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Published

2022

Journal Title

Global Change Biology

Version

Version of Record (VoR)

DOI

[10.1111/gcb.16267](https://doi.org/10.1111/gcb.16267)

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OPINION**Land-based climate solutions for the United States**

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Funding information

U.S. Department of Energy Great Lakes Bioenergy Research Center, Grant/Award Number: DE-SC0018409; U.S. National Science Foundation Long-term Ecological Research Program, Grant/Award Number: DEB1832042; USDA Long-term Agroecosystem Research Program; Michigan State University AgBioResearch; U.S. Department of Energy Advanced Research Projects Agency Energy Program, Grant/Award Number: DE-AR0000826; European Union Horizon 2020 Research and Innovation Programme, Grant/Award Number: 774378 and NE/P019455/1

Abstract

Meeting end-of-century global warming targets requires aggressive action on multiple fronts. Recent reports note the futility of addressing mitigation goals without fully engaging the agricultural sector, yet no available assessments combine both nature-based solutions (reforestation, grassland and wetland protection, and agricultural practice change) and cellulosic bioenergy for a single geographic region. Collectively, these solutions might offer a suite of climate, biodiversity, and other benefits greater than either alone. Nature-based solutions are largely constrained by the duration of carbon accrual in soils and forest biomass; each of these carbon pools will eventually saturate. Bioenergy solutions can last indefinitely but carry significant environmental risk if carelessly deployed. We detail a simplified scenario for the United States that illustrates the benefits of combining approaches. We assign a portion of non-forested former cropland to bioenergy sufficient to meet projected mid-century transportation needs, with the remainder assigned to nature-based solutions such as reforestation. Bottom-up mitigation potentials for the aggregate contributions of crop, grazing, forest, and bioenergy lands are assessed by including in a Monte Carlo model conservative ranges for cost-effective local mitigation capacities, together with ranges for (a) areal extents that avoid double counting and include realistic adoption rates and (b) the projected duration of different carbon sinks. The projected duration illustrates the net effect of eventually saturating soil carbon pools in the case of most strategies, and additionally saturating biomass carbon pools in the case of forest management. Results show a conservative end-of-century mitigation capacity of 110 (57–178) Gt CO₂e for the U.S., ~50% higher than existing estimates that prioritize nature-based or bioenergy solutions separately. Further research is needed to shrink uncertainties, but there is sufficient confidence in the general magnitude and direction of a combined approach to plan for deployment now.

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1 | INTRODUCTION

Efforts to curb emissions of CO₂ and other greenhouse gases (GHGs) have fallen well short of those needed to meet the international goal of limiting warming to 1.5 or even 2°C by the end of the century (IPCC, 2018). Consequently, we now face an urgent need for negative emissions technologies (NETs) capable of removing GHGs from the atmosphere. NETs fall into three broad categories (Field & Mach, 2017): improved ecosystem stewardship or nature-based solutions, whereby more carbon is stored in ecosystems via practices like reforestation and afforestation, conservation agriculture, and wetland restoration; biological carbon capture with geologic storage as in bioenergy with carbon capture and storage (BECCS) and ocean fertilization; and non-biological technologies such as enhanced rock weathering and direct air capture. Several NETs, including conservation agriculture and bioenergy, can also contribute to GHG avoidance by substituting renewable inputs for fossil fuel use. Socioeconomic projections of end-of-century concentrations of atmospheric GHGs—IPCC Shared Socioeconomic Pathways (IPCC, 2021)—show that all scenarios with a reasonable probability of meeting the 1.5°C target require the global removal of some 100–1000 Gt of CO₂e by 2100 (IPCC, 2018; Rogelj et al., 2018).

NETs vary dramatically in their technical maturity, requirements for land, GHG removal intensities, financial and environmental costs, and delivery of co-benefits such as pollution abatement and biodiversity conservation (Smith et al., 2016), and any single NET is unlikely to sustainably meet end-of-century removal goals (Minx et al., 2018). Nor, of course, are NETs alone a viable solution—deep mitigation also requires decarbonization and non-CO₂ GHG emission reductions (Anderson et al., 2019). Land-based mitigation approaches have the potential to contribute to both negative emissions and decarbonization, and fast action is urgently needed in order to minimize a mid-century temperature overshoot (IPCC, 2022); a plan that includes and assesses the mitigation potential of proven technologies that are available now—notably those related to agriculture, forestry, and bioenergy—seems crucial.

