What is the maximum efficiency with which photosynthesis can convert solar energy into biomass?

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Photosynthesis is the source of our food and fiber. Increasing world population, economic development, and diminishing land resources forecast that a doubling of productivity is critical in meeting agricultural demand before the end of this century. A starting point for evaluating the global potential to meet this goal is establishing the maximum efficiency of photosynthetic solar energy conversion. The potential efficiency of each step of the photosynthetic process from light capture to carbohydrate synthesis is examined. This reveals the maximum conversion efficiency of solar energy to biomass is 4.6% for C3 photosynthesis at 30 °C and today's 380 ppm atmospheric [CO_2], but 6% for C4 photosynthesis. This advantage over C3 will disappear as atmospheric [CO_2] nears 700 ppm.

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Introduction

The world population is projected to grow to ~10 billion before reaching a plateau in the later part of this century, and increasing economic prosperity of the developing world is forecast to soon place even greater demands on agricultural production than will population growth. With very few prospects to sustainably expand the 1.5 billion ha of cropland currently under cultivation [1], a doubling of productivity will be needed to meet the increasing demand before the end of this century. Current photosynthesis underlies the production of all of our food and fiber and biomass-based biofuel is increasingly being viewed as a source of renewable fuels. More solar energy reaches the Earth's surface every hour (4.3×10^{20} J) than is consumed on the planet in a year (4.1×10^{20} J) (Basic Research Needs for Solar Energy Utilization, DOE Solar Energy Workshop

report, http://www.sc.doe.gov/bes/reports/abstracts.html#-SEU_rpt.pdf). Despite its quantity, solar energy is diffuse, placing a premium in all sectors of production agriculture on the overall efficiency of photosynthetic solar energy conversion. In this context it is not surprising that 'application of the revolutionary advances in biology and biotechnology to the design of plants and organisms that are more efficient energy conversion machines' was identified as a major solar energy research goal for the coming decades (Basic Research Needs for Solar Energy Utilization, DOE Solar Energy Workshop report, http://www.sc.doe.gov/bes/reports/abstracts.html#SEU_rpt.pdf). A key starting point for identifying and evaluating biotechnology targets for improving photosynthetic solar conversion efficiency is a critical re-examination of the maximum efficiency of photosynthetic solar energy conversion that could theoretically be achieved in managed ecosystems. The purpose of the analysis undertaken here is to draw on the state-of-the art understanding of the mechanism of plant photosynthesis to establish the theoretical limit on photosynthetic solar energy conversion efficiency that improved agronomy, breeding, and biotechnology can hope to approach.

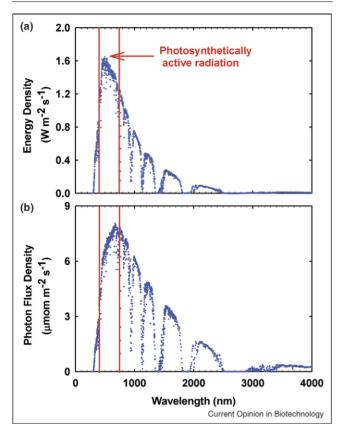## Photosynthetically active radiation in the solar spectrum

As photosynthesis uses different wavelengths of radiant energy with different efficiencies, the first step is to define the average energy spectrum at the Earth's surface. The relative radiant energy density of the solar spectrum at the surface of Earth's atmosphere is given by the Planck's radiation distribution formula:

relative energy flux density per unit wavelength interval

$$\propto \frac{\lambda^{-5}}{e^{hc/\lambda k T_s} - 1} \tag{1}$$

where λ is the wavelength (nm); T_s is the temperature at the surface of the Sun, which is about 5800 K; c is the speed of light (3×10^{17} nm s^{-1}); k is the Bolzmann's constant (1.38×10^{-23} kg m^{-2} s^{-2} K^{-1} or J K^{-1}); and h is the Planck's constant (6.626×10^{-34} J s). Heteroatomic gas molecules in the Earth's atmosphere (e.g. CO_2, H_2O, methane, nitrous oxide, etc.) absorb radiant energy at specific infrared wavelengths. These gases absorb most strongly in the wavelength ranges 900–950, 1100–1150, 1350–1450, 1800–1950 nm, while ozone and oxygen remove much of the energy below 400 nm (Figure 1). Photons above 740 nm in wavelength contain insufficient energy to drive higher plant photosynthesis. Based on the measured average solar spectrum at the Earth's surface,

The distributions of energy density **(a)** and photon flux density **(b)** of a solar spectrum, which represents the average spectrum for the 48 continuous states of the United States over a period of one year. The energy density distribution was obtained directly from American Society for Testing and Materials (http://rredc.nrel.gov/solar/spectra/am1.5/) [33,34]. The photon flux density at each wavelength was calculated based on the energy in the typical solar spectrum (a) and the energy in each photon at that wavelength. The band between the two vertical red lines represents the photosynthetically active radiation (400–740 nm).

the proportion of total solar energy within the photosynthetically active band (400–740) is 48.7%; that is 51.3% of the incident solar energy is unavailable to higher plant photosynthesis (Figures 1 and 2).

