i.e., boom sprayer, tandem disk, no-till drill, rotary mower/conditioner, hay merger, large rectangular baler, 75 hp tractor, 130 hp tractor, pull spreader, loader, and bale spike) to be  $3.6 \times 10^4$  kg. We assume for purposes of calculating the embodied energy of each piece of machinery that it consist entirely of steel and that it takes 25 MJ kg<sup>-1</sup> to produce steel (S17, S18) with an additional 50% for assembly (S19). We distribute this over a 30 year life of the prairie and a 240 ha size of the farm.

<sup>§</sup> We assume a first year 2.24 kg ha<sup>-1</sup> application rate of glyphosate, which requires 475 MJ/kg to produce and distribute (S20). We divide this energy input over an assumed 30 year life of the prairie. We assume phosphorus fertilizer, which takes 9.2 MJ/kg to produce and transport (S21), is applied every three years at a rate of 7.4 kg ha<sup>-1</sup> yr<sup>-1</sup> on degraded prairie and 12.0 kg ha<sup>-1</sup> yr<sup>-1</sup> on fertile prairie to replace phosphorus removed in harvested biomass.

<sup>||</sup> The 2004 U.S. per capita energy use was  $3.58 \times 10^5$  MJ (S22, S23). We assume household size of 2.5 people (S24), 50% of farm household labor devoted to farming (S25), and a 240 ha farm.

<sup>¶</sup> We estimate 24 and 38 L ha<sup>-1</sup> of diesel is used to move bales onto and off of tractor trailers for degraded and fertile prairies, respectively (S16). We assume bales weigh 680 kg, each tractor trailer can haul 27 bales, and bales are transported an average of 40 km to their point of end use. With an average fleet efficiency of 2.2 km/L (S26), 36.4 L of diesel are used in a single round trip to haul the bales produced on 4.9 ha of degraded prairie or 3.0 ha of fertile prairie.



**Table S3.** Greenhouse gas (GHG) sequestration (positive values) or release (negative values) from LIHD bioenergy sources (kg CO<sub>2</sub> equivalent ha<sup>-1</sup>). All three delivered energy sources created from LIHD biomass are carbon negative biofuels because net GHG reductions exceed the release of fossil GHG during biomass production, harvesting, transport, and processing.\*

Biomass use	GHG reductions or releases on prairie <sup>†</sup>			GHG release from biomass production <sup>‡</sup>	GHG avoided by displacing fossil fuels <sup>§</sup>	Net GHG reduction from bioenergy production
	CO <sub>2</sub> soil/root sequestration	N <sub>2</sub> O emissions	CH <sub>4</sub> mitigation			
Electricity	4,033	-160	150	-324	6,389	10,088
Ethanol	4,033	-160	150	-324	2,465	6,164
Synfuel	4,033	-160	150	-324	5,926	9,626

\* Although we have data on biomass production on fertile soils for prairie, we do not have comparable data on LIHD carbon storage in such soils, and thus do not present this case in this table.

<sup>†</sup> Values are from (S27).

<sup>‡</sup> This includes diesel used for producing prairie seed, planting and harvesting, and transporting bales. Diesel life cycle GHG emissions are  $3.01 \times 10^3$  g CO<sub>2</sub> eq. L<sup>-1</sup> (S28). We also include GHG release in pesticide production, sustaining farm households, and producing farm capital and machinery by assuming they require use of an amount of diesel equivalent to the energy expenditure of these inputs.

<sup>§</sup> This value is the amount of fossil fuels each use of biomass displaces (energy equivalent) multiplied by the life cycle GHG emissions of the displaced fossil fuels. We assume ethanol displaces gasoline (life cycle GHG emission = 96.9 g CO<sub>2</sub> eq. MJ<sup>-1</sup>) (S28), biomass-generated electricity displaces coal-generated electricity (life cycle GHG emission = 289.5 g CO<sub>2</sub> eq. MJ<sup>-1</sup>) (S29), and synfuel displaces 38% gasoline and 62% diesel (life cycle GHG emission = 82.3 g CO<sub>2</sub> eq. MJ<sup>-1</sup>) (S14, S28).