Recent analyses of potentials for land-based mitigation to contribute to end-of-century climate change goals underscore the importance of the food system in general (Clark et al., 2020) and agriculture and forestry in particular (Griscom et al., 2017) for creating the avoided and negative emissions necessary to meet 2100 climate change targets. Bioenergy in particular is used in all successful 1.5°C scenarios (Rogelj et al., 2018), and can be used to decarbonize transportation by producing liquid fuel or electricity (Field et al., 2020; Gelfand et al., 2020), and the co-production of non-fuel chemicals from biomass can as well help to decarbonize the substantial number of chemical products today produced with fossil fuels (Huang et al., 2021).

Driven by rising public demand, private sector interest, and increasingly dire scientific assessments, legislative initiatives in the U.S. signal the government's intent to engage agriculture and forestry to meet the CO₂ drawdown commitments of the Paris Climate Agreement and COP26. Still murky, however, is the degree to which

technical potentials can be met by realistic scenarios that balance available land against the relative strengths and durations of alternative carbon sequestration and emission avoidance strategies. Particularly missing from current discussions of land-based mitigation scenarios are quantitative assessments of potential solutions that include both nature-based (Fargione et al., 2018) and cellulosic bioenergy (Field et al., 2020) solutions.

We believe this oversight deserves attention in order to provide a more complete picture of land-based climate solution potentials. And it is especially important to understand alternative land-use choices in the context of sink strength durations—the period of time over which some land-based mitigation measures will approach saturation. Most ecosystems can store only so much carbon in soils and biomass; eventually these sinks will reach some new equilibrium beyond which no more carbon will accrue. And while end-of-century targets for limiting warming to 1.5 or 2°C are aggressive (IPCC, 2018), even larger draw-downs will be necessary to return atmospheric GHG levels closer to pre-industrial concentrations (IPCC, 2019).

Top-down integrated assessment models of the capacity for land-based mitigation to avoid or remove the 100–1000 Gt of atmospheric CO₂ globally necessary to limit the global temperature increase to 1.5°C by 2100 are, by design, high level simplifications that seek to capture cost-optimized interactions among global systems but lack the sector-level detail needed for effective policy- and decision-making (NASEM, 2019). Additionally, such estimates typically consider only a subset of available land-based strategies, with an emphasis on BECCS (e.g., Calvin et al., 2019). Bottom-up efforts, on the other hand, effectively identify specific practices with substantial mitigation potentials, whether carbon capture or emissions avoidance, but struggle to capture the spatial resolution needed to avoid double-counting activities with competing land needs (NASEM, 2019), or promote one set of practices (such as reforestation) to the exclusion of others (such as bioenergy) (Fargione et al., 2018). And no efforts to derive land-based estimates capture the combined uncertainties of local practice outcomes, available land base, likely adoption rates, and the durations of different carbon sink strengths.

Recent estimates of U.S. land-based sequestration potentials suggest a maximum sequestration capacity of 1.0–2.4 Gt of CO₂ equivalents (CO₂e) per year at mid-century (NASEM, 2019), and a recent spatial analysis of potential nature-based solutions (Fargione et al., 2018) suggests an end-of-century capacity for ~74 Gt CO₂e by 2100. This estimate excludes bioenergy, however, an especially important opportunity in the United States and other countries where an available land base allows capacity to scale appreciably (Hilaire et al., 2019). That liquid bioenergy can offset fossil fuel use and thereby provide benefits immediately during the 20–30 year transition to electric vehicles (Meier et al., 2015) and for much longer for hard-to-decarbonize petroleum needs (IPCC, 2018), that biomass can be used to produce electricity (Calvin et al., 2019), and that bioenergy's mitigation potential is substantially enhanced when coupled with geologic sequestration (Klein et al., 2014; Sanchez et al., 2018), are important considerations for long-term mitigation needs.

