

Biofuels on the landscape: Is “land sharing” preferable to “land sparing”?

KRISTINA J. ANDERSON-TEIXEIRA,^{1,2,3} BENJAMIN D. DUVAL,^{1,2,3} STEPHEN P. LONG,^{1,2,3,4} AND EVAN H. DELUCIA^{1,2,3,4,5}

¹Energy Biosciences Institute, University of Illinois, Urbana, Illinois 61801 USA

²Global Change Solutions LLC, Urbana, Illinois 61801 USA

³Institute of Genomic Biology, University of Illinois, Urbana, Illinois 61801 USA

⁴Department of Plant Biology, University of Illinois, Urbana, Illinois 61801 USA

Abstract. Widespread land use changes, and ensuing effects on ecosystem services, are expected from expanding bioenergy production. Although most U.S. production of ethanol is from corn, it is envisaged that future ethanol production will also draw from cellulosic sources such as perennial grasses. In selecting optimal bioenergy crops, there is debate as to whether it is preferable from an environmental standpoint to cultivate bioenergy crops with high ecosystem services (a “land-sharing” strategy) or to grow crops with lower ecosystem services but higher yield, thereby requiring less land to meet bioenergy demand (a “land-sparing” strategy). Here, we develop a simple model to address this question. Assuming that bioenergy crops are competing with uncultivated land, our model calculates land requirements to meet a given bioenergy demand intensity based upon the yields of bioenergy crops. The model combines fractional land cover of each ecosystem type with its associated ecosystem services to determine whether land-sharing or land-sparing strategies maximize ecosystem services at the landscape level. We apply this model to a case in which climate protection through GHG regulation—an ecosystem’s greenhouse gas value (GHGV)—is the ecosystem service of interest. Our results show that the relative advantages of land sparing and land sharing depend upon the type of ecosystem displaced by the bioenergy crop; as the GHGV of the unfarmed land increases, the preferable strategy shifts from land sharing to land sparing. Although it may be preferable to replace ecologically degraded land with high-GHGV, lower yielding bioenergy crops, average landscape GHGV will most often be maximized through high-yielding bioenergy crops that leave more land for uncultivated, high-GHGV ecosystems. Although our case study focuses on GHGV, the same principles will be applicable to any ecosystem service whose value does not depend upon the spatial configuration of the landscape. Whenever bioenergy crops have substantially lower ecosystem services than the ecosystems with which they are competing for land, the most effective strategy for meeting bioenergy demand while maximizing ecosystem services on a landscape level is one of land sparing: focusing simultaneously on maximizing the yield of bioenergy crops while preserving or restoring natural ecosystems.

Key words: bioenergy feedstocks; biofuels; biomass yield; climate mitigation; ecosystem services; greenhouse gas value, GHGV; land sharing vs. land sparing; land use; sustainability; trade-offs.

INTRODUCTION

Overview

Land use change by humans profoundly affects biodiversity and ecosystem services including climate regulation, regulation of water flow and quality, habitat provisioning, regulation of pests and diseases, and cultural services (Foley et al. 2005, Millennium Ecosystem Assessment 2005). Land use change is the number one factor responsible for losses of species diversity and ecosystem services (Sala et al. 2000, Foley et al. 2005).

Land use change is also a major driver in the climate system; gross CO₂ emissions from tropical deforestation equaled ~40% of global fossil fuel emissions from 1990 to 2007 (Pan et al. 2011), and biophysical effects of land use change can significantly modify climate on local and global scales (Foley et al. 2003, Bala et al. 2007, Anderson-Teixeira et al. 2012). Land use pressures and associated threats to biodiversity and ecosystem services are growing because of a growing world population, changing diets, and bioenergy demand (Foley et al. 2005, Tilman et al. 2009, von Braun 2009). In the face of these pressures, it becomes increasingly important that limited land resources be optimally allocated among food production, energy production, and protection of natural ecosystems. One question is key to making wise land use decisions: Is it preferable to grow “eco-friendly” crops, intentionally sacrificing maximum yield to protect

Manuscript received 2 May 2012; accepted 15 June 2012.
Corresponding Editor: C. C. Cleveland.

⁵ Corresponding author. Present address: Department of Plant Biology, University of Illinois at Urbana–Champaign, 265 Morrill Hall, 505 S. Goodwin Avenue, Urbana, Illinois 61801 USA. E-mail: delucia@illinois.edu

biodiversity and ecosystem services (“land sharing”), or to maximize crop yields, thereby using less land and sparing more land from cultivation (“land sparing”; Green et al. 2005, Godfray 2011, Phalan et al. 2011)?

Debate over the relative advantages of land sharing vs. land sparing takes on a new urgency in the face of expanding bioenergy production. Given that global food demand and associated land use pressures are increasing (Tilman et al. 2011), there is limited potential for widespread production of bioenergy crops on existing cropland without triggering indirect land use change (iLUC) elsewhere in the world (Searchinger et al. 2008, Plevin et al. 2010). This is the case in the United States, where a substantial proportion of existing cropland would need to be devoted to bioenergy crops to meet current biofuel targets (Fargione et al. 2010, Smith et al. 2012). Some current cropland could be made available for bioenergy without raising food prices by increasing yield on existing cropland or reducing allocation to animal feed; however, this same mechanism has also been identified as important to feeding a growing world population while reducing rates of deforestation (Foley et al. 2011, Tilman et al. 2011). Although current cropland that is not essential to food production (e.g., “marginal” or excessive cropland) may be ideally suited for bioenergy production (Campbell et al. 2008), an alternative use would be restoring natural vegetation or allowing this land to undergo natural succession (Righelato and Spracklen 2007, Kendall and Chang 2009), as occurs when land is abandoned or entered into conservation programs (e.g., the Conservation Reserve Program [CRP] in the United States). Thus, when considering land use for bioenergy, a precautionary approach to evaluating the environmental impacts of bioenergy production entails viewing any large-scale bioenergy production as competing primarily with nonfood land over the long run and on a global scale.

When it comes to selecting the most ecologically sustainable bioenergy crop, two leading arguments support ideals at the “land-sharing” and “land-sparing” ends of the spectrum. The first argument, representing the land-sharing ideal, is that bioenergy crops should maximize ecosystem services while maintaining satisfactory yield. Specifically, the ideal bioenergy cropping system would be one with high biodiversity and ecosystem services, such as a low-input high-diversity (LIHD) mix of native prairie species whose high biodiversity enhances productivity and reduces the need for chemical inputs (Tilman et al. 2006). The land-sharing approach favors ecosystems with high value in regulating greenhouse gases (GHGs); for example, crops with the potential to sequester soil carbon are valued for the climate mitigation potential (Anderson-Teixeira et al. 2009, DeLuca and Zabinski 2011). Unfortunately, there is often a trade-off between crop yield and protection of biodiversity and ecosystem services (Krebs et al. 1999, Green et al. 2005, Zhang et al. 2010, Hoben et al. 2011), and the land-sharing ideal would entail

sacrificing yield when such a trade-off exists. Therefore, crops that represent the land-sharing ideal typically require more land to meet a given demand and may thereby place more pressure on natural ecosystems (Green et al. 2005, Heaton et al. 2008, Hodgson et al. 2010). A second major drawback to this approach is that lower yields are less profitable, making this approach less economically viable (Jiang and Swinton 2009).

At the other end of the spectrum, the land-sparing ideal values maximization of crop yield, often at the expense of biodiversity and ecosystem services. This approach typically implies more intensive cultivation with higher chemical inputs, secondary concern for GHG regulation and other ecosystem services, and lower support of species diversity. For example, relative to LIHD prairie, corn (*Zea mays*) or perennial grass monocultures such as switchgrass (*Panicum virgatum* L.) or miscanthus (*Miscanthus × giganteus*) may have higher yields but increased need for chemical inputs and decreased support of species diversity (Tilman et al. 2006, Heaton et al. 2008). Although the high-yield ideal places environmental factors such as GHGV, support of biodiversity, and need for chemical inputs secondary to yield, it does not necessarily imply that all ecosystem services are sacrificed; for example, miscanthus shows promise of both high yield and favorable biogeochemical cycling (Beale and Long 1997, Heaton et al. 2009, Davis et al. 2010), albeit sacrificing native plant species diversity. The approach of using high-yielding bioenergy crops has the advantage of being more economically viable for landowners and bioenergy producers and is therefore viewed as more feasible by economists (e.g., Jiang and Swinton 2009, Jain et al. 2010). Although ecologists often shy away from this option out of concerns for biodiversity and ecosystem services, this approach has major potential benefits for ecological sustainability on the landscape level, in that it allows a given demand to be met with less land, thereby placing less pressure on natural ecosystems. The key question, then, is whether, and under what circumstances, it is preferable to adopt a land-sharing vs. a land-sparing approach.

Here, we develop a simple mathematical framework to address the question of whether ecological sustainability is better promoted through land sharing or land sparing. Specifically, we present a framework to calculate landscape-level ecosystem services as a function of (1) bioenergy crop yield and (2) the ecosystem services associated with the bioenergy crop and the unfarmed land with which it is competing for space. We then apply this framework in the context of five potential bioenergy crops in North America, considering one specific ecosystem service of great importance—climate protection through GHG regulation. We use our model to determine whether, and under what circumstances, land sparing or land sharing is preferable from a GHG perspective.

