Improving Photosynthetic Efficiency for Greater Yield

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Abstract

Increasing the yield potential of the major food grain crops has contributed very significantly to a rising food supply over the past 50 years, which has until recently more than kept pace with rising global demand. Whereas improved photosynthetic efficiency has played only a minor role in the remarkable increases in productivity achieved in the last half century, further increases in yield potential will rely in large part on improved photosynthesis. Here we examine inefficiencies in photosynthetic energy transduction in crops from light interception to carbohydrate synthesis, and how classical breeding, systems biology, and synthetic biology are providing new opportunities to develop more productive germplasm. Near-term opportunities include improving the display of leaves in crop canopies to avoid light saturation of individual leaves and further investigation of a photorespiratory bypass that has already improved the productivity of model species. Longer-term opportunities include engineering into plants carboxylases that are better adapted to current and forthcoming CO_2 concentrations, and the use of modeling to guide molecular optimization of resource investment among the components of the photosynthetic apparatus, to maximize carbon gain without increasing crop inputs. Collectively, these changes have the potential to more than double the yield potential of our major crops.

Contents

INTRODUCTION

In the last ten years, increases in yield for some major crops such as rice have shown little improvement (98). This slowing pace of yield increase is occurring in a context of increasing world population, climate change, the diversion of an increasing proportion of the grain harvest to meat production, and the emergence of bioenergy production. This is coupled with losses of agricultural land to urbanization and soil degradation. In 2008, the world saw the lowest wheat stockpiles of the past 30 years (136) and fears of a rice shortage incited riots in some countries. Adding to this, the rapid growth in the Chinese and Indian economies has resulted in never before seen demands on grain supplies. Increasing grain crop productivity is the foremost challenge facing agricultural research. Although photosynthesis is the ultimate basis of yield, improving photosynthetic efficiency has played only a minor role in improving yields to date. However, the yield traits that drove the remarkable yield increases during the green revolution appear to have little remaining potential for further increases. Globally, rice is the world's most important crop in terms of the number of people who depend upon it as their major source of calories and nutrition. After rapid increases in yield over the latter half of the twentieth century, further yield increases appear harder to obtain. As an example, between 1987 and 1997 China increased its average rice yields from 5.4 t ha^{-1} to 6.4 t ha^{-1}, yet between 1997 and 2007 no further clear increase has been achieved (**Figure 1**). Jacques Diouf, head of the United Nation's Food and Agriculture Organization, projected that it will be essential to double grain yields to meet increasing global demand across the next 50 years. As we show below, this may now be possible only by improving photosynthetic efficiency. Why might increasing photosynthesis be critical to gaining further grain crop yields?

While realized yields have improved in part through better fertilization and improved disease protection, they have also improved very substantially as a result of increased genetic yield potential (Y) (see the sidebar, Glossary of Terms and Abbreviations, below, for a summary of the abbreviations used in this review). This is defined as the yield that a crop can attain

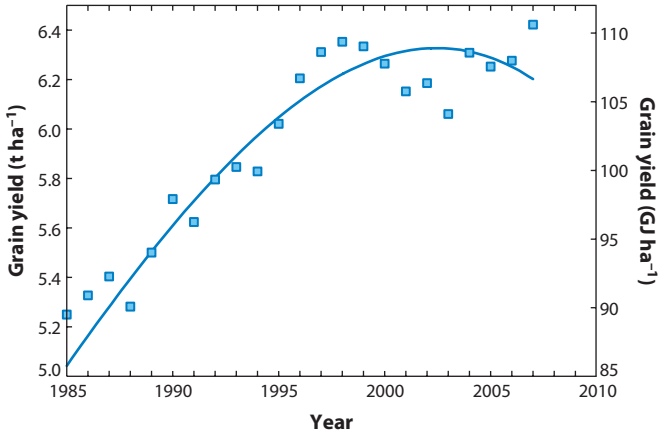

Figure 1

Average annual yield of rice per unit land area in China. Each data point is the average of all harvested areas in China (34). The line is a third-order polynomial best fit to the trend of yield against time.