Here we provide a quantitative assessment of the extent to which the active management of crop, grazing, and forest lands can help to meet U.S. mitigation targets by 2100. We emphasize that this is one of a number of different potential scenarios, chosen not to provide a single prescriptive solution but rather to show the mitigation potential of an integrated approach based on currently available technologies that balances competing land needs, considers the finite durations of nature-based carbon sinks, and includes a bioenergy potential constrained by expected light vehicle transportation fuel needs. We also emphasize that this U.S. example may or may not be relevant elsewhere, especially where land availability is limited. That said, the potential for restoring degraded lands while mitigating climate change through land management measures such as reforestation and perennial cellulosic bioenergy production is significant (Mosier, Córdova, et al., 2021).

We show a potential capacity for U.S. mitigation of 2.5 Gt CO₂e per year (95% confidence intervals: 1.4–3.8; Table S1) after mid-century vehicle electrification and deployment of geologic carbon capture and storage (CCS), which is included in all but the least energy intensive 1.5°C Shared Socioeconomic Pathway scenarios (IPCC, 2018). Our analysis provides a conservative end-of-century capacity of 110 (57–178) Gt CO₂e (Figure 1, Table S1), significantly more than that estimated by bottom-up assessments based on natural climate solutions (~74 Gt CO₂e), which exclude BECCS, and by top-down assessments based on integrated assessment models (~70 Gt CO₂e), which rely mostly on BECCS. Our land assignments

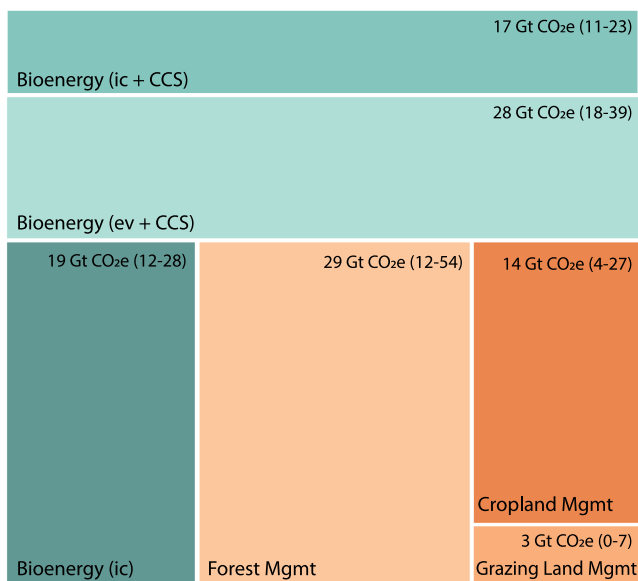


FIGURE 1 Mitigation potentials for U.S. land-based approaches totaling 110 Gt CO₂e to 2100 (95% confidence interval: 57–178 Gt CO₂e). Forest management includes afforestation and reforestation, and bioenergy is for light vehicle transportation. Bioenergy from 2050 includes carbon capture and storage with liquid fuel+internal combustion (ic) and then electricity production+electric vehicles (ev). Values in parentheses denote 95% confidence intervals. Values by emissions category and practice change appear in supplemental materials Table S1

explicitly avoid double counting and involve no changes in U.S. food production, and thus avoid food-fuel conflict and should not result in indirect land use change emissions elsewhere. Explicit consideration of sink durations demonstrates how the relative importance of different potential sinks changes throughout the century (Figure 2). In general, soil carbon reaches a new equilibrium after 40–50 years in most cases, while forest biomass carbon following reforestation does not saturate until sometime after 2100; that geologic CCS is projected to become available mid-century provides an additional, indefinite sink for carbon in bioenergy feedstocks.

We identify avoided and net negative emissions in four components of the agriculture and forestry sector, which comprises most of the Agriculture, Forestry, and Other Land Uses (AFOLU) category of IPCC assessments. In rank order, these include bioenergy after CCS deployment (58% of total capacity) and forest (26%), cropland (13%), and grazing land (3%) management (Figure 1, Table S1). As noted later, significant additional land-based mitigation could be provided by demand-side shifts to plant-based diets and reduced food waste (Clark et al., 2020; Roe et al., 2019).