## References and Notes

- S1. J. Knops *et al.*, *Ecology Letters* **2**, 286 (1999).
- S2. D. Tilman *et al.*, *Science* **294**, 843 (2001).
- S3. P. Camill *et al.*, *Ecol. Appl.* **14**, 1680 (2004).
- S4. C. E. Owensby, J. M Ham, A. K. Knapp, L. M Auen, *Global Change Biol.* **5**, 497 (1999).
- S5. S. E. Florine, K. J. Moore, S. L. Fales, T. A. White, C. Lee Burras, *Biomass and Bioenergy* **30**, 522 (2006).
- S6. M. K. Mann, P. L. Spath, *Clean Prod. Processes* **3**, 81 (2001).
- S7. X. Qin, T. Mohan, M. El-Halwagi, G. Cornforth, B. A. McCarl, *Clean Techn. Environ. Policy*, (2006); published online 9 Sept. 2006 (10.1007/s10098-006-0065-4).
- S8. *Annual Energy Outlook 2006* (DOE/EIA-0383(2006), U.S. Department of Energy – Energy Information Administration, Washington, DC, 2006).
- S9. J. Sheehan *et al.*, *J. Ind. Ecol.* **7**, 117 (2004).
- S10. C. N. Hamelinck, G. van Hooijdonk, A. P. C. Faaij, *Biomass and Bioenergy* **28**, 384 (2005).
- S11. M. J. Prins, K. J. Ptasincki, F. J. J. G. Janssen, *Fuel Processing Technology* **86**, 375 (2004).
- S12. M. J. A. Tijmensen, A. P. C. Faaij, C. N. Hamelinck, M. R. M. van Hardeveld, *Biomass and Bioenergy* **23**, 129 (2002).
- S13. C. N. Hamelinck, A. P. C. Faaij, H. den Uil, H. Boerrigter, *Energy* **29**, 1743 (2004).
- S14. E. D. Larson, R. H. Williams, H. Jin, paper presented at the 8th International Conference on Greenhouse Gas Control Technologies, Trondheim, Norway, 2006, in press.
- S15. C. E. Owensby, P. I. Coyne, L. M. Auen, *Plant Cell Environ.* **16**, 843 (1993).
- S16. W. Lazarus, R. Selley, “Farm Machinery Economic Cost Estimates for Late 2005” (University of Minnesota, St. Paul, MN, 2005)
- S17. J. de Beer, E. Worrell, K. Blok, *Annu. Rev. Energy Environ.* **23**, 123 (1998).
- S18. R. J. Fruehan, O. Fortini, H. W. Paxton, R. Brindle, “Theoretical minimum energies to produce steel for selected conditions” (OSTI ID: 769470 U.S. Department of Energy Office of Industrial Technologies, Washington, DC, 2000).

- S19. M. S. Graboski, "Fossil energy use in the manufacture of corn ethanol" (Prepared for the National Corn Growers Association, 2002).
- S20. Z. Helsel, in: Fluck, R.C. (Ed), *Energy in Farm Production* (Elsevier, New York, 1992), pp. 177-201.
- S21. J. Hill, E. Nelson, D. Tilman, S. Polasky, D. Tiffany, *Proc. Natl. Acad. Sci. USA* **103**, 11206 (2006).
- S22. *Annual Energy Review 2004* (Rep. No. DOE/EIA-0384(2004), U.S. Department of Energy – Energy Information Administration, Washington, DC, 2005).
- S23. *Population Estimates* (U.S. Census Bureau, Washington, DC, 2006).
- S24. J. Fields, "America's families and living arrangements: 2003" (U.S. Census Bureau, Current Population Reports P20-553, Washington, DC, 2003).
- S25. R. Green, M. C. Ahearn, paper presented at the Agricultural Outlook Forum 2005. Arlington, VA, 24-25 February 2005.
- S26. S. C. Davis, S. W. Diegel, "Transportation Energy Data Book: Edition 24" (U.S. Department of Energy Office, ORNL-6973, Oak Ridge, TN, 2004).
- S27. G. P. Robertson, E. A. Paul, R. R. Harwood, *Science* **289**, 1922 (2000).
- S28. N. Brinkman, M. Wang, T. Weber, T. Darlington, "Well-to-Wheels Analysis of Advanced Fuel/Vehicle Systems - A North American Study of Energy Use, Greenhouse Gas Emissions, and Criteria Pollutant Emissions" (Argonne National Laboratory, Argonne, IL, 2005).
- S29. P. L. Spath, M. K. Mann, D. R. Kerr, "Life Cycle Assessment of Coal-fired Power Production" (National Renewable Energy Laboratory, NREL/TP-570-25119, Golden, CO, 1999).