Theory

We begin with a landscape (total land area: L_T) where bioenergy production may occur (Fig. 1A). For simplicity, we assume that abiotic variables (e.g., climate, soil type) are uniform across this landscape. The land is divided among three major uses: food production (L_F), bioenergy production (L_B), and other, unfarmed land (L_O). For simplicity we assume that L_F is constant, such that decisions regarding the amount and type of bioenergy production will affect only the nonfood (NF) landscape ($L_T - L_F$). Although bioenergy production is likely to affect food prices and eating habits (Mitchell 2008, Searchinger et al. 2008), implying that L_F , L_B , and L_O are all interdependent, our analysis makes the precautionary assumption that trade-offs will ultimately occur between bioenergy production and uncultivated land. Assuming that the ecosystem services associated with each land type are independent of L_F , the question of whether land sharing or land sparing is preferable from a landscape ecosystem services perspective will depend only upon how the nonfood (NF) landscape is divided between L_B and L_O .

In this model, changes in L_B are directly offset by equal and opposite changes in L_O . That is, the fraction of the NF landscape allocated to bioenergy production, $f_B = L_B / (L_T - L_F)$, and the fraction left unfarmed, $f_O = L_O / (L_T - L_F)$, sum to one. These fractions will be determined by the amount of land required to meet a certain bioenergy demand (D ; in liters per year)—which we assume to be independent of the bioenergy crop selected or the amount of land required to grow it—relative to the ethanol yield (Y ; in liters per hectare per year) of the bioenergy crop:

$$f_B = \frac{D/Y}{L_T - L_F} \quad (1a)$$

$$f_O = 1 - \frac{D/Y}{L_T - L_F} \quad (1b)$$

When $[L_T - L_F]$ and D are held constant, f_B and f_O vary solely with respect to Y . Specifically, land allocation to bioenergy is inversely related to yield, and the amount of land left unfarmed increases with yield (Fig. 1B). Of course, the likelihood that land managers will actually grow bioenergy crops will depend upon a number of agronomic and economic factors—in particular, biomass yield and ensuing profitability; however, our model is specifically designed to address ecological, not economic, trade-offs.

Once we know how land is divided among bioenergy crops and other land, we can combine this with metrics of the ecosystem services of bioenergy crops (ES_B) and natural ecosystems (ES_N) to quantify the total ecosystem services associated with the NF landscape (ES_{NF}):

$$ES_{NF} = f_B \times ES_B + f_O \times ES_O. \quad (2)$$

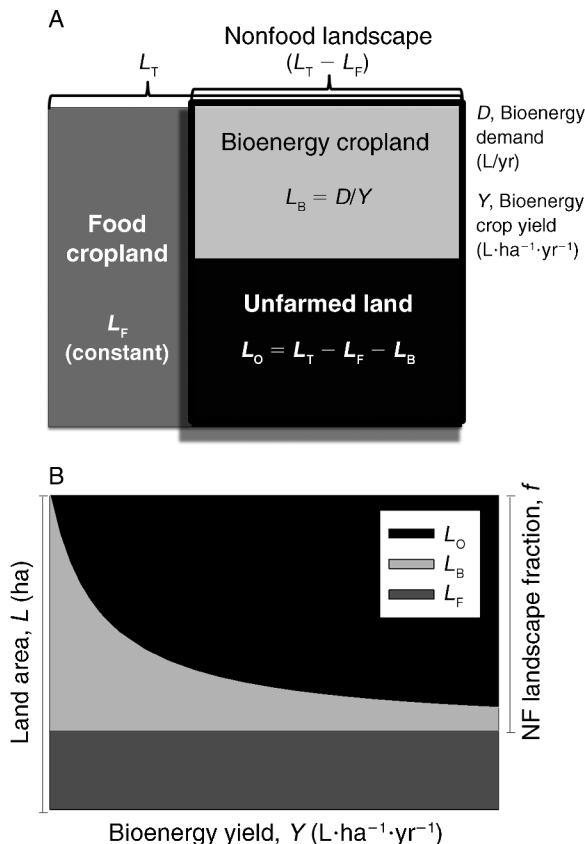


FIG. 1. Schematic diagram illustrating (A) landscape division in our model, which depends upon bioenergy demand and the bioenergy crop yield (Eq. 1), and (B) how land allocation to bioenergy crops varies as a function of bioenergy demand. Model terms are: L , land area, with subscripts T [total], F [food production], B [bioenergy production], or O [other unfarmed land]; Y , bioenergy crop yield; D , bioenergy demand. NF refers to the nonfood landscape. For model details, see *Introduction: theory*.

Thus, the total ecosystem services associated with the NF landscape depend on (1) the fraction of land required for bioenergy crops (Eq. 1a) and (2) the relative ES values of bioenergy crops and the ecosystem that it replaces (Fig. 2).

This framework can be used to understand whether the total ecosystem services of the NF landscape are higher under land-sharing or land-sparing strategies (Fig. 2). Its application is straightforward when there are no significant interactions among ES and landscape configuration, such as edge or patch size effects.

We apply this model to address whether landscape-level GHG regulation is better under land-sharing or land-sparing strategies for a range of bioenergy crop–unfarmed ecosystem type combinations. Here, the ES in Eq. 2 is GHGV, or the total GHG benefit of maintaining an ecosystem over a multiple year time frame—or, conversely, the cost of clearing it (Anderson-Teixeira and DeLucia 2011). We determine the extent to

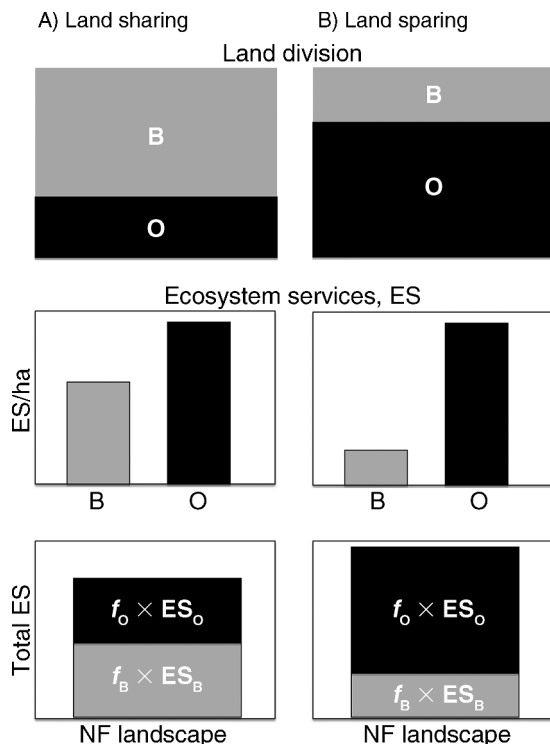


FIG. 2. Schematic diagram illustrating trade-offs between (A) land-sharing and (B) land-sparing strategies, where “B” and “O” represent land allocated to bioenergy crops and unfarmed land, respectively. Under the land-sharing strategy, more land is allocated to high-ES bioenergy crops, whereas under the land-sparing strategy, less land is allocated to low-ES bioenergy crops (where ES stands for ecosystem services). The resultant total ES of the nonfood (NF) landscape will depend upon the fraction of the nonfood landscape allocated to bioenergy production (f_B), the fraction of unfarmed land (f_O), the ecosystem services of bioenergy crops (ES_B), and the ecosystem service of natural ecosystems (ES_O). In theory, either strategy may be preferable.

which bioenergy crops conform to the land-sharing or land-sparing ideal based on their yield and GHGV.

METHODS

Our case study concerns potential bioethanol production in the north central and eastern United States. We consider five bioenergy crops and five other ecosystem types with which these bioenergy crops may compete (Table 1).

Our model is not sensitive to the size of land area considered, but to the ethanol demand intensity relative to the size of the NF landscape ($D/[L_T - L_F]$; Eq. 1). Ethanol demand intensity will vary spatially, being concentrated around ethanol production plants. We considered the hypothetical case of a cellulosic ethanol plant with a production, D , of 136 million L ethanol per year, which is the expected capacity of a commercial-scale cellulosic ethanol plant currently under construction in Highlands County, Florida, USA (Graham-Rowe 2011). We assumed that the biofuel production

facility would draw feedstocks from within 25 miles ($L_T = 510\,000$ ha) and that 75% of the land within this area is devoted to food production ($L_F = 382\,500$ ha). This implied that the 136 million L of ethanol per year must be obtained from the remaining 127 500 ha, resulting in an ethanol demand intensity, $D/[L_T - L_F]$, of $1067\text{ L}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for the NF landscape surrounding an ethanol plant. We used this as a default value for our analysis, noting that the answer to the question addressed here—whether land-sharing or land-sparing strategies are preferable from an ecosystem services perspective—is independent of the value of $D/[L_T - L_F]$ (see Appendix).

Potential ethanol yields for each crop type were calculated based upon biomass yields and ethanol conversion efficiencies (Table 2). Yield estimates were obtained from the USDA for corn grain (USDA National Agricultural Statistics Service 2011) and from published data on yields of cellulosic sources (sources detailed in Table 2). Yield estimates were consistent with the ranges given by the U.S. DOE (2011). We assumed a conversion efficiency of 310 L ethanol/Mg dry matter for cellulosic ethanol and 420 L ethanol/Mg grain for corn ethanol (Perrin et al. 2009, Somerville et al. 2010). Substantial variation in yield was driven by a range of factors including geographic location and management practices (Scurlock et al. 2002, Heaton et al. 2004, Miguez et al. 2008, Wang et al. 2010). Our analysis considered both average and maximum yield estimates for each bioenergy crop. We assumed that bioenergy crops are unlikely to be cultivated under conditions in which below-average yields would be obtained.