2 | SECTOR-LEVEL CONTRIBUTIONS

2.1 | Cellulosic bioenergy

Cellulosic bioenergy (Robertson et al., 2017), not to be confused with grain-based bioenergy (Lark et al., 2022), plays a substantial role in IPCC 1.5°C-consistent pathways both with and without CCS

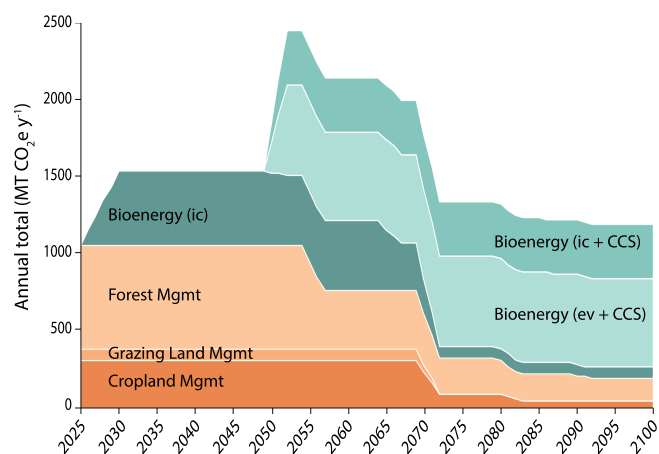


FIGURE 2 Annual mitigation potentials through 2100 for different emissions categories considering the strengths and durations of various sinks (Table S1), and the presumed availability of geologic carbon capture and storage beginning ca. 2050. The steep declines in nature-based sinks (soil organic carbon and tree biomass) reflect the assumption in the calculations of an abrupt termination of their effectiveness (Table S1), when in reality they would approach carbon saturation in a more gradual and asymptotic manner. The 2025 start date (2030 for bioenergy) is arbitrary but useful for comparison with other efforts; the entire timeline could be shifted to a later date with no change to the 75 years potential. See Figure 1 legend for a description of terms

(IPCC, 2018). We include here cellulosic biomass production that avoids interfering with food production to prevent food-fuel conflicts and emissions that might arise from agricultural production displaced to other parts of the world (so-called Indirect Land Use Change effects [Plevin & Kammen, 2013]) and that also avoids the conversion of carbon-dense ecosystems such as forests, wetlands, and conservation lands in order to avert long-term carbon debt and biodiversity harm (Robertson et al., 2017). Eligible feedstocks thus include purpose-grown perennial (but not annual) biomass crops and corn (*Zea mays* L.) residue (stover). We constrain land assigned to purpose-grown bioenergy production to that required to supply expected 2050 transportation fuel biomass needs not provided by waste and residue streams (U.S. Department of Energy, 2011) based on current field-scale yields of switchgrass (*Panicum virgatum* L.) and other native grasses (Gelfand et al., 2020; Robertson et al., 2011). Field-scale yields of woody crops like hybrid poplar (*Populus* spp.) could also have been used with similar results (Gelfand et al., 2020). Less land would be required for a more productive crop like giant miscanthus (*Miscanthus × giganteus*) but with considerably less biodiversity value (e.g., Williams & Feest, 2019) and potential invasiveness (Pittman et al., 2015). More land would be required for restored prairie, which is less productive but much more biodiverse (Gelfand et al., 2020).

Perennial cellulosic bioenergy lands include 41 Mha of the 70–100 Mha of former cropland still unforested (Bandaru et al., 2015; Campbell et al., 2013), planted grasslands now enrolled in the USDA Conservation Reserve Program, and lands now used to grow corn for grain ethanol production. Cellulosic biofuels from perennial crops offer >5 times the climate benefit of grain-based fuels, with CO₂e emissions reductions relative to gasoline >100% as compared to corn grain ethanol's <20%, and as well numerous co-benefits such as soil and water conservation and biodiversity enhancement (Mosier, Córdova, et al., 2021). We exclude annual biomass crops like energy sorghum (*Sorghum bicolor* L. Moench) because of their currently low GHG reduction potentials (Kent et al., 2020).

Growing perennial cellulosic bioenergy crops on current grain ethanol land could, with proper incentives, remove the least productive annual cropland from intensive cultivation with little to no impact on current food supplies but with substantial environmental benefit, since these lands are disproportionately prone to soil erosion and excess nutrient export. Much of this perennial cropland conversion could be focused on consistently low-yielding subfield areas that comprise up to 25% of Midwest agricultural lands (Basso et al., 2019), avoiding the need to convert entire fields to perennial cellulosic crops and ameliorating the disproportionately high global warming impacts of these patches due to their low nitrogen use efficiencies, savings that are not included in our mitigation calculations here. Alternatively, were our 10 Mha of current grain ethanol land kept in corn to meet new food demands, a portion of the co-produced corn residue could be harvested as a cellulosic feedstock to provide by 2100 about 40% of the perennial cropland conversion's climate impact (1.8 vs. 4.4 Gt CO₂e;

Table S1, note x), but without the environmental benefits of perennial systems.