# Comment on “Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass”

Michael P. Russelle,<sup>1\*</sup> R. Vance Morey,<sup>2</sup> John M. Baker,<sup>1</sup>  
Paul M. Porter,<sup>3</sup> Hans-Joachim G. Jung<sup>1</sup>

Tilman *et al.* (Reports, 8 December 2006, p. 1598) argued that low-input high-diversity grasslands can provide a substantial proportion of global energy needs. We contend that their conclusions are not substantiated by their experimental protocol. The authors understated the management inputs required to establish prairies, extrapolated globally from site-specific results, and presented potentially misleading energy accounting.

Tilman *et al.* (1) reported that biofuels derived from diverse mixtures of native grassland perennials can provide greater energy yields and environmental benefits than monoculture grown on fertile soils. We agree that growing herbaceous perennial species on land of marginal value for agriculture is desirable for several reasons, but we take issue with the authors' contention that low-input high-diversity (LIHD) prairie can provide a substantial contribution to our nation's energy needs. We argue that their experimental results do not substantiate their conclusions and that the authors overstated the global importance of their results.

Tilman *et al.* suggest that LIHD plantings could provide a sustainable source of harvestable biomass for fuel production, but they reported sample yields from an experiment in which nearly all the biomass was burned in situ, not harvested. Although several plant nutrients are lost from burned vegetation as gases or particulates, most cations are returned to the soil (2). With mechanical harvest, all nutrients are removed. Although legumes can replace nitrogen, nutrient replacement will be an important requirement for many marginal, and especially acidic, soils if yields are to be sustained. Limestone additions would be required to maintain symbiotic N<sub>2</sub> fixation on soils with poor pH buffering capacity. Liming represents a major energy input (3, 4).

More seriously, the experimental approach of Tilman *et al.* is a form of double accounting with respect to carbon. The authors estimated harvestable biomass from small samples taken in late summer, then burned the remaining bio-

mass on the plots the following spring [see supporting online material for (1)]. Combustion of this sort is incomplete, so some, if not most, of the soil C sequestration they measured is almost certainly due to charcoal additions that would not have occurred with harvest for biofuel production. Burning also has multiple, and often unpredictable, effects on prairie plant ecology. In general, burning reduces the presence of woody species in mixed stands, as the authors observed (1), but also helps control other undesirable species and may increase root biomass, tillering, soil temperature, and nitrification (2). With the exception of the decline in woody species, these benefits would not accrue with mechanical harvest of herbaceous perennials.

Tilman *et al.* (1) also ignored the difficulty of establishing and maintaining stands of native prairie species. Species composition was maintained artificially in the Cedar Creek plots with hand-weeding four times per year [see supporting online material for (5)], a practice that would be impossible in a commercial biomass production system. Because phenology differs among plant species, timing of biomass removal will influence species survival and composition of the grassland through interspecific competition. For instance, switchgrass, one of the dominant North American tallgrass prairie species, requires 6 weeks of regrowth to persist if harvested during the growing season (6). Resulting alterations in species dominance could affect grassland productivity and yield resilience under stress. Thus, the yields reported by Tilman *et al.* and their assumption of a 30-year useful stand life may need to be reconsidered. In temperate climates, delaying harvest until after a killing frost in the fall would avoid the problem of interspecific competition during late summer regrowth, but it would also remove protective winter cover of great value for wildlife.

