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 [CO₂], but 6% for C4 photosynthesis. This advantage over C3 will disappear as atmospheric [CO₂] 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 × 10²⁰ J) than is consumed on the planet in a year (4.1 × 10²⁰ 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:

\[ \frac{\lambda^{-5}}{\exp(\lambda T_e/\hbar) - 1} \]  

where \( \lambda \) is the wavelength (nm); \( T_e \) is the temperature at the surface of the Sun, which is about 5800 K; \( \epsilon \) is the speed of light \( (3 \times 10^{17} \text{ nm s}^{-1}) \); \( h \) is the Bolzmann’s constant \( (1.38 \times 10^{-23} \text{ kg m}^2 \text{s}^{-2} \text{K}^{-1} \text{ or J K}^{-1}) \); and \( k \) is the Planck’s constant \( (6.626 \times 10^{-34} \text{ J s}) \). Heteroatomic gas molecules in the Earth’s atmosphere (e.g., CO₂, H₂O, 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 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 $h \nu / \lambda$, 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
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 ($e_C$) 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) subtype, 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 ($e_C$) 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
The fact that one CO2 is released for every two oxygenations 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 CO2 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 CO2 [11]. Oxygenation is competitively inhibited by CO2, such that in C4 plants the concentration of CO2 at Rubisco in bundle sheath cells largely eliminates photorespiration. However, some leakage may occur releasing CO2 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 + 3.5ϕ, 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 CO2 fixation is (3 + 3.5ϕ)/(1 − 0.5ϕ) where 0.5 represents the fact that one CO2 is released for two oxygenations. The decrease in εc caused by photorespiration (encedpr) is therefore:

\[ d_{pr} = 1 - \frac{3(1 - 0.5\phi)}{3 + 3.5\phi} \]  

The ratio of oxygenations to carboxylations (ϕ) is

\[ \phi = \frac{O}{C} \times \tau \]  

The symbols O and C represent the intercellular O2 and CO2 concentrations. τ is the specificity factor of Rubisco for CO2 where specificity is the ratio of the probabilities of carboxylation to oxygenation. Specificity declines with an increase in temperature, as does the solubility of CO2 in solution as well as the specificity of Rubisco to CO2 relative to O2, which together drive the decrease in energy conversion efficiency with increase in temperature. The effects of temperature and [CO2] on energy conversion efficiencies of C3 and C4 photosynthesis for the past, current, and future atmospheric conditions. We used three CO2 concentrations, that is, 220, 380, and 700 ppm, which correspond to the average [CO2] of the past 25 My [16,17], current, and projected for year 2100. The O2 concentration was as 21% in all cases. Temperature influences both the solubility of CO2 and O2 in solution as well as the specificity of Rubisco to CO2 relative to O2, which together drive the decrease in energy conversion efficiency with increase in temperature. The 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 CO2 loss as a fraction of photosynthetic CO2 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 εc 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 control of photosynthesis is shared between Rubisco leaves. In C3 leaves metabolic flux analysis suggests [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 b6f 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] 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 CO2. 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 CO2. 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] 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 CO2 at Rubisco. Based on the lower apparent CO2 compensation points in the absence of mitochondrial respiration of the transformed plants [32], we computed that these transformed plants would have 14% more CO2 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

<table>
<thead>
<tr>
<th>Term</th>
<th>Units</th>
<th>Definition</th>
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<tbody>
<tr>
<td>c</td>
<td>nm·s⁻¹</td>
<td>Speed of light (3 × 10⁸)</td>
</tr>
<tr>
<td>CO₂</td>
<td>μmol·mol⁻¹</td>
<td>Atmospheric CO₂ concentration (380)</td>
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<tr>
<td>C</td>
<td>μmol·mol⁻¹</td>
<td>Intercellular CO₂ concentration (266)</td>
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<tr>
<td>dᵦᵣ</td>
<td>–</td>
<td>Decrease in εₛ caused by photorespiration</td>
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Appendix (Continued)

<table>
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<tr>
<th>Term</th>
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<tr>
<td>h</td>
<td>J s</td>
<td>Planck’s constant (6.626 × 10⁻³⁴)</td>
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<tr>
<td>I</td>
<td>μmol m⁻² s⁻¹</td>
<td>Photon flux density</td>
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<tr>
<td>k</td>
<td>J K⁻¹</td>
<td>Boltzmann’s constant (1.38 × 10⁻²³)</td>
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<tr>
<td>kᵣ</td>
<td>s⁻¹</td>
<td>Number of carboxylation reactions per active site of Rubisco per second</td>
</tr>
<tr>
<td>kₒ</td>
<td>s⁻¹</td>
<td>Number of oxygenation reactions per active site of Rubisco per second</td>
</tr>
<tr>
<td>Kᵣ</td>
<td>μmol mol⁻¹</td>
<td>Rubisco Michaelis–Menten constant for CO₂ (683 at 30 °C)</td>
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<tr>
<td>Kₒ</td>
<td>mmol mol⁻¹</td>
<td>Atmospheric O₂ concentration (210)</td>
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<td>O₂</td>
<td>mmol mol⁻¹</td>
<td>Intercellular O₂ concentration (210)</td>
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<td>NAD-ME</td>
<td>–</td>
<td>NAD-Malic Enzyme subtype C4 photosynthesis</td>
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<td>PSI</td>
<td>–</td>
<td>Photosystem II</td>
</tr>
<tr>
<td>𝜃ₛ</td>
<td>K</td>
<td>Temperature at sun’s surface (5800)</td>
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<tr>
<td>φ</td>
<td>–</td>
<td>The ratio of oxygenations to each carboxylation</td>
</tr>
<tr>
<td>𝜌</td>
<td>–</td>
<td>The specificity of Rubisco for CO₂ relative to O₂ (91.3 at 25 °C)</td>
</tr>
<tr>
<td>𝜆</td>
<td>nm</td>
<td>Wavelength</td>
</tr>
<tr>
<td>𝜂ᵣ</td>
<td>–</td>
<td>Energy conversion efficiency</td>
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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

● of special interest
●● of outstanding interest


This paper reviews the mechanisms of photosystem II-dependent cyclic electron flow and proton pumping in chloroplasts which has only recently been elucidated.


A new summary of the current understanding of the mechanisms of temperature responses of C₃ and C₄ photosynthesis across temperature ranges that do not damage the photosynthetic apparatus.


An evolutionary algorithm was applied to an advanced 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 to show that substantial re-arrangement in investment of $N$ among the photosynthetic proteins resulted in a predicted 60% increase in photosynthetic capacity without any increase in the total $N$ invested into the photosynthetic apparatus as a whole.


This paper reported the insertion of the *E. coli* glycolate catabolic pathway into Arabidopsis chloroplasts thereby introducing a by-pass of the normal photorespiratory pathway by converting glycolate to glycerate directly in the chloroplast. Although CO$_2$ is still generated in this bypass pathway, the release is in the direct vicinity of Rubisco thereby partially repressing oxygenation.