Energy loss by reflectance of photosynthetically active light

Owing primarily to the relatively weak absorbance of chlorophyll in the green band, vegetation is not a perfect absorber of photosynthetically active radiation (400–740 nm). This, of course, is why most plants are green and not black and it therefore limits maximum interception of 400–740 nm light to 90%, that is, ~10% of photosynthetically active radiation is reflected. This represents a minimum loss of 4.9% of the total incident solar radiation by reflection (Figure 2). Some plants contain varying amounts of nonphotosynthetic pigments that absorb light

of these wavelengths (e.g. anthocyanins in the epidermis) but the energy is not transferred to photosynthesis. This inactive absorption, to the extent that it happens, would further lower photosynthetic conversion efficiency [2].

Energy loss in rapid relaxation of higher excited states of chlorophyll

The energy of a photon is determined by hc/λ, with the result that the energy of a blue photon (400 nm) is 75% greater than that of a red photon (700 nm). However, higher excited states of chlorophyll very rapidly relax and photochemistry is driven in the photosynthetic reaction center with the energy of a red photon regardless of the wavelength that was originally absorbed. Consequently, photosynthesis is unable to store the additional energy of blue photons. For the surface solar spectrum in the photosynthetically active range (400–740 nm) the average energy per mole of photons is 205 kJ. The energy required to drive a charge separation event in Photosystem II (PSII) is approximately 176 kJ mol^{-1} (equal to the energy of a photon of wavelength 680 nm) or 171 kJ mol^{-1} ($\lambda = 700$ nm) for Photosystem I (PSI). Therefore the average energy loss between absorption and charge-separation in the photosystems will be approximately $(205 - (176 + 171)/2)$ kJ mol^{-1}; that is, a minimum of 6.6% of the incident solar energy is lost irretrievably as heat because of relaxation of higher excited states of chlorophyll (Figure 2).
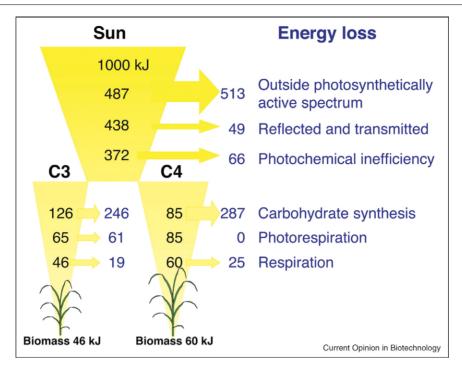
Energy loss between the reaction center and carbohydrate synthesis

The size of this loss differs between C4 and C3 species because of different ATP requirements of the two photosynthetic pathways.

C3 photosynthesis

Examination of the Calvin cycle shows that three ATP and two NADPH are required to assimilate one molecule of CO_2 into carbohydrate and to regenerate one ribulose-1,5-bisphosphate (RuBP) to complete the cycle. In whole chain linear electron transport the absorption of four photons will reduce one molecule of NADPH while translocating a maximum of six protons into the thylakoid lumen; two from water oxidation and four from plastoquinol oxidation by the cytochrome b_6/f complex [3]. Since two NADPH, and therefore the absorption of eight photons, are required for the assimilation of one CO_2 into carbohydrate, a maximum of 12 protons are transported into the lumen for each CO_2 assimilated. With 4 protons required for the synthesis of 1 ATP [4–6], the 12 protons transported would therefore be just sufficient to support the synthesis of the 3 ATP required to balance 2 NADPH in the assimilation of one CO_2. The eight moles of red photons, the minimum required to convert 1 mol of CO_2 to carbohydrate, represents 1388 kJ energy. One-sixth of a mole of glucose, that is, a 1C carbohydrate unit, contains 477 kJ energy. The minimum energy loss in electron

Figure 2

Minimum energy losses calculated for 1000 kJ of incident solar radiation at each discrete step of the plant photosynthetic process from interception of radiation to the formation of stored chemical energy in biomass. Both C3 and C4 (NADP–Malic Enzyme type) photosynthesis are considered. Calculations assume a leaf temperature of 30 °C and an atmospheric $[CO_2]$ of 380 ppm. The theoretical maximal photosynthetic energy conversion efficiency is 4.6% for C3 and 6% C4 plants, calculated based on the total initial solar energy and the final energy stored in biomass. The arrows indicate the amount of energy losses at different processes.

transport and synthesis of carbohydrate within the Calvin cycle – between energy trapping at the reaction centers and carbohydrate production – is $1 - (477/1388)$; this amounts to a loss of 24.6% of the energy contained in the original incident solar radiation (Figure 2). Therefore, the maximal energy conversion efficiency (ε_c) of C3 photosynthesis, before photorespiration and respiration is 12.6% (Figure 2).