Tilman *et al.* base most of their report (1) on one experiment, yet extrapolate their results globally. The experiment was conducted at one

site in central Minnesota, USA, on soils that have low soil organic C, low water-holding capacity, and relatively shallow groundwater. The authors then estimated the amount of energy that might be provided by LIHD biomass, assuming  $5 \times 10^8$  ha of “abandoned and degraded land.” This land area, attributed to (7), derives from studies estimating the potential for reforestation of degraded lands primarily in the tropics (8). However, we are not aware of large areas of “abandoned and degraded” agricultural lands in temperate regions of the globe that would permit establishment of large-scale LIHD biomass prairies without affecting food production, as the authors claim. In the entire United States for example, there are only about  $1.5 \times 10^7$  ha of land classified as idle cropland (9), and a substantial fraction of that area is in regions too arid to support the annual biomass yields projected in (1). We contend that, rather than attempt to make global calculations, the authors should have limited their interpretations to similar soil and climatic conditions in the United States, on clearly identified land where these practices could be implemented.

Finally, Tilman *et al.* make the misleading claim that LIHD biomass from degraded infertile land would produce more usable energy per hectare than corn grain ethanol from fertile soils [figure 2 in (1)]. The biofuel energy output (GJ ha<sup>-1</sup>) for corn grain ethanol is four times as large as either of the two LIHD alternatives that include biofuel outputs. It also appears that most of the energy for the conversion process for LIHD biofuels, but not corn grain ethanol, was assumed to come from biomass co-products. Co-products from corn grain ethanol can provide all of the conversion energy (10), and applying them as conversion energy rather than co-product energy credit to their net energy balance ratios [figure 2 in (1)] results in a net energy of more than 50 GJ ha<sup>-1</sup> for corn grain ethanol, with corresponding reductions in greenhouse gas emissions. Alternatively, using only half the corn stover produced from each hectare of corn grain that is used for ethanol production could provide all the energy required for distillation, or at least as much cellulosic ethanol as a hectare of LIHD prairie, thereby substantially improving the energy balance of corn-based ethanol. To be meaningful, net energy and greenhouse gas emission comparisons among biofuel systems must be based on consistent assumptions about conversion technologies.

Alternative energy based on biomass has captured public attention, and considerable resources are being devoted to research, development, and implementation. There is potential for substantial environmental benefit, but also for unproductive expenditure. Many agree that no single biomass feedstock or product will suffice because of the disparate economic, environmental, edaphic, climatic, technological, and logistical factors involved. We suggest

<sup>1</sup>U.S. Department of Agriculture, Agricultural Research Service, St. Paul, MN 55108, USA. <sup>2</sup>Department of Bioproducts and Biosystems Engineering, University of Minnesota, St. Paul, MN 55108, USA. <sup>3</sup>Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108, USA.

\*To whom correspondence should be addressed: E-mail: michael.russelle@ars.usda.org

that the results and conclusions presented by Tilman *et al.* be treated with appropriate caution until they have been subjected to more rigorous examination.

