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The Theoretical Limit to Plant Productivity

Evan H. DeLucia,*,[†,‡,§] Nuria Gomez-Casanovas,[‡] Jonathan A. Greenberg,[∥] Tara W. Hudiburg,[‡] Ilsa B. Kantola,[‡] Stephen P. Long,[†,‡,⊥] Adam D. Miller,[‡] Donald R. Ort,[†,⊥,#] and William J. Parton[∇]

[†]Department of Plant Biology, University of Illinois, Urbana, Illinois 61801, United States
[‡]Energy Biosciences Institute, University of Illinois, Urbana, Illinois 61801, United States
[§]Institute for Sustainability, Energy, and Environment, University of Illinois, Urbana, Illinois 61801, United States
[∥]Department of Geography and Geographic Information Science, University of Illinois, Urbana, Illinois 61801, United States
[⊥]Department of Crop Science, University of Illinois, Urbana, Illinois 61801, United States
[#]Photosynthesis Research Unit, USDA/ARS, Urbana, Illinois 61801, United States
[∇]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, United States

Supporting Information

ABSTRACT: Human population and economic growth are accelerating the demand for plant biomass to provide food, fuel, and fiber. The annual increment of biomass to meet these needs is quantified as net primary production (NPP). Here we show that an underlying assumption in some current models may lead to underestimates of the potential production from managed landscapes, particularly of bioenergy crops that have low nitrogen requirements. Using a simple light-use efficiency model and the theoretical maximum efficiency with which plant canopies convert solar radiation to biomass, we provide an upper-envelope NPP unconstrained by resource limitations. This theoretical maximum NPP approached 200 tC ha^{-1} yr^{-1} at point locations, roughly 2 orders of magnitude higher than most current managed or natural ecosystems. Recalculating the upper envelope estimate of NPP limited by available water reduced it by half or more in 91% of the land area globally. While the high conversion efficiencies observed in some extant plants indicate great potential to increase crop yields without changes to the basic mechanism of photosynthesis, particularly for crops with low nitrogen requirements, realizing such high yields will require improvements in water use efficiency.

INTRODUCTION

As the demand for food, feed, and fuel from crops and managed forests increases, understanding the limits of natural and managed ecosystems to sustainably provide biomass becomes critically important. Net primary production (NPP) is the difference between carbon captured during photosynthesis and carbon released during respiration, and represents the amount of energy stored in plant material annually that is available as a source of food and fiber for the planet including its human inhabitants.[1] Estimates of terrestrial NPP derived from satellite images of vegetation cover and model assumptions suggest an annual terrestrial value of ~54 Pg C y^{-1}. This value has remained stable for the past several decades, leading to the conclusion that it represents a planetary boundary[2] — an upper limit on global biomass production. Increases in NPP by human activities, for example improvements to the productivity of agricultural crops, presents a challenge to the concept that global NPP represents a planetary boundary.[3] Whether NPP is fixed or dynamic, there is, however, little question that humans are co-opting a considerable fraction of it. By directly consuming plant material, feeding it to livestock, by burning it, or otherwise converting land to a lower productivity state, humans currently appropriate approximately one-third of total terrestrial NPP.[4,5]

Concerns about the amount of NPP that can be used sustainably by humans are heightened by the allocation of land to bioenergy production. Approximately 13% of global energy consumption is derived from biomass, and deep concerns over global change accelerated by increasing atmospheric CO_2, as well as the desire for national energy security are increasing reliance on plant material as an energy source.[6] Most liquid fuel from biomass, primarily ethanol, is derived from the food crops maize and sugar cane, putting upward pressure on food and feed prices and potentially driving agricultural expansion into native ecosystems.[7] Transitioning to second-generation feedstocks that utilize lignocellulose rather than sugar and starch for fuel production will reduce direct competition with the food supply.[8] However, because of their relatively low energy density compared to fossil fuels, meeting a substantial portion of the demand for liquid fuel with second-generation feedstocks could require considerable land area, although this will depend critically on the productivity that can be achieved per unit land area.[6]