C4 photosynthesis
For simplicity among the three major C4 subtypes, we will consider only the NADP–Malic Enzyme (ME) sub-type, which includes all the major C4 crops, such as maize, sorghum, and sugar cane, and is considered to be the most efficient [7]. Here, five ATP and two NADPH are required to assimilate one CO_2 since, in addition to the energy requirement of the Calvin cycle, two additional ATP are required for the phosphorylation of pyruvate to phosphoenol pyruvate. In effect these two extra ATP represent a light-energy driven pump, which transports CO_2 from the outer mesophyll and concentrates it at the site of Rubisco in the inner photosynthetic bundle sheath. The ∼10-fold higher concentration of CO_2 around Rubisco in C4 leaves eliminates or minimizes photorespiration [8]. In C3 photosynthesis, we have shown that translocation of protons in the reduction of

the two NADPH required to fix one CO_2 is just sufficient to generate the three ATP also required. In C4, requiring two additional ATP, then even at maximum efficiency, proton translocation resulting from the reduction of NADPH in noncyclic electron transport will be inadequate. Cyclic electron transport returns electrons from PSI back to the cytochrome b_6/f complex resulting in the translocation of two protons per photon into the thylakoid lumen [9[•],10]. In order for the cyclic flow to provide the additional eight protons needed to synthesize the two additional ATP, absorption of four additional photons at PSI for a minimum total of 12 will be required per CO_2 assimilated in C4 photosynthesis. Following our reasoning above for C3 photosynthesis, the minimum energy loss in electron transport and synthesis of carbohydrate in C4 photosynthesis, between reaction center primary photochemistry and carbohydrate production is $1 - (477/2052)$; this amounts to a loss of 28.7% of the energy contained in the original incident solar radiation (Figure 2). Therefore, the maximal energy conversion efficiency (ε_c) of C4 photosynthesis, prior to respiration, is 8.5% (Figure 2).

Energy loss because of photorespiration
In all eukaryotes photosynthetic CO_2 assimilation is via Rubisco, which catalyzes both the carboxylation and

oxygenation of RuBP. Each oxygenation results in the formation of one molecule of glycolate. Two molecules of glycolate are metabolized through the C2 pathway releasing one CO_2 and forming one molecule of phosphoglycerate, which re-enters the Calvin cycle. This process known as photorespiration lowers the efficiency of photosynthesis both in requiring ATP and reductive energy, and in releasing recently assimilated CO_2 [11]. Oxygenation is competitively inhibited by CO_2, such that in C4 plants the concentration of CO_2 at Rubisco in bundle sheath cells largely eliminates photorespiration. However, some leakage may occur releasing CO_2 back to the mesophyll where it will be re-fixed at the cost of additional energy. Here we consider the maximum potential efficiency, that is, zero photorespiration in C4 species. To determine the energetic cost of photorespiration we define the ratio of RuBP oxygenation to carboxylation as Φ, and compute the amount of ATP associated with one carboxylation and Φ oxygenation as $3 + 3.5\Phi$, where 3.5 represents the net ATP use in the C2 pathway and the Calvin cycle associated with one oxygenation event. Therefore, the number of ATP per CO_2 fixation is $(3 + 3.5\Phi)/(1 - 0.5\Phi)$ where 0.5 represents the fact that one CO_2 is released for every two oxygenations. The decrease in ε_c caused by photorespiration (d_{pr}) is therefore:
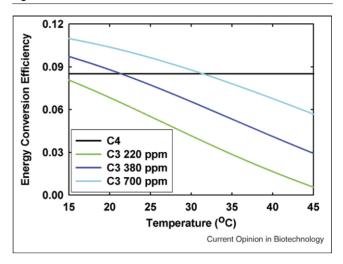
$$d_{pr} = 1 - \frac{3(1 - 0.5\Phi)}{3 + 3.5\Phi} \qquad (2)$$