Bioenergy for transportation, with CCS and electric vehicles after 2050, represents ~58% of U.S. land-based mitigation potential over the entire period (Figure 1), and by the end of the century represents ~80% of total land-based mitigation capacity once most soil carbon sinks saturate (Figure 2). We include in this analysis (Table S1) harvested corn residue, limited to corn not grown on land now producing grain ethanol (since land now growing grain ethanol is assigned to perennial bioenergy crops) and also limited to harvest of only 40% of a crop's available residue to protect soil carbon stores (Jones et al., 2018; Xu et al., 2019). We also include the CO₂e fertilizer savings from reduced nitrogen use on former grain ethanol lands. Even with the eventual saturation of soil carbon accrual by mid-century, bioenergy to meet transportation needs can provide mitigation of 19.1 Gt CO₂e (11.7–27.7) from 2030 through 2100 in the absence of CCS (Table S1). The conversion of biomass to liquid fuel provides the opportunity to capture ~50% of its carbon as CO₂, and 90% upon conversion of biomass to electricity (Klein et al., 2014), creating an additional mitigation opportunity of 16.8 (10.8–23.3) Gt CO₂e were CCS available for liquid fuel production by 2050, and additionally 28.0 (17.8–39.1) Gt CO₂e upon also electrifying the U.S. light vehicle fleet (Gelfand et al., 2020). Together this creates as much as 64 (40–90) Gt CO₂e of overall bioenergy mitigation, close to the median 70 Gt CO₂e (range: 0–136) of BECCS attributed to the U.S. by integrated assessment models that target limiting the global temperature increase to <2°C (Nemet et al., 2018).

2.2 | Forest management

In the conterminous United States, harvested natural forests cover ~218 Mha mainly in the west. Extending harvest intervals about a decade to increase the mean standing biomass over an entire growth cycle and improving stand management to increase soil carbon stores could, if implemented on about half of this acreage, capture ~11.8 (7.4–18.0) Gt CO₂e by 2100 (Table S1). This is additional to the current U.S. forest soil background carbon sink (Nave et al., 2018). Prescribed burning and thinning to suppress fires in the west together with longer rotations for eastern plantations increases the mitigation potential for harvested forests by an additional 1.8 (0.5–3.3) Gt CO₂e. A similar amount of mitigation (~11.4 [2.0–27.6] Gt CO₂e) could be provided by reforestation on 22 Mha of former croplands; this could be increased to 63 Mha (Fargione et al., 2018) were 41 Mha not already assigned to perennial bioenergy crops – a tradeoff that we bend towards the indefinite long-term mitigation potential of bioenergy. Planting trees for windbreaks and riparian buffers in cropland landscapes plus urban tree plantings could provide additional mitigation of 3.4 (2.2–5.0) Gt CO₂e by 2100. All told, improved forest management could provide ~28.5 (11.9–53.8) Gt CO₂e of mitigation by 2100 in this analysis, representing ~26% of U.S. land-based mitigation potentials to 2100.

2.3 | Advanced cropland management

Well-studied options for managing agricultural systems to sequester soil carbon or avoid existing GHG emissions include cover crops and reduced tillage, diversified crop rotations, nitrogen fertilizer management, rice water management, and the restoration of cropped peatlands. Winter cover crops in mesic climates have by far the greatest potential impact because of their high initial rate of soil carbon capture (1.8 tons of CO₂e ha⁻¹ y⁻¹ on average; Table S1) and their potential extent (35–83 Mha) on available cropland, capable of mitigating ~5.2 (1.1–10.4) Gt CO₂e by 2100 (Table S1). Adoption of continuous no-till captures carbon at average rates ~40% lower than this (1.1 tons of CO₂e ha⁻¹ y⁻¹ on average; Table S1); adoption on ~60% of available cropland (in particular, excluding cooler and wetter areas) could potentially mitigate ~2.9 (0.5–6.4) Gt CO₂e by 2100.