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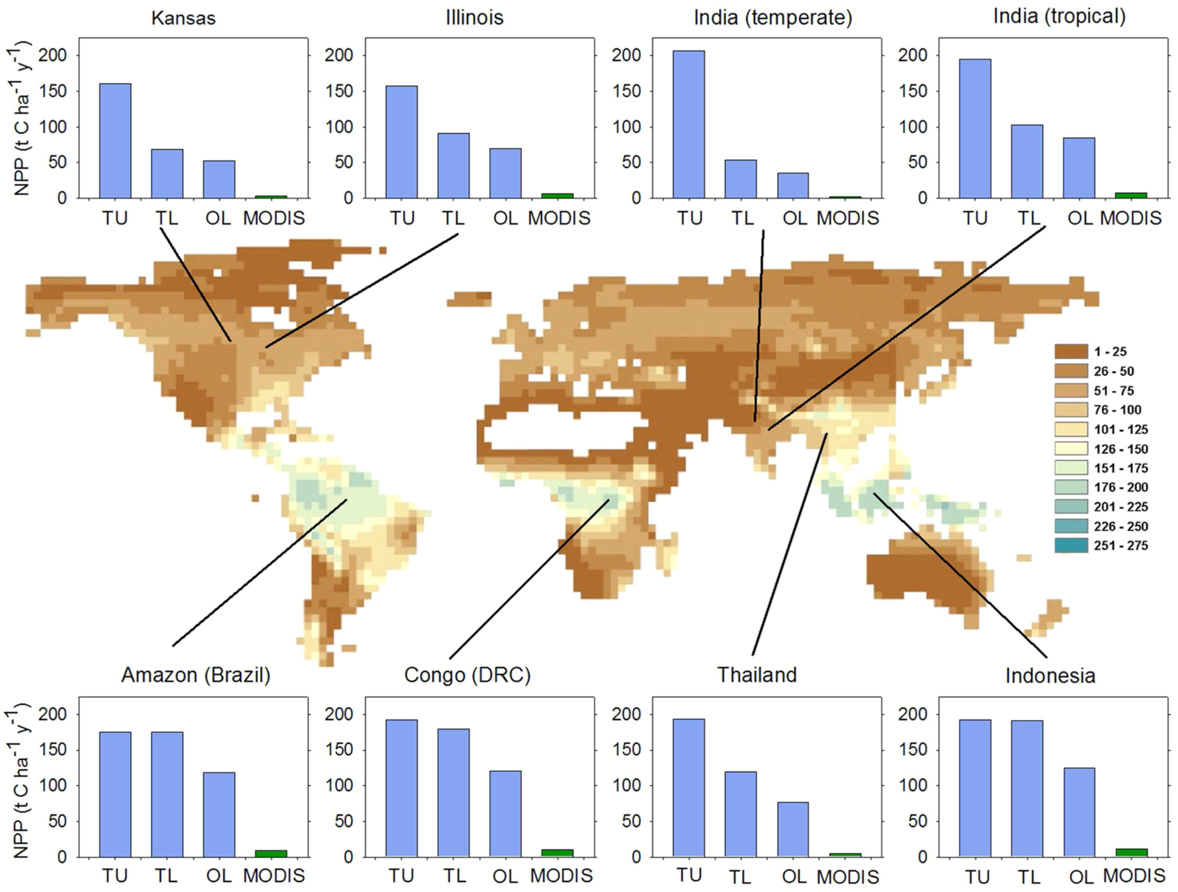

Figure 1. Global distribution of predicted maximum net primary production (NPP; tC ha^{-1} y^{-1}) based on the theoretical maximum light conversion efficiency and accounting for water limitation. Each pixel (2.5°) was populated with data for a predicted C_3 or C_4 crop depending on which had greater NPP at a given location (SI Figure S2). Predicted maximum total NPP (TU), maximum NPP supported by local water availability (TL), NPP calculated using actual maximum observed conversion efficiency for C_3 or C_4 plants and local water availability (OL), and NPP for native vegetation estimated from global satellite images (MODIS), are shown for selected locations.