The ratio of oxygenations to carboxylations (Φ) is

$$\Phi = \frac{O}{C \times \tau} \qquad (3)$$

The symbols O and C represent the intercellular O_2 and CO_2 concentrations. τ is the specificity factor of Rubisco for CO_2 where specificity is the ratio of the probabilities of carboxylation to oxygenation. Specificity declines with an increase in temperature, as does the solubility of CO_2 relative to O_2 [12]. As a result, the loss in the efficiency caused by photorespiration increases with temperature. The effect of temperature on τ is calculated from the empirically derived equations of Bernacchi *et al.* [13], which yield a τ of 71 at 30 °C. Given this value of τ, a $[CO_2]$ of 380 ppm and an $[O_2]$ of 21%, the maximal ε_c of C3 plants would be decreased by 49% at 30 °C, equivalent to a loss of 6.1% of the originally intercepted solar radiation (Figure 2). Because this loss is dependent on both temperature and atmospheric $[CO_2]$ (see [14•]), Figure 3 shows how conversion efficiency varies from 15 to 45 °C and at different $[CO_2]$ which represent the average of Pleistocene conditions (220 ppm), current (380 ppm) and forecast levels for 2100 (700 ppm) [15,16]. These simulations show a very strong advantage for C4 photosynthesis at the atmospheric $[CO_2]$ that prevailed for most of the past 25 M years [17] (Figure 3). This advantage has been diminished by the recent rise in $[CO_2]$ and may be eliminated, except at the

Figure 3

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The effects of temperature and $[CO_2]$ on energy conversion efficiencies of C3 and C4 photosynthesis for the past, current, and future atmospheric conditions. We used three CO_2 concentrations, that is, 220, 380, and 700 ppm, which correspond to the average $[CO_2]$ of the past 25 My [16,17], current, and projected for year 2100. The O_2 concentration was as 21% in all cases. Temperature influences both the solubility of CO_2 and O_2 in solution as well as the specificity of Rubisco to CO_2 relative to O_2, which together drive the decrease in energy conversion efficiency with increase in temperature.

highest temperatures, by the end of this century (Figure 3).

Energy loss due to respiration

The energy losses so far computed have been derived from the known, well-understood and conserved mechanisms of photosynthesis. By contrast there is no quantitatively defined mechanism of linkage between photosynthetic rate and mitochondrial respiration. This final loss (Figure 2) can therefore only be an estimate based on empirical measurements. Measured ratios of respiratory CO_2 loss as a fraction of photosynthetic CO_2 uptake for major crops vary from 30% to 60% [18,19]. It has been shown that there is heritable variation in this ratio within crop species, and selection for a lower ratio in the case of ryegrass (*Lolium perenne*) resulted apparently in higher yielding lines [20]. We assume 30% here as the minimum respiratory loss that might be achieved without otherwise adversely affecting plant growth. This represents a loss of the original incident solar energy of 1.9% (C3) and 2.5% (C4), with the result that the maximum conversion efficiencies of solar radiation into biomass ε_c are 4.6% (C3) and 6.0% (C4) at 30 °C.

Closing the gap between theoretical and achieved conversion efficiencies

The highest solar energy conversion efficiency reported for C3 crops is about 2.4% and about 3.7% for C4 crops across a full growing season based on solar radiation intercepted by the leaf canopy [2,21–23]. Higher short-

term conversion efficiencies are observed for brief periods during the life of a crop reaching 3.5% for C3 and 4.3% for C4 [2]. A major factor that lowers the conversion efficiency below this theoretical value even for healthy canopies under optimal conditions is insufficient capacity to utilize all radiation incident on a leaf. The result is that although photosynthesis increases linearly with light at low radiant energy fluxes, above about one quarter of full sunlight, the increase in photosynthesis with further increase in light diminishes and there will often be no further increase above about half of full sunlight [24]. Efficiency can be further lowered by the fact that excess energy will engage photoprotective mechanisms which will further impair efficiency [25–27]. There are two potential solutions: improved canopy architecture or/ and increased photosynthetic capacity per unit leaf area. First, canopy architecture. If for example, the sun is overhead, then high leaf angles will distribute the light more evenly through the canopy and could reduce the proportion of leaves that become light saturated. This design can increase photosynthetic efficiency by as much as 45% relative to a canopy made up of horizontal leaves [28]. Second, photosynthetic capacity of individual leaves. In C3 leaves metabolic flux analysis suggests control of photosynthesis is shared between Rubisco and proteins involved in the regeneration of RuBP; the cytochrome b_6/f complex and sedoheptulose-1:7-bisphosphatase are most frequently implicated, reviewed in [29]. However, Rubisco already accounts for about 50% of leaf soluble protein and it is first, doubtful that more protein could be added to chloroplasts of a healthy mature leaf and second, undesirable in modern agriculture to increase nitrogen fertilizer requirements. Zhu *et al*. [30$^{\bullet\bullet}$] built a metabolic model of the photosynthetic carbon metabolism which described and linked every enzyme-catalyzed step of the Calvin cycle, C2 pathway, and starch and sucrose synthesis in the leaf. Using an evolutionary algorithm they showed that by substantial rearrangement in the investment of nitrogen among the proteins a 60% increase in photosynthetic capacity might be achieved without any increase in the total nitrogen invested into the photosynthetic apparatus as a whole.