Crop rotation changes—reducing the proportion of western farmland in summer fallow, and elsewhere diversifying crop rotations away from continuous corn and 2-year corn-soybean cropping cycles—could together mitigate ~1.0 (0–2.3) Gt CO₂e by 2100 (Table S1). Likewise, advanced nitrogen management, including the redistribution of manure from many soils where it is now applied in excess to soils now receiving no manure, and more efficient fertilizer practices to reduce N₂O and CO₂ from fertilizer application and production, respectively, could mitigate another 3.5 (2.2–5.1) Gt CO₂e. In total, advanced cropland management using today's technology could mitigate ~14.2 (4.3–27.0) Gt CO₂e by 2100, or ~13% of the nationwide potential for land-based mitigation.

2.4 | Grazing land management

The vast extent of U.S. grasslands grazed for livestock production – ~252 Mha – catapults even small changes in soil organic carbon to nationally significant levels. Improving stocking rates by better matching livestock foraging intensity to forage production has been shown to increase soil carbon accrual, albeit at low rates (0–1.0 ton of CO₂e ha⁻¹ y⁻¹; Table S1), and current forage models suggest accrual will occur on only ~35% of available U.S. rangeland. Interseeding existing grasslands with improved grass species can also increase soil carbon accrual (0–1.1 tons of CO₂e ha⁻¹ y⁻¹) and, together with improved stocking rates, could likely provide 3.0 (0.5–6.6) Gt CO₂e mitigation by 2100 (Table S1). Improved stocking rates and forage species composition on pastures—the wetter and more intensively stocked paddocks mostly in the eastern United States—can increase soil carbon stocks to a greater extent (e.g., Mosier, Apfelbaum, et al., 2021), but the areal extent of these lands is low so they do not contribute much to the total grazing lands mitigation potential of ~3.1 (0.2–7.3) Gt CO₂e by 2100, which represents ~3% of U.S. total land-based mitigation capacity. Ongoing research such as adaptive multi-paddock grazing and enteric methane suppression in ruminants may identify additional sequestration and avoidance capacities (NASSEM, 2019).

2.5 | Demand-side mitigation measures and future technologies

Missing from this analysis are demand-side measures that reduce the need for current and future food production. Recent estimates of global impacts suggest that shifting to plant-rich diets and reducing food waste can amplify mitigation by land-based practices by at least 14% (Roe et al., 2019) and that a plant-rich diet by itself might reduce total food system emissions by ~50%, or ~678 Gt CO₂e globally (Clark et al., 2020).

Also missing are a number of land-based mitigation technologies under active investigation but not yet sufficiently tested to allow estimates with reasonable confidence. Genetic improvements to bioenergy crop productivity, for example, should soon increase rates of bioenergy carbon capture especially on infertile soils (e.g., Casler & Vogel, 2014), as could the potential for designing crops that better promote soil carbon stabilization via root architecture changes and exudates that can alter rhizosphere microbiomes and promote soil carbon retention (e.g., Kravchenko et al., 2019). Nitrification inhibitors have abated soil N₂O emissions in some field studies (Rose et al., 2018), and genetic and management improvements to crop nitrogen use efficiency (Udvardi et al., 2021) should eventually allow greater future savings of fertilizer-induced CO₂e emissions.

Biochar has been shown to persist in some soils, although its production from biomass must be balanced against the diversion of land from perennial cellulosic bioenergy production and reforestation, each with greater and more certain mitigation potentials (Paustian et al., 2016). Cropland reflectance of solar radiation (i.e., albedo), already contributing to climate cooling relative to pre-conversion reflectance (Abraha et al., 2021; Dominique et al., 2018), might be managed to further enhance reflectance. Ruminant methane production, already somewhat reduced by dietary changes in confined animals (Kumar et al., 2014), may eventually be attenuated in grazed livestock by further manipulating the rumen microbiome, thereby enlarging the grazing land contribution to agricultural mitigation.

Not missing from this analysis, but requiring greater research attention, are the potentials for carbon accrual in forest soils and grazing lands in particular. In contrast to a voluminous literature on soil carbon gain by croplands under different management practices, there are few long-term empirical studies of management-induced changes in forest soil carbon other than soil carbon loss and recovery following forest clearing and regrowth (Nave et al., 2018). Likewise, a lack of long-term studies of soil carbon accretion in grasslands—especially in extensive rangelands at scale (Teague et al., 2013)—hampers our predictions of which practices will generally increase carbon stocks (Conant et al., 2017). And missing from all ecosystems is information on the potential for soil carbon change at depth, that is, accrual or loss of carbon in deeper horizons, inadequately sampled in most soil carbon accretion studies (Kravchenko & Robertson, 2011).