GLOSSARY OF TERMS AND ABBREVIATIONS

A	Rate of leaf photosynthetic CO_2 uptake per unit leaf area.
A_c'	Integrated daily canopy carbon uptake.
A_{sat}	Light-saturated rate of photosynthetic CO_2 uptake.
C3	Plants in which the primary carboxylase is Rubisco and the primary carboxylation product of RuBP is a three-carbon sugar. Rubisco in C3 plants also catalyzes the oxygenation of RuBP, the initial step of photorespiration.
C4	Plants in which the primary carboxylase is PEPcase and the primary carboxylation product in the light is a four-carbon compound. Rubisco is a secondary carboxylase in C4 plants that functions in a high-CO_2 environment suppressing oxygenation and photorespiration.
C_a	CO_2 concentration in the ambient atmosphere surrounding the leaf.
C_c	CO_2 concentration at the site of carboxylation in the chloroplast.
C_i	CO_2 concentration in inner cellular airspaces within the leaf.
D1	A protein of the photosystem II reaction center involved in charge separation, and vulnerable to oxidative damage, with the result of a high repair turnover.
FACE	Free Air Concentration Enrichment is employed under field conditions to raise the concentration of CO_2 to mimic future atmospheric conditions without disturbing other interactions.
g_m	Mesophyll conductance; numerical measure of the rate of diffusion of CO_2 from the intercellular airspace through the liquid phase to the site of carboxylation in the chloroplast.
g_s	Stomatal conductance; numerical measure of the rate of diffusion of water vapor, carbon dioxide or other gases through the stomatal pore.
I	Photon flux density.
I'	Cumulative intercepted radiation.
J_{max}	Maximum capacity for regeneration of RuBP.
k^c_c	Maximum catalytic rate of Rubisco carboxylation per active site.
LAI	Leaf Area Index is defined as the one sided green leaf area per unit ground area in broadleaf canopies, or as the projected needle leaf area per unit ground area in needle canopies.
LHCII	The light-harvesting complex. An array of protein-chlorophyll molecules within the thylakoid membrane containing both chlorophylls a and b that transfer light energy to the photosystem II reaction center.
LSU	Large subunit of Rubisco; eukaryotic Rubisco has eight large chloroplast-encoded and eight small nuclear-encoded protein subunits.
NPQ	Nonphotochemical quenching of chlorophyll fluorescence due to the thermal dissipation of chlorophyll excited states, which competes with photosystem II fluorescence emission as well as with photochemistry.
PEP	Phosphoenol pyruvate is the three carbon carboxylation substrate for PEPcase in C4 plants.
PEPcase	Phosphoenol pyruvate (PEP) carboxylase; the primary carboxylase of C4 photosynthesis, which catalyzes the fixation of CO_2 to phosphoenol pyruvate.
PPDK	Pyruvate Pi dikinase regenerates PEP in the mesophyll cells during C4 photosynthesis.
PsbS	A protein of photosystem II that is involved in NPQ and heat dissipation of excess absorbed energy.
Q cycle	Describes a series of redox reactions by the cytochrome b_6f complex located in the thylakoid membrane, which results in the net oxidation of one plastoquinol molecule, the net reduction of two plastocyanin molecules, and the translocation of four protons into the thylakoid lumen storing energy in the form of a transmembrane electrochemical potential of protons.
Rubisco	Ribulose-1,5-bisphosphate carboxylase oxygenase; the primary carboxylase in C3 plants and the secondary carboxylase in C4 plants that carboxylates RuBP to form a three-carbon sugar.