Prevailing models predict that biomass crops grown on marginal or abandoned land where they will not compete with the food supply, can only displace a small portion of world energy consumption.[9−11] Considerable spatial variation in factors affecting crop productivity, including variability in climate, soils, management practices, and social, political and economic factors, makes estimating global biomass yields challenging.[12] To overcome this challenge, model calculations often make the simplifying assumption that the maximum achievable biomass production of a managed system cannot exceed that of the natural ecosystem that would otherwise occur there.[9−11] This assumption stems from the observation that current biomass production of agricultural crops often is below that of native vegetation.[3,13,14] Recent estimates suggest that in the absence of irrigation and fertilization, agricultural conversion has reduced terrestrial NPP globally by ∼7%.[15] This assumption has been questioned in part because it does not embrace the potential for improving the productivity of emerging energy or food crops,[3,16] and perhaps more importantly, that it may not be consistent with ecological theory.

In natural communities, where plants often struggle with too little water or limiting nutrients, and must fend off competitors and predators, evolution rarely favors maximum growth rates.[17,18] The evolution of strategies to manage biotic or environmental stresses, including allocation of resources to deep root systems for water and nutrient acquisition, or tall woody stems to shade competitors, or antiherbivore defenses, all necessarily reduce growth rates. Most plant species have life history strategies that favor success in stressful or competitive environments at the expense of maximizing NPP.[19] In natural communities, the assemblage of many plant species may overcome some of the growth trade-offs faced by individual plants by making maximum use of resources at the community level.[20] However, plants under human management need not invest as much in nonphotosynthetic tissue and thus are released from common natural constraints on growth.

Here, we show that the assumption that natural ecosystems represent the maximum NPP at a given location may not be appropriate when considering potential future NPP. We provide several examples where managed systems far exceed the NPP of the native system. We also use a simple light-use efficiency model to estimate the maximum NPP that is theoretically possible from physical and physiological principles, with and without water limitations. Our model provides a biologically and physically defined upper envelope for NPP in managed ecosystems, assuming the aspirations of crop improvement are met fully.

■ MATERIALS AND METHODS

To test the assumption that natural ecosystems represent the maximum NPP at a given location, we drew examples from the primary literature where productivity of non-native species in the absence of irrigation and fertilization, either agricultural plants, primarily plantations, or invasive species exceeded the NPP (aboveground) of native climax vegetation. This was not an exhaustive literature search, but sufficient to question the assumption that the native system represents the maximum achievable NPP.

We used a light-use efficiency model derived from theoretical and observed maximum efficiencies to calculate the theoretical maximum and achievable NPP at any given location. NPP was calculated as the product of total incident solar radiation during the growing season (S_t), the efficiency with which plant canopies absorb solar radiation (interception efficiency: ε_i), the efficiency with which absorbed solar radiation is converted into biomass (conversion efficiency: ε_c), and the inverse of the specific energy of plant biomass (K).[21] This approach is used by an extended family of global carbon cycling models.[22] S_t is total incoming solar radiation, about half of which is available for photosynthesis by higher plants, and we assume plant canopies absorb 90% of incoming photosynthetically active radiation, for example, ε_i is 0.9.[23,24] K was 18.2 MJ kg^{-1}.[25]

Conversion efficiency (ε_c) represents the difference between gross photosynthesis of the entire plant canopy and respiratory carbon losses from all plant tissues, including leaves, stems, and roots. At least for short periods during the growing season, values of ε_c for field-grown crops range from 0.032 to 0.046.[26,27] Energy losses in the initial absorption of solar radiation and in primary photochemistry ultimately leading to the production of NADPH and ATP can be at least 74% for plants using C_3 or C_4 photosynthetic pathways.[28] Inefficiencies in subsequent metabolic processes leading to the production of biomass diverge between plants using these two photosynthetic pathways. Notably, C_3 plants divert ~40% of the remaining energy to photorespiration, whereas C_4 plants effectively circumvent this loss but at a cost of two extra ATPs per CO_2 assimilated.