Ecosystem properties needed to compute GHGV (Anderson-Teixeira and DeLucia 2011) were obtained from the literature (Table 2). These variables include organic matter storage in various pools; annual exchange of CO_2 , CH_4 , and N_2O between the ecosystem and the atmosphere; and CO_2 emissions from management (e.g., on-site CO_2 emissions from farm machinery). In general, data on these ecosystem properties were limited, often being restricted to one or two locations considered being well suited to cultivation of the crop and meeting the criteria outlined in Table 1. Therefore, although it was possible to estimate GHGV for “typical” cultivation of each crop (Table 1), further research will be required to relate variation in the ecosystem properties that drive GHGV to geographic location, management practices, or yield. GHGV was calculated as in Anderson-Teixeira and DeLucia (2011; Table 2) by summing (1) the release of GHGs that would occur through the oxidation of stored organic material upon clearing of the ecosystem and (2) the annual GHG fluxes that would be displaced by clearing of the ecosystem (i.e., net ecosystem exchange of CO_2 , annual CH_4 exchange, annual N_2O release, associated management emissions). Ecosystem-atmosphere GHG exchanges over a 30 year “ecosystem” time frame (T_E) were translated into changes in atmospheric GHG

TABLE 1. Description of ecosystem types considered in this analysis.

Ecosystem type	Description
Bioethanol crops	
Corn grain	<i>Zea mays</i> grain used for first-generation bioethanol production. We assume conventional management practices, including annual tillage, stover (residue) returned to field, and average U.S. agricultural inputs. Soil organic carbon (SOC) assumed to be at steady state.
Corn grain + stover	<i>Zea mays</i> grain used for first-generation bioethanol production together with 100% residue (stover) harvest for the production of cellulosic ethanol. We assume that initiation of residue harvest is accompanied by a switch to no-till agriculture (Adler et al. 2007). Assumed that SOC accumulation would continue for >30 years.
Miscanthus	<i>Miscanthus</i> × <i>giganteus</i> agroecosystem in the USA. No tillage; N fertilization < 100 kg N·ha ⁻¹ ·yr ⁻¹ (Heaton et al. 2008, Miguez et al. 2008); assumed recent conversion from annually tilled agroecosystem. Establishment phase (first 2–3 years) is excluded. Assumed that SOC accumulation would continue for >30 years.
Switchgrass	<i>Panicum virgatum</i> agroecosystem in the USA. No tillage; N fertilization < 100 kg N·ha ⁻¹ ·yr ⁻¹ (Adler et al. 2007, Fargione et al. 2010); assumed recent conversion from annually tilled agroecosystem. Establishment phase (first 2–3 years) is excluded. Assumed that SOC accumulation would continue for >30 years.
LIHD prairie	Low-input, high-diversity (LIHD) native prairie mix (Tilman et al. 2006). Annual harvest; no tillage; no fertilization; assumed recent conversion from annual tillage. Assumed that SOC accumulation would continue for >30 years.
Other	
Pasture	Moderately grazed grassland pasture in the central USA. Assumed that half of aboveground biomass was removed by grazing.
CRP grassland	Grassland established on former cropland, often through the U.S. Conservation Reserve Program (CRP). Assumed that SOC accumulation would continue for >30 years.
Native grassland	Great plains grassland in the central USA. Because natural fires occur frequently, recently burned sites were not excluded.
Aggrading forest	Eastern deciduous forest regrowing following stand-clearing disturbance. Assumed that GHG exchange would approximate that of mature forests beginning at age 72 (Anderson-Teixeira and DeLucia 2011).
Eastern deciduous forest	Eastern deciduous forest with no recent disturbance.

concentrations and were multiplied by the radiative efficiency of each GHG to obtain total radiative forcing from GHGs. Cumulative radiative forcing was translated into CO₂-equivalents over a 100-year analytical time frame (T_A). This is analogous to the commonly used approach for computing GHG global warming potentials (Forster et al. 2007), which typically use $T_A = 100$, but differs in that $T_E > 1$ for GHGV whereas $T_E = 1$ for global warming potentials. Selection of T_E and T_A is inherently subjective (Anderson-Teixeira and DeLucia 2011); the time frames selected here ($T_E = 30$, $T_A = 100$) are typical of biofuels life cycle analyses (Anderson-Teixeira et al. 2011). Although GHGV varies with both T_E and T_A (Anderson-Teixeira and DeLucia 2011), a sensitivity analysis revealed that the general conclusions of our analysis are not sensitive to the time frames selected (data not shown).

Having calculated ethanol yield (Y) and GHGV for each ecosystem, we then used Eqs. 1 and 2 to calculate the average GHGV of the NF landscape. These calculations focused on a scenario in which $D/(L_T - L_F) = 1067 \text{ L} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (previously described). We also conducted a sensitivity analysis showing how results vary across the range of potential values for $D/[L_T - L_F]$ (see Appendix).

We note that our analysis does not consider the full life cycle GHG effects of bioenergy production, which includes GHG benefits of fossil fuel displacement and

GHG emissions from the ethanol production process (Davis et al. 2009). However, GHG benefits from fossil fuel displacement will be equal for all bioenergy crops because ethanol production (D) is held constant. Differences may arise from differences between grain- and cellulosic-ethanol production costs, co-product crediting, or differences in transport costs. The first two, which may influence comparisons between grain- and cellulosic-based ethanol but do not systematically bias the analysis in favor of land sharing or land sparing, are beyond the scope of this analysis. The latter introduces a systematic bias in favor of the land-sharing strategy, because lower Y implies higher L_B and therefore greater transport costs, which are not factored into this analysis; however, feedstock transport contributes so little to the net GHG balance of bioenergy production systems (U.S. EPA 2010) that this bias is unlikely to alter conclusions.

RESULTS

Yields and GHGVs

Yields of bioenergy crops varied substantially both across and within crop types (Table 2). Based upon average yields, the ethanol productivity of bioenergy crops was ranked as follows: LIHD prairie < switchgrass < corn grain < corn grain + stover < miscanthus (Table 2). There was, however, substantial variation in the range of yield estimates. In particular, there remains considerably uncertainty as to the potential yield of

TABLE 2. Yield, GHGV, and ecosystem properties used to compute GHGV for ecosystem types considered in this analysis; uppercase letters indicate data sources.

Plant source	Dry matter yield (Mg·ha ⁻¹ ·yr ⁻¹)	Ethanol yield (L·ha ⁻¹ ·yr ⁻¹)	GHGV (Mg CO ₂ -eq·ha ⁻¹ ·30 yr ⁻¹)	Organic matter storage (Mg/ha)	
				Aboveground biomass	Root biomass
Bioethanol crops					
Corn grain	9.3 (7–10) [A]	3900 (2940–4200)	–52	8.5 (3.3) [B, C]	0.25 [B]
Corn grain + stover ^c	grain, 8.2 (6.2–8.8); ^d stover, 7.4 (5–16) [A, F, G, H]	6560 (4170–8720)	–47	8.5	0.25
Miscanthus	22.4 (2.2–45.5) ^e [J, K, L]	6940 (680–14 100)	160	17.2 (6.2) [B, K, L, M]	19.8 (10.9) [M]
Switchgrass	11.2 (1.6–27) ^f [R]	3470 (500–8370)	80	5.8 (2.9) [B, K]	12.9 (2.7) [C, M, S, T]
LIHD prairie	4.2 (3.1–6.2) [B, U, V, W, X]	1310 (960–1920)	115	4.3 [B]	14 ^g [B]
Other					
Grassland pasture [Z]			72	2.8 ⁱ	9.9 ^j
CRP grassland ^k [Z]			125	5.6	14
Native grassland [DD]			200	5.6 (1.1)	14
Aggrading forest [Z]			422	0	2
Eastern deciduous forest [DD]			1066	271 (121)	35 (11)

Notes: Where multiple reliable estimates were available, we report the range or SD in parentheses following the mean. Values assume that, in perennial grass bioenergy crops and CRP grassland, organic storage in biomass and litter plateaus in a negligible amount of time such that subsequent CO₂ uptake is represented by changes in soil organic carbon. Organic matter storage for bioenergy crops (columns 5–8) changes dramatically during the year; it was calculated as average storage throughout the year. Source data collected over a year were linearly extrapolated to obtain biomass estimates for every day of the year. We assumed that aboveground biomass dropped to zero at time of harvest and remained there until time of emergence. For perennial grasses, an unknown date of emergence was assumed to be Julian day 100 (10 April). Values were averaged over the 1-yr period; when data for more than one year existed for one site, annual averages were averaged across years. Mean and SD values presented here represent cross-site averages.

Superscript lowercase letters refer to source data details: a, all values are from Le Mer and Roger (2001); b, includes CO₂ emissions from farm machinery and agricultural inputs (fertilizer, lime); c, assumed same biomass, roots, litter, and N₂O emissions as conventional corn; d, grain yield based on U.S. average, assuming 12% reduction associated with 100% residue harvest (Blanco-Canqui and Lal 2007); e, includes trials outside the United States; f, assumed CO₂ emissions associated with agricultural inputs and farm machinery fuel emissions equal to those of switchgrass (Adler et al. 2007); g, assumed equal to native grassland; h, assumed CO₂ emissions associated with agricultural inputs equal to those for switchgrass, minus N fertilizer and herbicides, and farm machinery fuel emissions equal to those of switchgrass (Adler et al. 2007); i, assumed that aboveground biomass of moderately grazed grassland is ~50% that of ungrazed grassland; j, assumed that root biomass of moderately grazed grassland is ~70% that of ungrazed grassland (Biondini et al. 1998); k, assumed biomass, litter, and N₂O flux equal to grassland; l, assumed equal to forest.