RuBP	Ribulose-1,5-bisphosphate is the five-carbon carboxylation substrate for Rubisco.
S_t	Total solar full-spectrum radiation across the growing season incident at the earth's surface.
$V_{c,max}$	Maximum capacity for Rubisco catalyzed carboxylation of RuBP.
W	Total above ground crop biomass.
W′	Cumulative above ground crop biomass.
Y	Genetic yield potential; the yield that a crop can attain under optimal management practices and in the absence of biotic and abiotic stresses
α_c	Fraction of incident light intercepted by a plant canopy.
ε_c	Conversion efficiency is the ratio of biomass energy produced over a given period to the radiative energy intercepted by the canopy over the same period.
ε_i	Light interception efficiency of photosynthetically active radiation (400–700 nm).
ε_p	Partitioning efficiency, also termed harvest index, is the amount of the total biomass energy partitioned into the harvested portion of the crop.
θ	Convexity of the nonrectangular hyperbola that describes the dependence of photosynthesis on light intensity (I).
λ	Rubisco specificity factor represents the discrimination between CO_2 and O_2, the two competing substrates of Rubisco that will lead to either the carboxylation or the oxygenation of RuBP.
τ_c	Fraction of incident light transmitted by a plant canopy.
Φ_{CO_2}	Maximum quantum efficiency of CO_2 fixation, or the maximal fractional number of CO_2 molecules that can be fixed with the absorption of one photon.

under optimal management practices and in the absence of biotic and abiotic stresses. Adapting the equation of Monteith (83):

$$Y = 0.487 \cdot S_t \cdot \varepsilon_i \cdot \varepsilon_c \cdot \varepsilon_p \qquad 1.$$

where S_t (GJ m^{-2}) is the total incident solar radiation across the growing season. Leaves of healthy crops typically absorb approximately 90% of the photosynthetically active radiation (400–700 nm) but transmit most of the near infrared radiation (>700 nm), approximately half of the energy of sunlight. To limit the analysis to photosynthetically active radiation, S_t is multiplied by 0.487. Light interception efficiency (ε_i) of photosynthetically active radiation is determined by the speed of canopy development and closure, leaf absorbance, canopy longevity, size, and architecture. Conversion efficiency (ε_c) is the combined gross photosynthesis of all leaves within the canopy, less all plant respiratory losses. Partitioning efficiency (ε_p), also termed harvest index, is the amount of the total biomass energy partitioned into the harvested portion of the crop. The equation gives the harvestable yield in MJ m^{-2}; converting this to mass depends on the energy content of the harvested material. For nonoil grains this will be 18 MJ g^{-1} but can rise to 35–40 MJ g^{-1} for oil-rich seeds. In the context of Equation 1, increase in potential yield over the past 50 years has resulted largely from increase in ε_p and ε_i. Increased ε_p has resulted in large part through dwarfing of the stem and increase in the potential number of seeds set. Increased ε_i has resulted through the development of larger-leafed cultivars and more rapid coverage of the ground after germination. Dwarfing has also indirectly improved realized ε_i by improving the standing power of the crop to adverse weather conditions, such as rain, wind, and/or hail (i.e., decreased lodging) (12, 31, 47).

Healthy crops of modern cultivars at optimized spacing intercept most of the available radiation within their growing season, limiting prospects for any further improvement of ε_i. One caveat is that most crops do not currently

Y: genetic yield potential; the yield that a crop can attain under optimal management practices and in the absence of biotic and abiotic stresses

S_t: total solar full-spectrum radiation across the growing season incident at the earth's surface

Table 1 Analysis of determinants of soybean yield when grown under ambient and elevated [CO_2]

Measure (units)[a]	Y	W[b,c]	S_t	ε_i	ε_c	ε_p[c]
	MJ m^{-2} (t ha^{-1})	MJ m^{-2} (t ha^{-1})	MJ m^{-2}	(Dimensionless: 0–1)		
380 ppm	10.6 (4.60)	17.7 (8.76)	620	0.89	0.032	0.60
550 ppm	12.2 (5.29)	20.9 (10.40)	620	0.89	0.038	0.58
% difference	15.0	18.2	0	0	18.8	−2.7

Component analysis of the yield of soybean (Glycine max L., cv. 93B15) grown in 2002 at SoyFACE (soybean Free Air Concentration Enrichment facility, Urbana, Illinois), based on Equation 1. Yields are based on four control and four elevated CO_2 plots. The analysis is based on the data of Morgan et al. (84) and Dermody et al. (24).