Photorespiration is strongly temperature and CO_2 dependent; consequently ε_c for C_3 plants varies with these parameters (Supporting Information (SI) Figure S1). A general theory of carbon allocation to construction and maintenance of plant structures including root systems and stems remains elusive,[29] but carbon allocation to meet the respiratory costs associated with the construction and maintenance of plant tissues typically represents 30−35% of gross photosynthesis.[27−29] Considering all potential losses in energy transduction from incident sunlight to the formation of carbohydrate, the maximum theoretical ε_c for C_4 and C_3 plants is 0.060 and 0.046, respectively.[28] Observed values of ε_c are about one-third of these theoretical maxima[30] leaving ample room to increase this value through crop improvement.

Using theoretical maximum ε_c we estimate the maximum theoretical NPP for crops growing in terrestrial habitats globally (e.g., theoretical upper limit; TU, Figure 1). We assume plants grow when the minimum temperature is above 0 °C and that they absorb 90% of photosynthetically active radiation during the frost-free growing season. Furthermore, we assume that water and nitrogen is sufficient to fully meet plant growth potential. These assumptions set the theoretical upper bounds of what might be possible for NPP through crop improvement, with full irrigation and fertilization, but without changing the basic mechanisms of photosynthesis. Not all of the biomass would be available to meet human needs, as our estimate does not differentiate biomass allocated to roots or other non-harvestable structures.

The maximum ε_c for a full growing season currently observed in nature for C_3 and C_4 plants is 0.024 and 0.037, respectively.[31] Estimates using these actual values of ε_c represent potential NPP if plants could use all available solar radiation during the frost-free growing season.

During some portion of the growing season most natural and managed ecosystems suffer from water limitations,[32−34] raising the question as to how much biomass could theoretically be produced given limited water availability at a given location. To determine how much water would be necessary to produce a unit of NPP in a specific location, we divided estimated biomass production by the average water use efficiency for a C_3 (0.049 t DM/ha/mm·kPa) or C_4 (0.091 t DM/ha/mm·kPa) crop (SI Table S1). Dividing the amount of water available during the growing season by crop water demand is the fraction of demand that is met by local water supply, and multiplying the theoretical NPP by this value produces the NPP that is possible at a given location with the local water availability (e.g., theoretical water limited; TL, Figure 1).

A "bucket model" estimated total annual water availability for plant growth. The model was run daily and summed to create annual values during the frost-free period. For each day available water was calculated as total precipitation plus water already stored in soil (the bucket), minus losses, where losses included surface runoff and drainage from the bottom of the soil profile. The maximum transpiration for each location was set by the potential evapotranspiration (PET), calculated from local temperature, net solar radiation, wind speed, dew point temperature, and elevation. Available water therefore could not exceed PET. Average environmental values for 2000−2009 were used to drive the model. Any water not used by the plant in a day was carried over to the next day. Because of its considerable seasonal variation,[35] we did not include direct evaporation from soil and plant surfaces, which average 20−30% of evapotranspiration,[36,37] in our estimates of available water. Global values for the soil water holding capacity at 2.5° resolution were based on the depth of the soil profile, and depth-dependent estimates of soil texture.[38] For native ecosystems globally, the actual NPP at each location was calculated with MODIS; average of annual values from 2000−2012; http://www.ntsg.umt.edu/project/mod17#data-product/).[39] MODIS accurately predicts NPP for native vegetation but may underestimate the value for crops (SI Figure S2).