Sources [in square brackets]: A, USDA National Agricultural Statistics Service (2011); B, K. J. Anderson-Teixeira et al., *unpublished manuscript*; C, Tufekcioglu et al. (2003); D, Smeets et al. (2009); E, West and Marland (2002); F, Perlack et al. (2005); G, Blanco-Canqui and Lal (2007); H, Fronning et al. (2008); I, Adler et al. (2007); J, Heaton et al. (2004); K, Heaton et al. (2008); L, Miguez et al. (2008); M, Dohleman (2009); N, Anderson-Teixeira et al. (2009); O, Jørgensen et al. (1997); P, Stehfest and Bouwman (2006); Q, Toma et al. (2010); R, Wang et al. (2010); S, Ma et al. (2000); T, McLaughlin and Kszos (2005); U, Knapp and Smith (2001); V, Scurlock et al. (2002); W, Huxman et al. (2004); X, Tilman et al. (2006); Y, Robertson et al. (2000); Z, Anderson-Teixeira and DeLucia (2011); AA, Biondini et al. (1998); BB, IPCC (2006); CC, U.S. EPA (2010); DD, Anderson-Teixeira et al. (2012); EE, Anderson et al. (2006).

perennial grass bioenergy crops throughout the United States. When ranked according to maximum reported yields, switchgrass surpassed corn grain. The observed range of yields implies that the ranking of achieved yields is likely to vary across locations.

Perennial grasses had substantially higher GHGVs than corn bioenergy systems (Table 2). All three perennial grasses had a GHGV exceeding 70 Mg CO₂-eq·ha⁻¹·30 yr⁻¹, whereas both corn grain and corn grain + stover had GHGVs of approximately –50 Mg CO₂-eq·ha⁻¹·30 yr⁻¹, indicating that the corn-based systems were a net source of GHGs to the atmosphere. This

difference was driven mainly by the GHG benefits of C storage in the root systems and soil C accumulation in the perennial grasses, and by substantially higher N₂O emissions from corn (Table 2).

Non-cropland ecosystems generally had higher GHGVs than bioenergy agroecosystems (Table 2). Exceptions were grassland pasture, which had a lower GHGV than all three perennial grasses, and CRP grassland, which had a lower GHGV than miscanthus. Although the grassland ecosystems had GHGVs of 200 Mg CO₂-eq·ha⁻¹·30 yr⁻¹ or less, regrowing or mature

TABLE 2. Extended.

Organic matter storage (Mg/ha)		CO ₂ flux (kmol·ha ⁻¹ ·yr ⁻¹)	CH ₄ flux ¹ (kmol·ha ⁻¹ ·yr ⁻¹) ^a	N ₂ O flux (kmol·ha ⁻¹ ·yr ⁻¹)	Management CO ₂ emissions ² (kmol·ha ⁻¹ ·yr ⁻¹) ^b
Litter	Vulnerable SOM				
3.2 (1.7) [B, C]	0	0	-0.13	0.165 [D]	19.0 [E]
0	0	-8.4 [H]	-0.13	0.165	19.4 [E, I]
3.1 [B]	0	-84.2 (240) [N]	-0.13	0.029 (0.009–0.07) [O, P, Q]	7.62 ^f
2.4 [B]	0	-56.7 (229) [N]	-0.13	0.045 [I]	7.62 [I]
2.4 [B]	0	-76.7 (220) [N]	-0.13	0.012 [Y]	3.85 ^h
1.4 [AA]	61 (34)	25.2 (145)	-0.15; [2.33 from cattle; [BB, CC]	0.067 (0.059)	
1.9	0	-76.7 (220) [N]	-0.15	0.012	
1.9 (1.5)	61 (34)	-33 (146)	-0.15	0.012 (0.015)	
1	0	-364 (65) [EE]	-0.23	0.026 ⁱ	
50 (6); dead wood 16 (20)	90 (56)	-308 (138)	-0.23	0.026 (0.036)	

forests had high GHGVs of 420 and 1070 Mg CO₂-eq·ha⁻¹·30 yr⁻¹, respectively.

In bioenergy crops, ethanol yield and GHGV of the agroecosystem did not covary strongly (Fig. 3). Negative covariation, indicative of a sparing–sharing trade-off, occurred across the sequence LIHD prairie–

switchgrass–corn (either grain only or grain + stover). Corn grain and corn grain + stover had different yields but similar GHGVs, implying a consistent benefit of corn grain + stover over corn grain alone. Miscanthus had the highest yield and GHGV, indicating unilateral GHG benefits relative to the others.

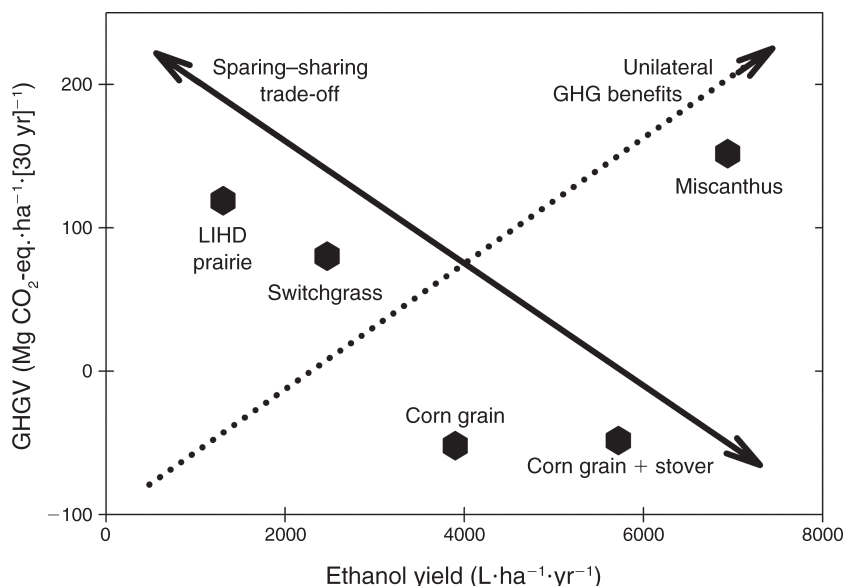


FIG. 3. Relationship between typical ethanol yields and greenhouse gas values (GHGVs) of the bioenergy crops considered here. GHGV is measured as CO₂ equivalents (CO₂-eq.) over a 30-year period. Negative covariation (solid line, two-headed arrow) implies a trade-off between land-sharing and land-sparing strategies, whereas positive covariation (dotted arrow) implies unilateral GHG benefits of one bioenergy crop over another. LIHD is a low-input, high-diversity native prairie mix; stover is corn residue.

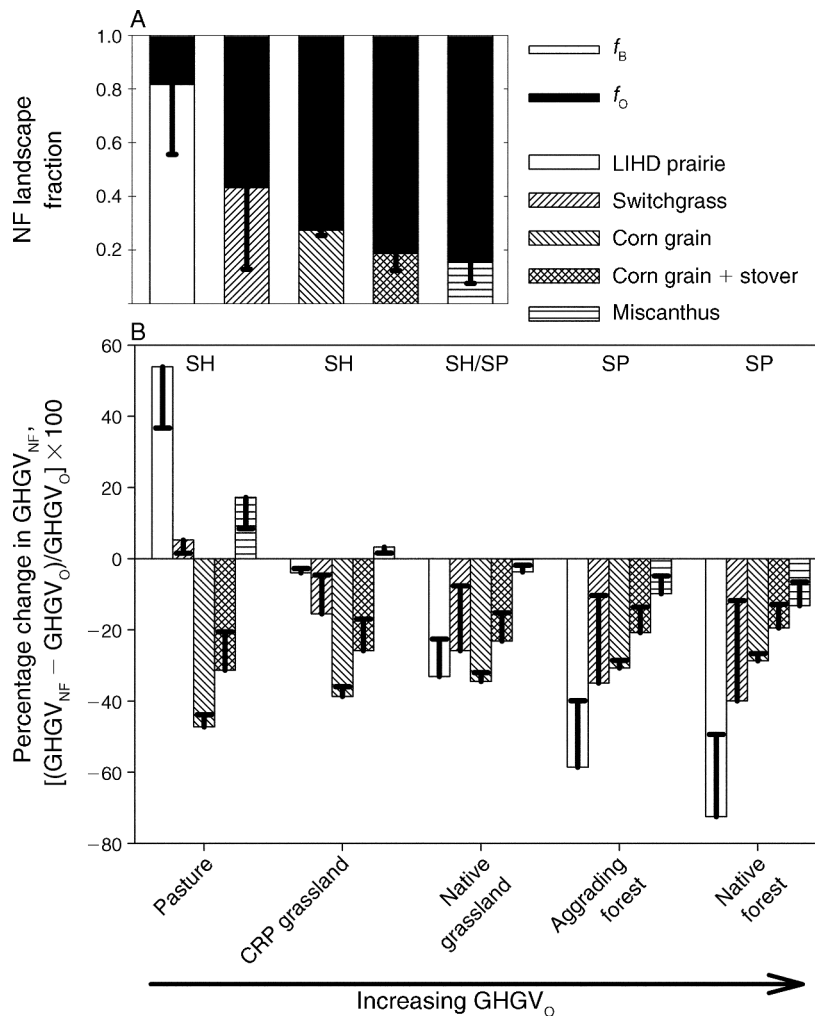


FIG. 4. Landscape division and GHGV_{NF} (NF, nonfood) for our focal scenario with an ethanol demand intensity of $1067 \text{ L} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. (A) Fractional allocation of the NF landscape to bioenergy crops (f_B) and other, uncultivated land (f_O). (B) Percentage change in GHGV_{NF} with addition of bioenergy crops to the landscape. Error bars represent values for maximum reported bioenergy yields. “SH” and “SP” annotations indicate that land-sharing and land-sparing strategies, respectively, maximize GHGV_{NF} . Note that negative values do not imply a net unfavorable life cycle GHG balance of bioethanol production, because we are considering only the GHGV of ecosystems and not fossil fuel displacement or ethanol production costs. CRP is the Conservation Reserve Program.