These observed solar energy conversion efficiencies noted above for C3 and C4 crops, while well below the theoretical maximums that we computed in Figure 2, are nevertheless threefold to fourfold larger than the average conversion efficiency attained for major crops in the U.S. [31]. This difference is largely because of unfavorable physical environments for plant growth and reveals opportunities for biotechnological improvement of productivity through understanding crop stress tolerance.

Raising the ceiling on the maximum conversion efficiency

Finally, are there realistic opportunities to raise the theoretical maximum conversion efficiency? For C3 plants, overcoming photorespiration is an obvious target. This may be achieved by converting C3 crops to C4 or by improving the specificity of Rubisco for CO_2. Conversion of a C3 to C4 crop would theoretically raise the maximum solar energy conversion efficiency at 30 °C from 4.6% to 6%. If Rubisco can be engineered to completely eliminate the oxygenation reaction, this would raise efficiency to 8.8%. This increase above the theoretical efficiency for C4 photosynthesis is because no additional ATP is required for concentrating CO_2. At present no Rubisco that lacks oxygenation capacity has been identified, indeed most evidence suggests that increase in specificity is at the expense of catalytic rate [16]. However, by engineering the *E. coli* glycolate catabolic pathway into Arabidopsis (*Arabidopsis thaliana*) chloroplasts [32$^{\bullet\bullet}$] NADH would be generated in the conversion of the oxygenation product, glycolate, to phosphoglycerate rather than reduced ferredoxin consumed as in normal higher plant photorespiratory metabolism. This pathway also uses only half the ATP of the higher plant pathway, and serves to concentrate CO_2 at Rubisco. Based on the lower apparent CO_2 compensation points in the absence of mitochondrial respiration of the transformed plants [32$^{\bullet\bullet}$], we computed that these transformed plants would have 14% more CO_2 at Rubisco in the light. Taking this and the halving of the ATP requirement into account, if this introduction were completely successful in bypassing the normal photorespiratory pathway through the mitochondria and peroxisomes, it would raise the maximum efficiency in C3 plants from the 4.6% of Figure 2 to 5.2% at 30 °C. If the plants are able to take advantage of the NADH generated in the chloroplast by the introduced *E. coli* glycolate catabolic pathway (e.g. production of ATP via a chloroplast/mitochondria shuttle) even greater improvement of the efficiency might be possible.

Appendix:. List of abbreviations. Values in parenthesis are those used in the analysis

Term	Units	Definition
c	$nm\ s^{-1}$	Speed of light (3×10^{17})
CO_2	$\mu mol\ mol^{-1}$	Atmospheric CO_2 concentration (380)
C	$\mu mol\ mol^{-1}$	Intercellular CO_2 concentration (266)
d_{pr}	–	Decrease in ε_c caused by photorespiration

Appendix (*Continued*)

Term	Units	Definition
h	J s	Planck's constant (6.626×10^{-34})
I	μmol m^{-2} s^{-1}	Photon flux density
k	J K^{-1}	Bolzmann's constant (1.38×10^{-23})
k_c^c	s^{-1}	Number of carboxylation reactions per active site of Rubisco per second
k_c^o	s^{-1}	Number of oxygenation reactions per active site of Rubisco per second
K_m^c	μmol mol^{-1}	Rubisco Michaelis–Menten constant for CO_2 (683 at 30 $^\circ$C)
K_m^o	mmol mol^{-1}	Rubisco Michaelis–Menten constant for O_2 (353 at 30 $^\circ$C)
O_2	mmol mol^{-1}	Atmospheric O_2 concentration (210)
O	mmol mol^{-1}	Intercellular O_2 concentration (210)
NAD-ME	–	NAD-Malic Enzyme subtype C4 photosynthesis
PSII	–	Photosystem II
T_s	K	Temperature at sun's surface (5800)
Φ	–	The ratio of oxygenations to each carboxylation
τ	–	The specificity of Rubisco for CO_2 relative to O_2 (91.3 at 25 $^\circ$C)
λ	nm	Wavelength
ε_c	–	Energy conversion efficiency

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