RESULTS AND DISCUSSION

The assumption that the maximum productivity at any given location is best represented by natural vegetation, an assumption underlying many estimates of global NPP,[9−11] is not uniformly supported (Table 1). While this assumption has proven useful in calculations of global NPP, it does not incorporate the potential to improve future yields through breeding and management,[3,5,16] and may underestimate the capacity of the biosphere to produce biomass for food, feed, and bioenergy. In the major grain producing region of the U.S., aboveground NPP (ANPP) of no-till maize and *Miscanthus x giganteus*, a perennial grass for bioenergy production, without fertilization or irrigation can exceed that of native prairie in the same location by more than 300% (Table 1). In woody ecosystems, NPP of poplar, teak, and bamboo plantations greatly exceed that of native vegetation on average by 106%.

Table 1. Location, Vegetation, and Productivity (Aboveground NPP; tC ha^{-1} yr^{-1}) of Eight Sites Where Annual Productivity Changes with Conversion to Non-Native or Cultivated Vegetation[a]

location	native vegetation	ANPP	introduced vegetation	ANPP	ANPP increase
Wisconsin, U.S.	restored prairie	0.8	no-til maize	5.1	540%
Iceland	boreal dwarf birch	1.0[b]	Nootka lupine	5.0[b]	400%
Illinois, U.S.	native prairie	3.2	*Miscanthus giganteus*	8.2	322%
Thailand	dry deciduous tropical forest	3.8	teak plantation	11.5	206%
Hawaii, U.S.	wet tropical forest	2.0	*Falcataria*-invaded forest	5.4	170%
Kansas, U.S.	tallgrass prairie	2.4	*Juniperus* shrubland	4.9	102%
India	moist tarai sal forest	7.3	*Populus* plantation	12.5	71%
Texas, U.S.	coastal prairie	1.6	*Prosopis* shrubland	2.6	63%
India	dry deciduous tropical forest	9.6[b]	bamboo plantation	13.5	40%

[a] When native vegetation yield was not available in the cited article, it was drawn from a separate literature source from the same ecoregion. ANPP was converted to ANPP-carbon (ANPP-C) by a factor of 0.46 for grasslands, 0.47 for tropical species, and 0.5 for temperate woody species. [b] ANPP unavailable, NPP shown. References are provided in SI, Table S2.

Invasive species cause untold damage to many ecosystems precisely because they have life history, morphological, and physiological attributes, including high resource use efficiency,[40] that maximize growth rates.[41,42] Across much of the western U.S., juniper is invading grassland and juniper NPP is almost twice that of the native vegetation that it is replacing (Table 1). In a meta-analysis of 94 studies the average increase in NPP of invasive species relative to native species was over 80%.[43] These examples, while by no means an exhaustive survey, represent cases where without irrigation or fertilization, managed or introduced species greatly outperform native vegetation in terms of NPP and illustrate the untapped potential for managed crops to produce biomass. The average annual dry biomass production on abandoned land is 4.3 tDM/ha[10] and the average value globally for crops currently is below this value,[44] but the highest annual dry matter production for a C_4 plant observed thus far is 100 tDM/ha,[45] raising the question what is the upper envelope of NPP.

A light-use efficiency model that incorporated the theoretical maximum or the maximum observed ε_c and solar radiation absorbed during nonfreezing days was used here to estimate theoretical maximum NPP at point locations globally. Estimates of theoretical upper-envelope NPP unconstrained by resource limitations greatly exceeded the production of natural and managed ecosystems (Figure 1; TU), indicating that there is considerable genetically established potential to increase crop yields. The global distribution of C_3 and C_4 plants was populated on our map by whichever of these two had the highest NPP for a given location. Because of the extended growing season—all periods above 0 °C—and their high ε_c at low temperature (SI Figure S1), C_3 crops achieved greater NPP in more locations globally than C_4 crops (SI Figure S3). In many locations, the theoretical upper limit to NPP (Figure 1) approached 200 tC ha^{-1} yr^{-1} − roughly 2 orders of magnitude higher than most current managed or natural ecosystems. The average upper envelope NPP (TU) on current managed land globally (http://databasin.org/datasets/e84a0e2e71b94ab091751fef8d0b6fc5) was 40 times greater than MODIS NPP for these locations. In all but some equatorial regions, however, this theoretical maximum was greatly reduced by water limitations.