#### References

1. D. Tilman, J. Hill, C. Lehman, *Science* **314**, 1598 (2006).
2. K. F. Higgins, A. D. Kruse, J. L. Piehl, *Effects of Fire in the Northern Great Plains*. South Dakota Extension Circular 761; [www.npwr.usgs.gov/resource/habitat/fire/index.htm](http://www.npwr.usgs.gov/resource/habitat/fire/index.htm) (Version 16MAY2000) (1989).
3. M. S. Graboski, *Fossil Energy Use in the Manufacture of Ethanol* (National Corn Growers Association, St. Louis, 2002).
4. H. Shapouri, J. A. Duffield, M. Wang, *The Energy Balance of Corn Ethanol: An Update*, USDA Office of the Chief Economist, Agric. Econ., Rep. no. 814. (2002).
5. D. Tilman *et al.*, *Science* **294**, 843 (2001).
6. L. E. Moser, K. P. Vogel, in *Forages: An Introduction to Grassland Agriculture*, R. F. Barnes *et al.*, Eds. (Blackwell, Oxford, 1995), pp. 409–420.
7. M. Hoogwijk *et al.*, *Biomass Bioenergy* **25**, 119 (2003).
8. A. Grainger, *Int. Tree Crops J.* **5**, 31 (1988).
9. National Agricultural Statistics Service, *2002 Census of Agriculture, Vol. 1, State Level Data*. United States Table 8; [www.nass.usda.gov/census/census02/volume1/us/st99\\_1\\_008\\_008.pdf](http://www.nass.usda.gov/census/census02/volume1/us/st99_1_008_008.pdf) (2004).
10. R. V. Morey, D. G. Tiffany, D. L. Hatfield, *Appl. Eng. Agric.* **22**, 723 (2006).

28 December 2006; accepted 16 May 2007  
10.1126/science.1139388

# Response to Comment on “Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass”

David Tilman,<sup>1\*</sup> Jason Hill,<sup>1,2</sup> Clarence Lehman<sup>1</sup>

We discovered that biofuels from low-input high-diversity mixtures of native perennial prairie plants grown on degraded soil can provide similar bioenergy gains and greater greenhouse gas benefits than current corn ethanol produced from crops grown in monoculture on fertile soil with high inputs. Russelle *et al.*'s technical concerns are refuted by a substantial body of research on prairie ecosystems and managed perennial grasslands.

Russelle *et al.* (1) raise several technical concerns that lead them to question our conclusions about the energetic and environmental advantages of biofuels derived from diverse mixtures of native perennial prairie plant species over biofuels from high-input annual food crops such as corn (2). The nature of their comments suggests that research results well known in ecology may be less familiar to those outside the discipline. Indeed, our approach stands in marked contrast to that of conventional high-input agriculture. Each of their concerns, addressed below, is refuted by published studies of the ecology of high-diversity grasslands, and none of them has substantive effect on our original conclusions.

Russelle *et al.* (1) question the ability of low-input high-diversity (LIHD) prairie biomass to grow sustainably with low nutrient inputs. U.S. corn, in contrast, requires substantial inputs: 148 kg/ha of nitrogen, 23 kg/ha of phosphorus, and 50 kg/ha of potassium annually (3). Leaching and erosional nutrient losses are much lower for perennial grasslands than for annually tilled row crops such as corn; hence, much lower inputs are needed. Moreover, we recommended harvesting prairie biomass when senescent in late autumn because this would “both yield greater biomass and decrease ecosystem loss of N, P, and other nutrients” [supporting online material for (4)]. Replacing nutrients removed by harvesting would require about 4 kg/ha of P and 6 kg/ha of K, should they be limiting (5, 6). LIHD mixtures needed no N fertilization because N fixation by legumes more than compensated for N exports in harvested biomass. Also, unlike some cultivated legumes, our native legumes grow well and fix N on acidic soils without liming (7). Moreover, several studies have shown that biomass yields of high-diversity grasslands are

sustainable with low inputs. Annual hay yields from high-diversity Kansas prairie (8) showed no declines over 55 years despite no fertilization. Similarly, hay yields increased slightly during 150 years of twice-annual biomass removal in high-diversity unfertilized plots of the Park Grass experiment (9, 10). In total, nutrient inputs sufficient to sustain LIHD biomass production are an order of magnitude lower than for corn.