Nonfood (NF) landscape division and GHGV for focal scenario

When $D/(L_T - L_F) = 1067 \text{ L} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, the fraction of the nonfood (NF) landscape required to support bioenergy demand ranged from 0.15 (0.08 at max Y) for miscanthus to 0.82 (0.56 at max Y) for LIHD prairie (Fig. 4A). Combining this result with the GHGVs of bioenergy crops and other land types (Table 2), we calculated the percentage change in GHGV for the average NF landscape (GHGV_{NF}) that would occur as a result of bioenergy production for each bioenergy crop–unfarmed land combination (Fig. 4B). It should be emphasized that this change in GHGV_{NF} does not represent the net life cycle GHG effect of bioenergy production, only the GHG effects of land use change.

The net effects of allocating land to bioenergy production depended upon the GHGV of the bioenergy crop relative to that of the unfarmed land; GHGV_{NF} increased when the bioenergy crop had a higher GHGV than the unfarmed land, and vice versa. For example, displacing pasture with LIHD prairie, switchgrass, or miscanthus increased the GHGV of the combined biofuel and nonfarmed landscape, whereas displacing native forest with any biofuel crop reduced the GHGV of the combined biofuel and nonfarmed landscape.

The relative advantages of land sparing and land sharing shifted as a function of the GHGV of the unfarmed land (Figs. 4B and 5). This is best illustrated by focusing on the GHGV_{NF} values achieved across the sparing–sharing trade-off continuum of LIHD prairie,

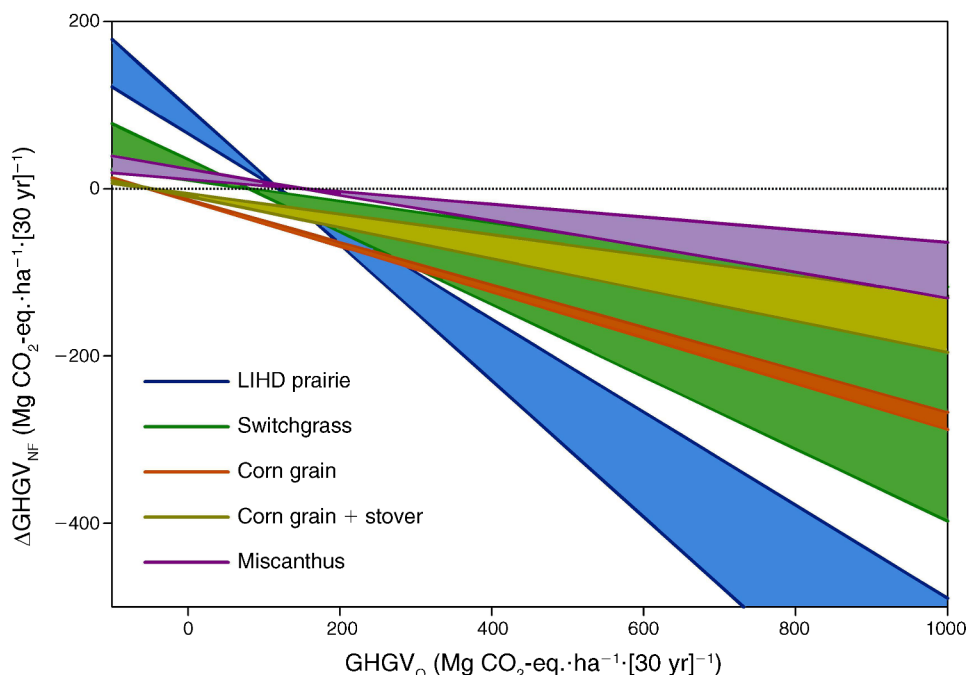


FIG. 5. Change in landscape GHGV ($\Delta\text{GHGV}_{\text{NF}}$) with the addition of various bioenergy crops to the landscape as a function of the GHGV of the ecosystem with which bioenergy crops are competing for space on the landscape (GHGV_{O}). For each bioenergy crop, the shaded area portrays values derived based on yields ranging from mean to maximum. Note that negative values do not imply a net unfavorable life cycle GHG balance of bioethanol production, because we are considering only the GHGV of ecosystems and not fossil fuel displacement or ethanol production costs.

switchgrass, and corn (either grain or grain + stover; Fig. 3). When the GHGV of the unfarmed land was relatively low (pasture, CRP grassland), there was a clear advantage to land sharing. That is, across the sparing–sharing trade-off continuum of LIHD prairie–switchgrass–corn, GHGV_{NF} was greatest for LIHD prairie, intermediate for switchgrass, and lowest for corn (Figs. 4B and 5), indicating the success of the land-sharing approach. When the GHGV of the unfarmed land was intermediate (native grassland), land-sparing and land-sharing strategies were approximately equal. Specifically, GHGV_{NF} was similar, with overlapping confidence intervals, for switchgrass, prairie, and the two corn systems (Fig. 4B), indicating that the GHGV benefits associated with LIHD prairie and switchgrass were approximately balanced by the benefits of lower land requirements associated with corn. Finally, when the GHGV of the unfarmed land was high (regrowing or mature forests), a land-sparing approach had strong benefits over a land-sharing approach. In these cases, GHGV_{NF} was driven primarily by the division of the landscape (Fig. 4A). The differences in GHGV among bioenergy crops were dwarfed by the large differences between GHGVs of forests and bioenergy crops. When the unfarmed land was mature forest, GHGV_{NF} was reduced by 772, 426, 306, 208, and 141 $\text{Mg CO}_2\text{-eq.}\cdot\text{ha}^{-1}\cdot 30\text{ yr}^{-1}$ when LIHD prairie, switchgrass, corn

grain, corn grain + stover, and miscanthus were the bioenergy crops, respectively.

Of course, when comparing bioenergy crops with positive covariation between yield and GHGV (Fig. 3), the high- Y , high-GHGV bioenergy crop was generally associated with a higher GHGV_{NF} (Figs. 4B and 5). Specifically, corn grain + stover consistently had a higher GHGV_{NF} than corn grain alone. Miscanthus typically had the most favorable GHGV_{NF} , with the notable exception that a land-sharing strategy was favored when GHGV_{O} was low (Fig. 5). When the unfarmed land was pasture, which had the lowest GHGV of all unfarmed land types considered here, LIHD prairie had a higher GHGV_{NF} than miscanthus (Fig. 4B). This occurred because 82% of the pasture was replaced with a higher-GHGV bioenergy crop in the case of LIHD prairie, compared to only 15% in the case of miscanthus (Fig. 4A).

Under many situations, yield uncertainty resulted in overlapping confidence intervals for f_{B} or GHGV_{NF} (Figs. 4 and 5). For example, although average-yielding switchgrass performed worse than corn grain or corn grain + stover when GHGV_{O} was relatively high, switchgrass attaining maximum yield would outperform both of these feedstocks (Figs. 4 and 5). Of course, maximally yielding switchgrass would no longer fall along the sparing–sharing trade-off illustrated in Fig. 3,

as its yield would exceed that of corn grain (Table 2). Thus, although the relative performance of the various bioenergy crops is subject to yield uncertainty, the general finding that the optimal strategy shifted from land sharing at low GHGV_O to land sparing at high GHGV_O values is robust.

DISCUSSION

As illustrated by a case in which GHGV is the ecosystem service of interest, the relative advantages of land sparing vs. land sharing depend upon the type of ecosystem with which the bioenergy crop is competing for land and its associated ecosystem services (Figs. 4 and 5). When the unmanaged land had a relatively low GHGV, land sharing yielded higher landscape ecosystem services than land sparing. In instances where bioenergy crops had higher GHGVs than the unfarmed land, the best crop was typically the one with the lowest yield, because this replaced the greatest amount of low-GHGV land. As the GHGV of the unfarmed land increased, the advantage shifted from land sharing to land sparing. When the unfarmed land had a much higher GHGV than the bioenergy crops, the most influential driver of landscape ecosystem services was the fraction of land left unfarmed, and land sparing was categorically the best strategy. These results parallel findings of studies comparing land-sharing and land-sparing strategies in a food production context, where GHG emissions or species diversity losses are minimized through a land-sparing strategy when the unfarmed land (e.g., forest) has a much higher ES value than the cropland (Burney et al. 2010, Hodgson et al. 2010, Godfray 2011, Phalan et al. 2011).