3 | CONCLUSIONS

The adoption of mitigation practices by land managers will involve tradeoffs, including financial. Some options are mutually exclusive

and the least expensive options will not stay that way for long—marginal cost abatement analyses make it clear that costs differ by farm size, geography, access to technology, and other factors, such that mitigation becomes more costly as adoption rates increase (Smith et al., 2014). Moreover, a dynamic agricultural economy makes future opportunity costs hard to predict. That said, the initial costs of all practices described here are known to be well below the informal benchmark of US\$100 per ton CO₂e⁻¹ (Fargione et al., 2018; NASEM, 2019), and in some cases an order of magnitude lower (Smith et al., 2014). Even so, the willingness of farmers, ranchers, and other land managers to participate in mitigation opportunities is not always driven by economic returns; many landowners as well as the public place high value on other ecosystem services—biodiversity conservation, recreation, and cultural amenities, among others. In some cases, co-benefits may enhance these services, as in the case of native grasses or restored prairie for bioenergy feedstocks. Thus, although economic incentives are important, they will not alone drive adoption. Moreover, it will be crucial to establish a governance structure for fairly monitoring, reporting, compensating, and verifying participation, and as well for dissuading farmers and land managers from re-instituting practices in the future that release captured CO₂ back to the atmosphere, thereby undercutting mitigation targets.

Policy should always serve to protect and enhance conservation and biodiversity services. Fortunately, all of the mitigation measures noted here, including bioenergy, have environmental co-benefits when implemented judiciously: enhanced soil fertility, drought resilience, and flood abatement derive from greater soil carbon stores; more diverse landscapes and cropping systems that favor native species promote biodiversity (IPBES, 2019; Werling et al., 2014); and advanced cropland and forest management attenuates wildfires, soil erosion, and nutrient runoff. That said, there are also tradeoffs, some insufficiently known, such as the potential for additional water requirements of CCS (Rosa et al., 2020), that will need to be carefully balanced against expected benefits.

While highly simplified, our analysis illustrates that with affordable technologies available today, advanced land management in the United States can provide ~110 (57–178) Gt CO₂e of mitigation by 2100 while protecting and enhancing the productivity and environmental benefits of crop, forest, and grazinglands. This value is ~50% greater than either prior bottom-up estimates that exclude bioenergy (Fargione et al., 2018) or top-down estimates that rely mostly on bioenergy (Hilaire et al., 2019; Nemet et al., 2018). Although not a panacea, and insufficient by itself (Anderson et al., 2019), the potential for U.S. land-based climate mitigation that includes both natural climate solutions and bioenergy is significant and deserves sensible support.

ACKNOWLEDGMENTS

We thank many colleagues for helpful discussion and feedback during the preparation of this analysis, anonymous reviewers for constructive criticism, and J.L. Schuette for help with data assembly. Financial support was provided by the U.S. Department of Energy Great Lakes

Bioenergy Research Center (Award DE-SC0018409), the U.S. National Science Foundation Long-term Ecological Research Program (DEB 1832042), the USDA Long-term Agroecosystem Research program, and Michigan State University AgBioResearch. Additional support (PS) is from the Soils-R-GGREAT (NE/P019455/1) and CIRCASA (Agreement 774378) projects of the European Union's Horizon 2020 Research and Innovation Programme (Award 774378); and (KP) the U.S. Department of Energy Advanced Research Projects Agency-Energy program (Award DE-AR0000826). KP serves as a part-time advisor to Indigo Ag, Inc., a company that markets soil carbon sequestration credits. The authors declare no other potential conflicts of interest.

DATA AVAILABILITY STATEMENT

All data in supplementary materials are available in Dryad (<https://doi.org/10.5061/dryad.ghx3ffbr1>).

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How to cite this article: Robertson, G. P., Hamilton, S. K., Paustian, K., & Smith, P. (2022). Land-based climate solutions for the United States. *Global Change Biology*, 28, 4912–4919. <https://doi.org/10.1111/gcb.16267>