[a]Abbreviations are as given for Equation 1.

[b]W is the total dry matter content in both energy and mass.

[c]W and ε_p were modified from Dermody et al. (24) to include root biomass, which was 18.5% of the total biomass, with the proportion unaffected by the CO_2 treatment. The energy content of the seeds was assumed to be 23 MJ/kg and the remainder of the biomass, 17 MJ/kg (24).

use the full potential growing season, i.e., the period when temperatures and water are adequate for plant growth. The effects on biomass production of extending the growing season can be seen by comparing biomass production of the unusually cold-tolerant perennial C4 grass *Miscanthus* x *giganteus* with its relative maize. Although its ε_c was almost identical to maize, it produced 60% more biomass in the Midwest, where recorded yields of maize are among the highest in the world. The higher productivity of *M.* x *giganteus* was due simply to its having produced a closed canopy, with an $\varepsilon_i > 0.9$, four weeks before maize and having maintained it for a further four weeks after the maize had senesced (25). Extending the growing season increased the cumulative intercepted radiation by approximately 60% (8, 14).

Soybean is the most important dicotyledonous crop, in terms of total global grain production, and the fourth most important grain crop, after maize, rice, and wheat. **Table 1** shows that a modern soybean cultivar developed for Midwest conditions, grown under normal production conditions and at current atmospheric [CO_2], intercepted almost 90% ($\varepsilon_i = 0.89$) of the photosynthetically active radiation across the growing season. Further, 60% of the biomass energy was partitioned into the harvested seed ($\varepsilon_p = 0.60$). This shows that breeding has succeeded in maximizing both ε_i and ε_p in soybean. Given that the crop will inevitably fail to intercept some radiation between sowing and canopy closure and that cell wall material cannot be recycled to the seed from leaves, roots, and stems, there is little or no prospect of further improving ε_i or ε_p. Analyses of the other major grain crops (maize, wheat, and rice) provide similar findings (31, 47, 115) (**Figure 1**). With reference to Equation 1, therefore, only two prospects may remain: extending the growing season to increase S_t, as noted above, or increasing ε_c. There has been a reluctance to invest in increased photosynthesis, and therefore increased ε_c. As reviewed previously (72), such reluctance arises from the argument that, first, there is no correlation between the yield of a broad range of crops and photosynthesis and, second, yield is limited by sinks for photosynthate and not by photosynthetic capacity. **Table 1** illustrates one of several data sets that now disprove these expectations. Elevated [CO_2] increased leaf photosynthesis in this soybean crop by 22.6% over the growing season (17), corresponding in turn to an 18.8% increase in ε_c and an 18.2% increase of total above ground biomass (W) shown in **Table 1**. This experiment, in which photosynthesis was increased by artificial elevation of [CO_2], provides direct evidence that increasing photosynthesis in a crop under standard field production conditions does result in an increase in yield. The increase in yield of 15% as compared to a 23% increase in photosynthesis reflects an increase in respiration associated with

ε_i: light interception efficiency of photosynthetically active radiation (400–700 nm)

ε_c: conversion efficiency; the ratio of biomass energy produced over a given period to the radiative energy intercepted by the canopy over the same period

ε_p: partitioning efficiency, also termed harvest index; the amount of the total biomass energy partitioned into the harvested portion of the crop

W: total above ground crop biomass

C3: plants in which the primary carboxylase is Rubisco and the primary carboxylation product of RuBP is a three-carbon sugar. Rubisco in C3 plants also catalyzes the oxygenation of RuBP, the initial step of photorespiration

the greater biomass and yield (63) and may also indicate a lack of adequate sink capacity to fully utilize the increased supply of photosynthate, but it nevertheless results in a large increase in yield. This review examines the prospects for genetically achieving a similar result, i.e., without increasing [CO_2]. **Table 1** shows an ε_c of 0.032 calculated on the basis of photosynthetically active radiation, which would amount to an efficiency of conversion of full-spectrum solar radiation into biomass of approximately 1.5%.