We showed that the dense root mass of LIHD prairie led to high rates of soil carbon sequestration (2). Russelle *et al.* (1) express concern that fire may have caused carbon storage through charcoal formation. However, published studies show that annual accumulation of charcoal carbon in frequently burned grasslands was <1% of our observed rate of soil carbon accumulation (11, 12). Similarly, fire had no effect on soil black carbon levels in a 6-year study of mixed-grass savanna (13). The concern about effects of late autumn mowing versus burning is also unfounded. Annual mowing and burning have similar effects on prairie biomass production (14, 15), and mowing does not cause prairie yields to decrease (8).

We proposed using mixtures of native prairie perennials for biofuels in part because, contrary to the assertion of Russelle *et al.* (1), such mixtures are easily established and require low or no inputs for maintenance. Indeed, prairie readily reestablishes itself from seed and displaces exotic plant species during natural succession on many degraded agricultural lands in the Great Plains (16). Prairie restoration, such as on the 6000 ha restored recently in Minnesota by The Nature Conservancy, is performed using agricultural machinery, not manual labor as Russelle *et al.* suggest. Our hand-weeding was done to maintain monoculture and low-diversity treatments. In contrast, the LIHD treatment led to rapid competitive displacement of exotic weedy and pasture species. LIHD plots were strikingly resistant to subsequent plant invasion and disease (17, 18). In portions of LIHD plots for which weeding had been stopped for 3 years, only 1.7% of total biomass came from invaders,

which themselves were mainly native prairie perennials, and this invasion did not impact energy production.

Our one-sentence “rough global estimate” of the energy LIHD biomass might potentially provide was brief, but well-supported and conservative. As to our estimated land base,  $9 \times 10^8$  ha of global agricultural lands have been degraded so as to have “great reductions” in agricultural productivity, and an additional  $3 \times 10^8$  ha are “severely degraded” and offer no agricultural utility (19, 20). A review of 17 studies found a median value of  $7.1 \times 10^8$  ha of degraded land available globally for biofuel production (21). Our suggestion of  $5 \times 10^8$  ha is 30% lower and is therefore a conservative estimate.

In our experiment (2), severely degraded land planted to LIHD mixtures had biomass production that was 46% as much as its native biome, temperate grassland (22). To be conservative, we assumed that LIHD mixtures of native species planted on degraded land would produce 20% less than we observed, i.e., just 37% of the average of its native biome (22). Weighting this LIHD production estimate by the global area for each biome produced our estimate of  $90 \text{ GJ ha}^{-1} \text{ year}^{-1}$  globally and of degraded lands potentially providing—through the integrated gasification combined cycle (IGCC)/Fischer-Tropsch process—about one-seventh of the global transportation and electricity demand. We stand by that estimate. Further, we urge that the energy and carbon sequestration potential of low-input high-diversity mixtures of locally native plant species be explored for degraded lands around the world.

Our energy accounting was thorough and correct. We reported actual energy balances for U.S. corn ethanol and soybean biodiesel as currently produced (both of which cause net increases in greenhouse gases), and we compared them to three ways that LIHD prairie biomass might be used to produce carbon-negative biofuels (i.e., biofuels that, in total for their life cycle, decrease greenhouse gas levels). We showed that these new carbon-negative biofuels could provide similar or greater net energy gains per hectare than current biofuels.

The concerns of Russelle *et al.* (1) are refuted by a thorough consideration of the published literature. As to current biofuels, we agree that the energy and greenhouse gas benefits of corn ethanol could be improved, but we disagree about methods. First, burning the high-protein co-product of corn ethanol production to power ethanol production facilities, as Russelle *et al.* suggest, seems unwise because greater protein production is required to meet global nutritional needs. Burning this protein is not an industry standard, nor is it discussed in any recent ethanol energy balance reviews (23, 24). Second, harvest and use of corn stover (the senescent stalks and leaves of corn plants) to power ethanol plants would likely cause soil organic

<sup>1</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA. <sup>2</sup>Department of Applied Economics, University of Minnesota, St. Paul, MN 55108, USA.