Recalculating the upper envelope estimate of NPP by available water reduced NPP by half or more in many locations, and 91% of the land area globally had water-limited maximum NPP, defined as ≥20% lower than the theoretical maximum NPP (Figure 1.; TL). Nonetheless, water-limited NPP (Figure 1; TL) still was considerably higher than native ecosystems (Figure 1; MODIS). For example, in Kansas, the upper envelope NPP was ∼160 tC ha^{-1} yr^{-1}, and this value dropped to ∼69 tC ha^{-1} yr^{-1} when limited by available water, a value still considerably greater than native grasslands in this region (∼3 tC ha^{-1} yr^{-1}). In the Amazon, Indonesia, Congo, and other equatorial locations with abundant precipitation, water-limited NPP (Figure 1; TL) approached or was equal to the upper envelope estimate of NPP, indicating that water did not significantly limit productivity in these regions.

A meaningful target for crop improvement would be to achieve the maximum ε_c already expressed in some plant species. Calculating potential NPP limited by water supply but using actual observed ε_c revealed substantial gains relative to native and managed ecosystems. Observed ε_c typically is one-third or less of theoretical,[29] but there are notable exceptions. In the tropics, the C_4 grass *Echinochloa plystachya* growing without water or nutrient limitations achieved an NPP of ∼49 tC ha^{-1} y^{-1}, among the highest recorded for native vegetation.[46] The conversion efficiency for this species was ∼0.04, two-thirds of the theoretical maximum for C_4 plants. *Miscanthus x giganteus* achieved a similar ε_c in a temperate climate.[47]

NPP calculated with the maximum observed ε_c for C_4 and C_3 crops[31] was considerably greater than native vegetation. The local NPP for native temperate deciduous forest in Illinois, for example, was ∼7 tC ha^{-1} yr^{-1} (Figure 1), similar to maize at this location.[48] A plant growing with the maximum observed ε_c but with local radiation and water inputs (Figure 1; OL) could theoretically achieve a NPP of ∼70 tC ha^{-1} yr^{-1}. The achievable NPP with water limitations (OL) globally was on average 10× greater than MODIS NPP for these locations. The highest conversion efficiencies observed in nature provide a blueprint for what may be possible through crop improvement even without changes to the basic mechanism of photosynthesis.[28]

While our estimates of the theoretical upper envelope of NPP incorporated limitations imposed by local water availability, they assumed unlimited access to soil nitrogen (and other mineral nutrients). Fertilization increases ε_c[27] and crop yields[49] but at great risk to the environment. Excess nitrogen contaminates groundwater, causes eutrophication of water bodies, and produces N_2O, a potent greenhouse gas.[50] However, the genetic potential for extraordinarily high nitrogen use efficiency is evident in modern unimproved crops. For example, much of the aboveground nitrogen in the perennial grass *Miscanthus x giganteus* is transported by the plant to the rhizome prior to senescence, leaving the harvested stems and leaves with a median carbon/nitrogen ratio of 200.[51] As a result of this high carbon/nitrogen ratio, very little nitrogen is removed during biomass harvest. Even for the theoretical water-limited NPP in Illinois of 91.2 tC ha^{-1} y^{-1}, measured soil nitrogen mineralization rates of 0.58 tN ha^{-1} y^{-1}[52] would be sufficient to meet nitrogen removals over an extended period of time for a plant with such a high carbon/nitrogen ratio, without additional nitrogen fertilizer (N requirement: 91.2 tC ha^{-1} y^{-1}/200 C/N = 0.46 tN ha^{-1} y^{-1}).