The sparing–sharing trade-offs observed for GHGV would be fundamentally the same for any ecosystem service that does not depend upon the spatial configuration of the landscape, being driven by the same underlying mathematical principles (Eqs. 1 and 2). A more complex model would be necessary to address species diversity or ecosystem services that depend upon landscape characteristics such as patch size and connectivity (Hodgson et al. 2010). However, for any ecosystem service that is minimally affected by landscape configuration (e.g., GHGV, nutrient retention, soil formation), the mathematical behavior of the model depends only upon land division (a function of Y ; Eq. 1) and the ES values of the bioenergy crop and the ecosystem with which it is competing (Eqs. 1 and 2). Eqs. 1 and 2 can be manipulated algebraically to define a general rule for comparing the ecosystem service benefits of various bioenergy options. A land-sharing strategy (“SH” subscript) will be preferable to a land-sparing strategy (“SP” subscript) when the following inequality is true:

$$\frac{ES_{SH} - ES_O}{Y_{SH}} > \frac{ES_{SP} - ES_O}{Y_{SP}}. \quad (3)$$

From this, we can draw three general conclusions. First, land sharing is favored when the unfarmed land

provides minimal ecosystem services (i.e., when ES_O is low), whereas land sparing is favored when the ecosystem service value of the unfarmed land is high (Figs. 4B and 5). Second, the greater the ecosystem service value of a land-sharing bioenergy crop is relative to that of a land-sparing crop (i.e., the higher ES_{SH}/ES_{SP}), the more likely that the land-sharing strategy will be preferable. Third, the more the yield of a land-sharing bioenergy crop is reduced relative to that of a land-sparing crop (i.e., the lower Y_{SH}/Y_{SP}), the less likely that the land-sharing strategy will be preferable.

The relative advantages of land sharing and land sparing depend upon the relationship between ethanol yield and ecosystem services (Eq. 3; Green et al. 2005). The steeper the trade-off (i.e., the more ES_B is decreased per incremental increase in Y), the more likely a land-sharing strategy is to maximize landscape ecosystem services. For example, there is a steeper GHGV– Y trade-off between LIHD prairie and corn grain than between LIHD prairie and corn grain + stover (Fig. 3). When the GHGV_{NF} values for these bioenergy crops in combination with native grassland are compared (Fig. 4B), a land-sharing strategy (LIHD prairie) is slightly favored in the case of the LIHD prairie–corn grain trade-off, whereas a land-sparing strategy (corn grain + stover) is favored in the case of the LIHD prairie–corn grain + stover trade-off. Therefore, when optimizing land use to meet the interconnected goals of bioenergy production and ecosystem services, it is important to consider the relationship between ES_B and Y (Zhang et al. 2010). This will be particularly relevant when selecting optimal management practices for a specific bioenergy crop, and further research will be required to delineate the relationship between ES_B and Y for the various bioenergy crops (for an analysis of this relationship for corn, see Zhang et al. 2010). Both ethanol yield and ecosystem services depend upon management practices such as fertilization; for example, N fertilization may increase yield (Heaton et al. 2004, Wang et al. 2010), but it will also reduce GHGV by increasing N₂O emissions (Zhang et al. 2010, Hoben et al. 2011). Although agricultural intensification has generally benefited the global GHG balance by averting deforestation (Burney et al. 2010), excessive intensification may disproportionately reduce ES values in relation to Y (e.g., Hoben et al. 2011), and reduce the benefits of the land-sparing strategy. However, it is important to appreciate that although nutrients such as N are an essential component of the product in the case of food, feed and forage crops, biofuels require only C, H, and O. Therefore, nutrients such as N potentially can be recycled, thereby partially mitigating the costs of intensification in bioenergy crops. This might be achieved by using perennial feedstocks such as LIHD prairie, switchgrass, or miscanthus that recycle most of their nutrients to roots and rhizomes before harvest (Beale and Long 1997, Heaton et al. 2009), or by returning vinasse and

ash to the soil in the case of sugarcane ethanol (Ometto et al. 2009).

The outcomes of this analysis are sensitive to estimates of yield and GHGV, both of which are subject to uncertainty. Although experimental trials have produced yield estimates for cellulosic bioenergy sources at a variety of locations (Heaton et al. 2004, Miguez et al. 2008, Wang et al. 2010) and models have been used to estimate yields across the United States (Davis et al. 2011; Miguez et al. in press), uncertainty remains as to the actual yields that will be achieved in agricultural-scale settings and how these vary regionally. In our analysis, yield uncertainty commonly resulted in overlapping confidence intervals for f_B or $\Delta\text{GHGV}_{\text{NF}}$ (Figs. 4 and 5). Much of this variation is driven by regional differences in yield potential, and the optimal crop will vary regionally. For example, whereas miscanthus has the highest observed yield and most favorable GHGV under conditions that are favorable for its growth (Fig. 3; Heaton et al. 2008), its relative advantage over switchgrass is diminished under colder and drier conditions (Heaton et al. 2004). Similarly, both miscanthus and switchgrass are expected to perform poorly in the northern Great Plains (Miguez et al. 2012), whereas native prairies are well adapted to the cold climate of this region. Of course, ongoing development of crops, agronomic techniques, and biofuel production technology is likely to alter the ethanol yield potential of all bioenergy crops in the future. With regard to GHGV, further research will be required to understand how the parameters that drive GHGV vary regionally and with respect to yield. Thus, although the framework presented here is ideally suited for addressing the general question of whether a land-sharing or land-sparing approach will be most favorable in terms of ecosystem services, a more detailed analysis will be required to determine how the relative benefits of different crops vary regionally.

The model presented here assumes a closed system where a fixed amount of land is required to meet food demands (Fig. 1) and where land use changes within the landscape will not affect land use elsewhere. In theory, it is applicable at any scale, from the individual farm to the globe. In our simplified scenario, food cropland area is constant while land allocation to bioenergy trades off with uncultivated land including pastures, abandoned cropland, and native ecosystems within the same region (North America). In reality, global interconnectedness of food, energy, and economic systems implies that bioenergy production may trade off with food production in one region, altering food prices and triggering iLUC elsewhere in the world, particularly in tropical regions (Searchinger et al. 2008, Fargione et al. 2010). If bioenergy were to trade off with food production, replacement of low-GHGV crops (Table 2; Anderson-Teixeira and DeLucia 2011) with higher-GHGV perennial crops (Table 2) would result in a climate benefit, with the greatest benefit obtained from a land-sharing

strategy (Fig. 5); however, this benefit would be counteracted by any GHG emissions from iLUC. There is a high degree of uncertainty regarding the extent and location of iLUC; estimates of the extent of indirect land displacement range from 0.28 to 0.89 ha cleared per 1 ha cropland converted to bioenergy, with 19–52% of cleared land being forest (Plevin et al. 2010). Depending upon the amount and type of ecosystems cleared, the costs of iLUC may or may not outweigh GHG benefits from bioenergy crops, but $\Delta\text{GHGV}_{\text{NF}}$ will always be reduced—more so under land sharing than land sparing, because the iLUC cost will be proportional to L_B . A preliminary analysis using tropical ecosystem GHGV data from Anderson-Teixeira and DeLucia (2011) indicates that the optimal strategy will depend upon the extent of land use change and types of ecosystems cleared, with land sharing being favored when iLUC costs are relatively low (within the above ranges of uncertainty) and land sparing favored when they are relatively high. Realistic application of our model over a global spatial scale would require a more complex analysis including multiple types of ecosystems and modeling of the complex socioeconomic drivers of land use, the latter of which remains a key uncertainty in biofuels life cycle analyses (Plevin et al. 2010). However, increasing model complexity will not fundamentally alter the emergent mathematical behavior of the model and the resulting conclusions.

Effective application of this framework also requires farsighted analysis of current and future conditions. Although the relative advantages of different bioenergy crops do not depend upon future changes in land allocated to food production or bioenergy demand (Eq. 1, Fig. A1), several considerations may affect the long-term trade-offs of various bioenergy strategies. First, the model only gives accurate results for the time frame over which yields and ecosystem services are sustainable. An intensively managed, high-yielding bioenergy crop may provide the greatest benefits over the short term, but intensive management may deplete soil resources and reduce long-term yields (Blanco-Canqui and Lal 2007). Moreover, climate change and agronomic advances may significantly alter crop yields (Lobell and Field 2007) and ecosystem services of both bioenergy crops and natural ecosystems (Field et al. 2007, Xue et al. 2011). Second, effective decision making must take a long-term view of abandoned or idle land, considering not only its current ecosystem services, but also its potential ecosystem services were it to be put back into production, restored, or allowed to undergo natural succession (Kendall and Chang 2009). Third, long-range economic feedbacks may alter the future benefits of either the land-sparing or land-sharing scheme. Land-sparing strategies may be ineffective in practice if agricultural subsidies incentivize surplus production or if the “spared” land is used to produce other agricultural commodities (Ewers et al. 2009). The land-sharing strategy may be vulnerable to the danger that, after

putting a large fraction of available land into production of a crop with high ecosystem services, land managers may easily be tempted to intensify production to increase profits. Finally, effective implementation of either strategy requires consideration of local institutions, governance, and social dynamics (Bawa et al. 2004, Fischer et al. 2011). Appropriate analysis of long-term considerations such as these is crucial for creating effective strategies to maximize ecosystem services on bioenergy landscapes over the long run.