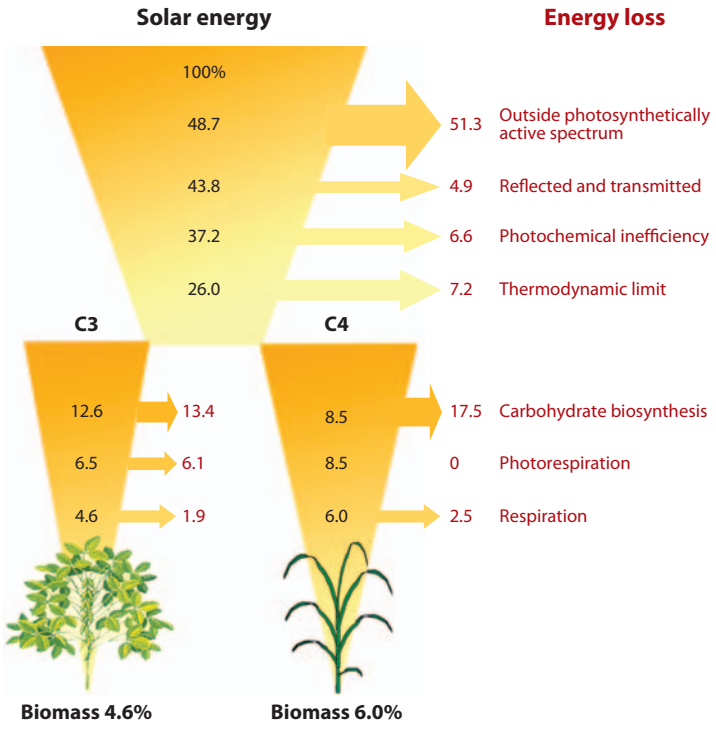

Figure 2

Minimum energy losses showing the percentage remaining (*inside arrows*) and percentage losses (*at right*) from an original 100% calculated for stage of photosynthetic energy transduction from sunlight incident on a leaf to plant biomass. Both C3 and C4 (NADP–malic enzyme type) photosynthesis are presented. Calculations assume a leaf temperature of 30 °C and an atmospheric [CO_2] of 387 ppm. The theoretical maximal photosynthetic energy conversion efficiency (ε_c) is 4.6% for C3 and 6% for C4 plants. These values are for total full-spectrum solar radiation. If the analysis is limited to photosynthetically active radiation (400–700 nm), then these values become 9.4% for C3 and 12.3% for C4. This analysis is redrawn, with modifications explained in the text, from (141).

Estimation of the Theoretical Maximal ε_c for both C3 and C4 Plants

The foregoing has established that realized efficiencies of two of the three efficiency components determining grain crop yield potential are close to their theoretical maxima for major crops. To determine whether there is potential to improve ε_c, it is first necessary to establish the theoretical maximum that could be attained under ideal conditions as it has evolved in C3 and C4 plants. A detailed stepwise biophysical and biochemical analysis of efficiency of energy transduction from interception of radiation to carbohydrate formation has been presented previously (142), and a slightly modified analysis is explained in **Figure 2**.