\*To whom correspondence should be addressed. E-mail: tilman@umn.edu

carbon levels to fall, and increase both carbon dioxide release and soil erosion. A better alternative would be powering corn ethanol plants with LIHD biomass, likely by gasification. If done properly, the ethanol produced could be carbon-neutral and have a markedly higher net energy gain than current corn ethanol.

The world's energy and climate problems are likely to be solved only by a combination of approaches and technologies, including wind and solar energy, increased energy efficiency, and renewable biofuels (25). Our research found that biofuels from LIHD biomass grown on degraded lands have substantial energy and greenhouse gas advantages over current U.S. biofuels. Moreover, LIHD production of renewable energy on agriculturally marginal lands could help ameliorate what might otherwise be an escalating conflict between food production, bioenergy production, and preservation of the world's re-

maining natural ecosystems. LIHD biofuels merit further exploration.

#### References

1. M. P. Russelle, R. V. Morey, J. M. Baker, P. M. Porter, H.-J. G. Jung, *Science* **316** (2007); [www.sciencemag.org/cgi/content/full/316/5831/1567b](http://www.sciencemag.org/cgi/content/full/316/5831/1567b).
2. D. Tilman, J. Hill, C. Lehman, *Science* **314**, 1598 (2006).
3. U.S. Department of Agriculture, *Agricultural Chemical Usage 2005 Field Crops Summary* (National Agricultural Statistics Service, USDA, Washington, DC, 2006).
4. D. Tilman, J. Hill, C. Lehman, *Science* **314**, 1598 (2006).
5. M. R. Koelling, C. L. Kucera, *Ecology* **46**, 529 (1965).
6. R. Samson *et al.*, *Crit. Rev. Plant Sci.* **24**, 461 (2005).
7. D. Tilman, *Oikos* **58**, 3 (1990).
8. J. Shortridge, *Geogr. Rev.* **63**, 533 (1973).
9. D. Jenkinson *et al.*, *J. Agric. Sci.* **122**, 365 (1994).
10. J. Silvertown, M. Dodd, K. McConway, J. Potts, M. Crawley, *Ecology* **75**, 2430 (1994).
11. B. Glaser, W. Amelung, *Global Biogeochem. Cycles* **17**, 1064 (2003).
12. X. Dai, T. Boutton, B. Glaser, R. Ansley, W. Zech, *Soil Biol. Biochem.* **37**, 1879 (2005).
13. R. J. Ansley, T. W. Boutton, J. O. Skjemstad, *Global Biogeochem. Cycles* **20**, GB3006 (2006).
14. L. Hulbert, *Ecology* **50**, 874 (1969).
15. S. L. Collins, A. K. Knapp, J. M. Briggs, J. M. Blair, E. M. Steinauer, *Science* **280**, 745 (1998).
16. R. S. Inouye *et al.*, *Ecology* **68**, 12 (1987).
17. J. Knops *et al.*, *Ecol. Lett.* **2**, 286 (1999).
18. J. Fargione, D. Tilman, *Ecol. Lett.* **8**, 604 (2005).
19. L. R. Olderman, R. T. A. Hakkeling, W. G. Sombroek, *World Map of the Status of Human Induced Soil Degradation: An Explanatory Note, rev.* (International Soil Reference and Information Center, Wageningen, Netherlands, rev. ed. 2, 1990).
20. G. Daily, *Science* **269**, 350 (1995).
21. G. Berndes, M. Hoogwijk, R. van den Broek, *Biomass Bioenergy* **25**, 1 (2003).
22. W. H. Schlesinger, *Biogeochemistry: An Analysis of Global Change* (Academic Press, San Diego, ed. 2, 1997).
23. A. E. Farrell *et al.*, *Science* **311**, 506 (2006).
24. R. Hammerschlag, *Environ. Sci. Technol.* **40**, 1744 (2006).
25. S. Pacala, R. Socolow, *Science* **305**, 968 (2004).

19 January 2007; accepted 22 May 2007  
10.1126/science.1140365