Our findings have several implications for the current debate on bioenergy production. Our results demonstrate that the relative advantages of land sparing and land sharing depend upon the type of ecosystem with which the bioenergy crop is competing for land; as the GHGV value of the unfarmed land increases, the preferable strategy shifts from land sharing to land sparing (Figs. 4 and 5). On one end of the spectrum is the proposal to grow high-ES bioenergy crops on marginal land or land unsuited for arable agriculture, thereby avoiding competition with food and improving ES values of the land (Tilman et al. 2006, Campbell et al. 2008, Fargione et al. 2010, Nijssen et al. 2012). Because degraded or abandoned land will generally have low ecosystem services, the land-sharing strategy may be preferable in this case (Fig. 4B). This strategy should, however, be weighed against an alternative strategy of growing the highest-yielding bioenergy crops on less of this land while restoring the remainder to high-ES unmanaged ecosystems (Kendall and Chang 2009). When considering productive, nondegraded land, the best strategy will generally be to select and develop bioenergy crops and management techniques so as to maximize yield while actively preserving or restoring natural land. A prime example of such a strategy is the “Midway Strategy” for the development of the sugarcane ethanol production system in Brazil, which involves improving the ethanol yield of sugarcane while preserving and restoring Atlantic Forest within the landscape (Buckeridge et al. 2012). On a policy level, GHG benefits of bioenergy production may best be ensured by coupling bioenergy production to mechanisms for forest protection (Thomson et al. 2010), such as REDD+ (United Nations mechanism to reduce deforestation and forest degradation; UNFCCC 2008). This conclusion is consistent with other research showing that land sparing in conjunction with protection of natural ecosystems is the most effective strategy for protecting biodiversity and ecosystem services (Burney et al. 2010, DeFries et al. 2010, Godfray 2011, Phalan et al. 2011). In sum, the economically favored strategy of maximizing yield is generally compatible with the ecologically preferable strategy of maximizing the yield of bioenergy crops while actively preserving or restoring natural land.

ACKNOWLEDGMENTS

This research was supported by the Energy Biosciences Institute (University of California–Berkeley and University of

Illinois) and by the BP (British Petroleum) Energy Sustainability Challenge.

LITERATURE CITED

- Adler, P. R., S. J. Del Grosso, and W. J. Parton. 2007. Life-cycle assessment of net greenhouse-gas flux for bioenergy cropping systems. *Ecological Applications* 17:675–691.
- Anderson, K. J., A. P. Allen, J. F. Gillooly, and J. H. Brown. 2006. Temperature-dependence of biomass accumulation rates during secondary succession. *Ecology Letters* 9:673–682.
- Anderson-Teixeira, K. J., S. C. Davis, M. D. Masters, and E. H. DeLucia. 2009. Changes in soil organic carbon under biofuel crops. *GCB Bioenergy* 1:75–96.
- Anderson-Teixeira, K. J., and E. H. DeLucia. 2011. The greenhouse gas value of ecosystems. *Global Change Biology* 17:425–438.
- Anderson-Teixeira, K. J., P. K. Snyder, and E. H. DeLucia. 2011. Do biofuels life cycle analyses accurately quantify the climate impacts of biofuels-related land use change? *Illinois Law Review* 2011:589–622.
- Anderson-Teixeira, K. J., P. K. Snyder, T. E. Twine, S. V. Cuadra, M. H. Costa, and E. H. DeLucia. 2012. Climate-regulation services of natural and agricultural ecoregions of the Americas. *Nature Climate Change* 2:177–181.
- Bala, G., K. Caldeira, M. Wickett, T. J. Phillips, D. B. Lobell, C. Delire, and A. Mirin. 2007. Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences USA* 104:6550–6555.
- Bawa, K. S., R. Seidler, and P. H. Raven. 2004. Reconciling conservation paradigms. *Conservation Biology* 18:859–860.
- Beale, C. V., and S. P. Long. 1997. Seasonal dynamics of nutrient accumulation and partitioning in the perennial C₄ grasses *Miscanthus × giganteus* and *Spartina cynosuroides*. *Biomass and Bioenergy* 12:419–428.
- Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications* 8:469–479.
- Blanco-Canqui, H., and R. Lal. 2007. Soil and crop response to harvesting corn residues for biofuel production. *Geoderma* 141:355–362.
- Buckeridge, M. S., A. P. de Souza, R. Arundale, K. J. Anderson-Teixeira, and E. H. DeLucia. 2012. Ethanol from sugarcane in Brazil: a “midway” strategy for increasing ethanol production while maximizing environmental benefits. *GCB [Global Change Biology] Bioenergy* 4:119–126.
- Burney, J. A., S. J. Davis, and D. B. Lobell. 2010. Greenhouse gas mitigation by agricultural intensification. *Proceedings of the National Academy of Sciences USA* 107:12052–12057.
- Campbell, J. E., D. B. Lobell, R. C. Genova, and C. B. Field. 2008. The global potential of bioenergy on abandoned agriculture lands. *Environmental Science and Technology* 42:5791–5794.
- Davis, S. C., K. J. Anderson-Teixeira, and E. H. DeLucia. 2009. Life-cycle analysis and the ecology of biofuels. *Trends in Plant Science* 14:140–146.
- Davis, S., W. Parton, F. Dohleman, C. Smith, S. Grosso, A. Kent, and E. DeLucia. 2010. Comparative biogeochemical cycles of bioenergy crops reveal nitrogen-fixation and low greenhouse gas emissions in a *Miscanthus × giganteus* agro-ecosystem. *Ecosystems* 13:144–156.
- Davis, S. C., W. J. Parton, S. J. Del Grosso, C. Keough, E. Marx, P. R. Adler, and E. H. DeLucia. 2011. Impact of second-generation biofuel agriculture on greenhouse-gas emissions in the corn-growing regions of the US. *Frontiers in Ecology and the Environment* 10:69–74.
- DeFries, R. S., T. Rudel, M. Uriarte, and M. Hansen. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geosci* 3:178–181.