For oxygen-evolving photosynthesis, only a limited portion of the solar spectrum can be used. Although photons in the waveband 350–740 nm may be used, below 400 nm and above 700 nm, photons can only be used at low efficiency, if at all. For the purposes of this review, photosynthetically active radiation is therefore defined for practical purposes as 400–700 nm, representing 48.7% of the total incident solar energy; i.e., 51.3% is lost at this point (**Figure 2**). Because of the weaker absorbance of chlorophyll in the green band, vegetation is not a perfect absorber of photosynthetically active radiation, which limits maximum interception of 400-nm to 700-nm light in healthy leaves to approximately 90%. Although a blue photon (400 nm) has 75% more energy than a red photon (700 nm), higher excited states of chlorophyll very rapidly relax, and all photochemistry is driven in the photosynthetic reaction centers with the energy of a red photon regardless of the wavelength that was originally absorbed, accounting for a 6.6% energy loss as heat, the "photochemical inefficiency" of **Figure 2**. It is assumed here that in noncyclic electron transport, the partitioning of photons between photosystem I and photosystem II is equal.

At the reaction centers, thermodynamics limit the amount of energy available to do photosynthetic work in terms of charge separation. In our previous analysis (142), the energy loss associated with the "thermodynamic

limit" over the efficiency of charge separation was considered together with energy losses associated with "carbohydrate biosynthesis." **Figure 2** separates these. Thermodynamics limit the energy available for work to 63% of the total energy in a red photon (685 nm), resulting in an energy loss of 37% (see **Supplemental material** for a more detailed quantitative explanation of the "thermodynamic limit" depicted in **Figure 2**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**).

There are energy expenditures associated with electron and proton transport and in the reduction of carbon dioxide to carbohydrate in the C3 cycle, with additional losses in the C_4-dicarboxylate cycle of C4 photosynthsis. In C3 photosynthesis, a minimum of 3 ATP and 2 NADPH is required to assimilate one molecule of CO_2 into carbohydrate and to regenerate 1 RuBP to complete the C3 cycle. In whole chain linear electron transport, the absorption of a minimum of 4 photons is needed to reduce one molecule of NADPH while translocating a maximum of 6 protons into the thylakoid lumen: 2 from water oxidation and 4 from plastoquinol oxidation by the cytochrome b_6/f complex via the Q cycle (59). Given that two NADPH are required for assimilation of one CO_2 into carbohydrate, the absorption of 8 photons results in a maximum of 12 protons transported into the lumen. Since 4 protons are needed for the synthesis of 1 ATP (36, 109, 124), these 12 protons transported are just sufficient to support the synthesis of the 3 ATP required to balance 2 NADPH in the assimilation of one CO_2. The 8 moles of red photons, the minimum required to convert 1 mole of CO_2 to carbohydrate, represents 874 kJ energy available for work. One-sixth of a mole of glucose, i.e., a 1-C carbohydrate unit, contains 477 kJ of energy. Therefore, the minimum energy expenditure in "carbohydrate biosynthesis" is 1-(477/874) or 10.78% of the original incident solar radiation (**Figure 2**). In turn, the maximal energy conversion efficiency (ε_c) of C3 photosynthesis, prior to photorespiration and respiration, is 12.6% (**Figure 2**) (142).

All the major C4 crops—maize, sorghum, and sugar cane, as well as the emerging bioenergy crop *Miscanthus*—belong to the most efficient C4 subtype (29) (NADP–malic enzyme). This subtype requires an additional 2 ATP relative to C3 photosynthesis for the phosphorylation of pyruvate to phosphoenol pyruvate; i.e., 5 ATP and 2 NADPH are required to assimilate 1 CO_2. Increased demand for ATP is underlined by the fact that the bundle sheath chloroplasts in this C4 subtype are often deficient in grana and photosystem II, implying increased cyclic electron transport. Here, electrons from photosystem I are returned to the Cyt b_6/f complex, resulting in the translocation of 2 protons per photon into the thylakoid lumen (22, 114). Thus the translocation of the 8 protons needed to produce the 2 additional ATP requires the absorption of an additional 4 photons by PSI, raising the minimum total quantum requirement for CO_2 assimilated in C4 photosynthesis to 12. Following earlier calculations for C3 photosynthesis (142), the maximal energy conversion efficiency (ε_c) of C4 photosynthesis, prior to respiration, is 8.5% (**Figure 2**).