Perennial bioenergy crops with deep, fibrous root systems and high retranslocation efficiency like *Miscanthus x giganteus* and *Panicum virgatum*, make very efficient use of nitrogen, losing little to groundwater or the atmosphere,[51] and illustrate what might be achieved through improvement of bioenergy crops where high nitrogen content in grain is not important. The situation would be quite different for food crops like maize where N removals in grain are high; to achieve high yields for grain crops would necessarily require exogenous N.

The approach toward improving ε_c is multifaceted and in the short term will involve reducing carbon losses to photorespiration and modifying the distribution of chlorophyll and nitrogen among leaves at different heights to take maximum advantage of rapidly attenuating light with canopy depth.[24,31] Over most of the globe, however, water limitations will present a significant obstacle to achieving maximum theoretical ε_c (Figure 1) and a concerted effort to improve crop water use efficiency will be necessary.[53] Crop breeding strategies that favor drought-resistance, increase photosynthetic capacity, or increase ability to extract water from soil are promising steps to improving water use efficiency,[54] as are agronomic practices, including minimum tillage and crop residue management, that reduce soil evaporation.[55,56] It is, however, concerning that at least in the limited data set compiled here (SI Table S1), variation in WUE among crops within the C_3 and C_4 photosynthetic types is low. Particularly if it is evident within a species, low variance might indicate limited opportunity to improve WUE through genetic selection.

To keep pace with a rapidly growing human population with expanding purchasing power, the ability to produce food, fiber, and fuel from plant material will need to increase. Agriculture currently uses 38% of the global ice-free land area,[57,58] and further expansion into sensitive ecological areas will accelerate atmospheric warming[59] and hasten the loss of biodiversity and other critical ecosystem services.[60] Agricultural land including pasture currently produces ~6Pg C annually[2,5] and increasing this amount through crop improvement and management in ways that are ecologically sustainable is of paramount importance. The maximum NPP with or without water limitations presented here represents a theoretical projection for a point location, and values integrated over larger spatial areas would be lower. At larger spatial scales many external factors reduce NPP on managed land, including local variation in resource availability, management practices, genetic constraints, and economic and ecological trade-offs[12,61,62]. Because their underlying assumptions do not include potential future improvements in crop yields, current models[9−11] may underestimate the capacity of land to produce biomass. Increasing ε_c even to the level currently observed in the highest NPP plants would greatly increase biomass production, however, over most of the land surface water limitations will stand in the way of achieving these high theoretical productivities. Our theoretical calculations indicate that there considerable opportunity to increase NPP by increasing ε_c, particularly for perennial energy crops where N removals from ecosystems are minimal; however, to fully realize this potential even at point locations will require parallel improvements in WUE.

■ ASSOCIATED CONTENT

Ⓢ Supporting Information

Supporting Figure 1. Temperature dependence of conversion efficiency used to model the theoretical upper limit to NPP; Supporting Figure 2. Maps of the difference between MODIS derived NPP and National Agricultural Statistics (NASS) derived NPP for counties in Iowa, Illinois, and Indiana (U.S. corn belt); Supporting Figure 3. Global distribution of predicted maximum net primary production (NPP; tC ha^{-1} y^{-1}) based on the theoretical maximum light conversion efficiency for a theoretical C_3 crop (A) or a theoretical C_4 crop (B); Supporting Table 1. Water use efficiency for C_3 and C_4 crops (t DM/ha/mm·kPa), where values are normalized to daytime atmospheric VPD during the growing season; Supporting Table 2. Location, vegetation, and productivity (aboveground NPP; tC ha^{-1} yr^{-1}) of eight sites where annual productivity changes with conversion to non-native or cultivated vegetation; with references. This material is available free of charge via the Internet at http://pubs.acs.org/.

■ AUTHOR INFORMATION

Corresponding Author

*Phone: 1 (217) 333 6177; e-mail: delucia@illinois.edu.

Notes

The authors declare no competing financial interest.

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