- DeLuca, T. H., and C. A. Zabinski. 2011. Prairie ecosystems and the carbon problem. *Frontiers in Ecology and the Environment* 9:407–413.
- Dohleman, F. 2009. Seasonal dynamics of productivity and photosynthesis of three biofuel feedstocks: Field comparisons of *Miscanthus* \times *giganteus*, *Panicum virgatum* and *Zea mays*. Dissertation. University of Illinois, Urbana–Champaign, Illinois, USA.
- Ewers, R. M., J. P. W. Scharlemann, A. Balmford, and R. E. Green. 2009. Do increases in agricultural yield spare land for nature? *Global Change Biology* 15:1716–1726.
- Fargione, J. E., R. J. Plevin, and J. D. Hill. 2010. The ecological impact of biofuels. *Annual Review of Ecology, Evolution, and Systematics* 41:351–377.
- Field, C. B., D. B. Lobell, H. A. Peters, and N. R. Chiariello. 2007. Feedbacks of terrestrial ecosystems to climate change. *Annual Review of Environment and Resources* 32:1–29.
- Fischer, J., et al. 2011. Conservation: limits of land sparing. *Science* 334:593.
- Foley, J. A., M. H. Costa, C. Delire, N. Ramankutty, and P. Snyder. 2003. Green surprise? How terrestrial ecosystems could affect earth's climate. *Frontiers in Ecology and the Environment* 1:38–44.
- Foley, J. A., et al. 2005. Global consequences of land use. *Science* 309:570–574.
- Foley, J. A., et al. 2011. Solutions for a cultivated planet. *Nature* 478:337–342.
- Forster, P., et al. 2007. Changes in atmospheric constituents and in radiative forcing. Pages in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Fronning, B. E., K. D. Thelen, and D.-H. Min. 2008. Use of manure, compost, and cover crops to supplant crop residue carbon in corn stover removed cropping systems. *Agronomy Journal* 100:1703–1710.
- Godfray, H. C. J. 2011. Food and biodiversity. *Science* 333:1231–1232.
- Graham-Rowe, D. 2011. Agriculture: Beyond food versus fuel. *Nature* 474:S6–S8.
- Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. *Science* 307:550–555.
- Heaton, E., F. G. Dohleman, and S. P. Long. 2008. Meeting US biofuel goals with less land: the potential of miscanthus. *Global Change Biology* 14:2000–2014.
- Heaton, E. A., F. G. Dohleman, and S. P. Long. 2009. Seasonal nitrogen dynamics of *Miscanthus* \times *giganteus* and *Panicum virgatum*. *GCB [Global Change Biology] Bioenergy* 1:297–307.
- Heaton, E., T. Voigt, and S. P. Long. 2004. A quantitative review comparing the yields of two candidate C₄ perennial biomass crops in relation to nitrogen, temperature and water. *Biomass and Bioenergy* 27:21–30.
- Hoben, J. P., R. J. Gehl, N. Millar, P. R. Grace, and G. P. Robertson. 2011. Nonlinear nitrous oxide (N₂O) response to nitrogen fertilizer in on-farm corn crops of the US Midwest. *Global Change Biology* 17:1140–1152.
- Hodgson, J. A., W. E. Kunin, C. D. Thomas, T. G. Benton, and D. Gabriel. 2010. Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecology Letters* 13:1358–1367.
- Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654.
- IPCC [Intergovernmental Panel on Climate Change]. 2006. Agriculture, forestry, and other land use. H. S. Eggleston, L. Buendia, K. Miwa, T. Ngara, and K. Tanabe, editors. 2006 IPCC guidelines for national greenhouse gas inventories. Institute for Global Environmental Strategies, Hayama, Japan.
- Jain, A. K., M. Khanna, M. Erickson, and H. Huang. 2010. An integrated biogeochemical and economic analysis of bioenergy crops in the Midwestern United States. *GCB [Global Change Biology] Bioenergy* 2:217–234.
- Jiang, Y., and S. Swinton. 2009. Market interactions, farmers' choices, and the sustainability of growing advanced biofuels: a missing perspective? *International Journal of Sustainable Development and World Ecology* 16:438–450.
- Jørgensen, R. N., B. J. Jørgensen, N. E. Nielsen, M. Maag, and A.-M. Lind. 1997. N₂O emission from energy crop fields of *Miscanthus* “*giganteus*” and winter rye. *Atmospheric Environment* 31:2899–2904.
- Kendall, A., and B. Chang. 2009. Estimating life cycle greenhouse gas emissions from corn–ethanol: a critical review of current U.S. practices. *Journal of Cleaner Production* 17:1175–1182.
- Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary productivity. *Science* 291:481–484.
- Krebs, J. R., J. D. Wilson, R. B. Bradbury, and G. M. Siriwardena. 1999. The second silent spring? *Nature* 400:611–612.
- Le Mer, J., and P. Roger. 2001. Production, oxidation, emission and consumption of methane by soils: A review. *European Journal of Soil Biology* 37:25–50.
- Lobell, D. B., and C. B. Field. 2007. Global scale climate–crop yield relationships and the impacts of recent warming. *Environmental Research Letters* 2:014002.
- Ma, Z., C. W. Wood, and D. I. Bransby. 2000. Soil management impacts on soil carbon sequestration by switchgrass. *Biomass and Bioenergy* 18:469–477.
- McLaughlin, S. B., and L. A. Kszos. 2005. Development of switchgrass (*Panicum virgatum*) as a bioenergy feedstock in the United States. *Biomass and Bioenergy* 28:515–535.
- Miguez, F. E., M. Maughan, G. A. Bollero, and S. P. Long. 2012. Modeling spatial and dynamic variation in growth, yield, and yield stability of the bioenergy crops *Miscanthus* \times *giganteus* and *Panicum virgatum* across the conterminous United States. *Global Change Biology—Bioenergy* 4:509–520.
- Miguez, F. E., M. B. Villamil, S. P. Long, and G. A. Bollero. 2008. Meta-analysis of the effects of management factors on *Miscanthus* \times *giganteus* growth and biomass production. *Agricultural and Forest Meteorology* 148:1280–1292.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C., USA.
- Mitchell, D. 2008. A note on rising food prices. World Bank Policy Research Working Paper 4682. Social Science Research Network SSRN eLibrary. http://papers.ssrn.com/sol3/papers.cfm?abstract_id=1233058
- Nijsen, M., E. Smeets, E. Stehfest, and D. P. Vuuren. 2012. An evaluation of the global potential of bioenergy production on degraded lands. *GCB [Global Change Biology] Bioenergy* 4:130–147.
- Ometto, A. R., M. Z. Hauschild, and W. N. L. Roma. 2009. Lifecycle assessment of fuel ethanol from sugarcane in Brazil. *International Journal of Life Cycle Assessment* 14:236–247.
- Pan, Y., et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- Perlack, R., L. Wright, A. Turhollow, R. Graham, B. Stokes, and D. Erbach. 2005. Biomass as feedstock for a bioenergy and bioproducts industry: the technical feasibility of a billion-ton annual supply. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA. <http://www.dtic.mil/cgi-bin/GetTRDoc?Location=U2&doc=GetTRDoc.pdf&AD=ADA436753>
- Perrin, R., N. Fretes, and J. Sesmero. 2009. Efficiency in Midwest US corn ethanol plants: A plant survey. *Energy Policy* 37:1309–1316.

- Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333:1289–1291.
- Plevin, R. J., Michael O'Hare, A. D. Jones, M. S. Torn, and H. K. Gibbs. 2010. Greenhouse gas emissions from biofuels' indirect land use change are uncertain but may be much greater than previously estimated. *Environmental Science and Technology* 44:8015–8021.
- Righelato, R., and D. V. Spracklen. 2007. Carbon mitigation by biofuels or by saving and restoring forests? *Science* 317:902.
- Robertson, G. P., E. A. Paul, and R. R. Harwood. 2000. Greenhouse gases in intensive agriculture: contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289:1922–1925.
- Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Scurlock, J. M. O., K. Johnson, and R. J. Olson. 2002. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology* 8:736–753.
- Searchinger, T., R. Heimlich, R. A. Houghton, F. Dong, A. Elobeid, J. Fabiosa, S. Tokgoz, D. Hayes, and T.-H. Yu. 2008. Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* 319:1238–1240.
- Smeets, E. M. W., L. F. Bouwman, E. Stehfest, D. P. van Vuuren, and A. Posthuma. 2009. Contribution of N₂O to the greenhouse gas balance of first-generation biofuels. *Global Change Biology* 15:1–23.
- Smith, W. K., C. C. Cleveland, S. C. Reed, N. L. Miller, and S. W. Running. 2012. Bioenergy potential of the United States constrained by satellite observations of existing productivity. *Environmental Science and Technology* 46:3536–3544.
- Somerville, C., H. Youngs, C. Taylor, S. C. Davis, and S. P. Long. 2010. Feedstocks for lignocellulosic biofuels. *Science* 329:790–792.
- Stehfest, E., and L. F. Bouwman. 2006. N₂O and NO emission from agricultural fields and soils under natural vegetation: summarizing available measurement data and modeling of global annual emissions. *Nutrient Cycling in Agroecosystems* 74:207–228.
- Thomson, A. M., K. V. Calvin, L. P. Chini, G. Hurtt, J. A. Edmonds, B. Bond-Lamberty, S. Frolking, M. A. Wise, and A. C. Janetos. 2010. Climate mitigation and the future of tropical landscapes. *Proceedings of the National Academy of Sciences USA* 107:19633–19638.
- Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences USA* 108:20260–20264.
- Tilman, D., J. Hill, and C. Lehman. 2006. Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314:1598–1600.
- Tilman, D., R. Socolow, J. A. Foley, J. Hill, E. Larson, L. Lynd, S. Pacala, J. Reilly, T. Searchinger, C. Somerville, and R. Williams. 2009. Beneficial biofuels—The food, energy, and environment trilemma. *Science* 325:270–271.
- Toma, Y. O., F. G. Fernández, A. Y. A. Nishiwaki, T. Yamada, G. Bollero, and J. R. Stewart. 2010. Aboveground plant biomass, carbon, and nitrogen dynamics before and after burning in a seminatural grassland of *Miscanthus sinensis* in Kumamoto, Japan. *GCB [Global Change Biology] Bioenergy* 2:52–62.
- Tufekcioglu, A., J. W. Raich, T. M. Isenhardt, and R. C. Schultz. 2003. Biomass, carbon and nitrogen dynamics of multi-species riparian buffers within an agricultural watershed in Iowa, USA. *Agroforestry Systems* 57:187–198.
- UNFCCC [United Nations Framework Convention on Climate Change]. 2008. Reducing emissions from deforestation in developing countries: approaches to stimulate action. Pages 8–11 in UNFCCC Report of the Third Conference of the Parties, Bali, 3–15 December 2007. <http://unfccc.int/resource/docs/2007/cop13/eng/06a01.pdf>
- USDA National Agricultural Statistics Service. 2011. National statistics for corn. United States Department of Agriculture. http://www.nass.usda.gov/Statistics_by_Subject/index.php?sector=CROPS
- U.S. DOE [Department of Energy]. 2011. U.S. billion-ton update: biomass supply for a bioenergy and bioproducts industry. R. D. Perlack and B. J. Stokes, leads. ORNL/TM-2011/224, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- U.S. EPA [Environmental Protection Agency]. 2010. Renewable fuel standard program (RFS2) regulatory impact analysis. EPA-420-R-10-006, U.S. Environmental Protection Agency, Washington, D.C., USA.
- Wang, D., D. S. Lebauer, and M. C. Dietze. 2010. A quantitative review comparing the yield of switchgrass in monocultures and mixtures in relation to climate and management factors. *GCB [Global Change Biology] Bioenergy* 2:16–25.
- West, T. O., and G. Marland. 2002. A synthesis of carbon sequestration, carbon emissions, and net carbon flux in agriculture: comparing tillage practices in the United States. *Agriculture, Ecosystems and Environment* 91:217–232.
- Xue, X., Y. Luo, X. Zhou, R. Sherry, and X. Jia. 2011. Climate warming increases soil erosion, carbon and nitrogen loss with biofuel feedstock harvest in tallgrass prairie. *GCB [Global Change Biology] Bioenergy* 3:198–207.
- Zhang, X., R. C. Izaurralde, D. Manowitz, T. O. West, W. M. Post, A. M. Thomson, V. P. Bandaru, J. Nichols, and J. R. Williams. 2010. An integrative modeling framework to evaluate the productivity and sustainability of biofuel crop production systems. *GCB [Global Change Biology] Bioenergy* 2:258–277.

SUPPLEMENTAL MATERIAL

Appendix

Sensitivity analysis to energy demand intensity (*Ecological Archives* A022-110-A1).