With the investment of 2 extra ATP, CO_2 is concentrated at the site of carboxylation by Rubisco in bundle sheath cells to a sufficient extent to competitively inhibit oxygenation (40) under most conditions. However, in C3 species, oxygenation and the ensuing photorespiratory metabolism represents a significant energy loss, essentially halving the maximum energy conversion efficiency from 12.6% to 6.1% (**Figure 2**). Thus the "quantum requirement penalty" for each oxygenation event is ~9 photons (4). The actual extent of this penalty in raising the quantum requirement for CO_2 fixation in a C3 leaf depends on the Rubisco specificity factor (λ), the temperature, and the [CO_2]. At 25 °C under current atmospheric [CO_2] of 387 ppm for a typical C3 crop λ, photorespiration raises the minimum quantum requirement of a C3 plant from 8 to 13 photons per CO_2 assimilated.

Mitochondrial respiration is another necessary expenditure of energy that must be subtracted in estimating the theoretical

C4: plants in which the primary carboxylase is PEPcase and the primary carboxylation product in the light is a four-carbon compound. Rubisco is a secondary carboxylase in C4 plants that functions in a high-CO_2 environment suppressing oxygenation and photorespiration

RuBP: ribulose-1,5-bisphosphate is the five-carbon carboxylation substrate for Rubisco

Q cycle: a series of redox reactions by the cytochrome b6f complex located in the thylakoid membrane, which results in the net oxidation of one plastoquinol molecule, the net reduction of two plastocyanin molecules, and the translocation of four protons into the thylakoid lumen storing energy in the form of a transmembrane electrochemical potential of protons

Rubisco: ribulose-1,5-bisphosphate carboxylase oxygenase; the primary carboxylase in C3 plants and the secondary carboxylase in C4 plants that carboxylates RuBP to form a three-carbon sugar

Supplemental Material

maximal ε_c. Mitochondrial respiration has been phenomenologically subdivided into maintenance respiration and growth respiration (99). Growth respiration is the portion invested in biosynthesis, whereas maintenance respiration accounts for the energy expenditure to maintain plant cells in dynamic environments, e.g., replacement of proteins, metabolite transport, and repair of cell damage. There is no known quantitative mechanistic link between photosynthetic and respiration rates. Negative correlations between the respiration of mature leaves and production have been reported for maize (27) and ryegrass (137, 138), implying that selection for lines with lower respiratory rates, while maintaining photosynthetic rate, may be an approach to improving ε_c. Ratios of respiratory CO_2 loss as a fraction of photosynthetic CO_2 uptake for major crops vary from 30% to 60% (3). In **Figure 2**, therefore, 30% is assumed to be the minimum respiratory expenditure 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 are 4.6% (C3) and 6.0% (C4) at 30 °C, or 9.4% and 12.3% of photosynthetically active radiation. The following section examines how the theoretical ε_c compares to achieved ε_c by crops under field production conditions.

λ: Rubisco specificity factor; represents the discrimination between CO_2 and O_2, the two competing substrates of Rubisco that will lead to either the carboxylation or the oxygenation of RuBP

α_c: fraction of incident light intercepted by a plant canopy

τ_c: fraction of incident light transmitted by a plant canopy

W': cumulative above ground crop biomass

I': cumulative intercepted radiation

Supplemental Material

THE PHOTOSYNTHETIC ENERGY CONVERSION EFFICIENCY IN THE FIELD

Measurements of ε_c in the Field

In the field ε_c is commonly measured as the mean slope of the relationship between the accumulation of biomass energy in the crop versus the cumulative amount of intercepted radiation. It can be measured over any portion or the entire growing season, by combining sequential harvests of biomass with measurements of intercepted radiation. The amount of intercepted radiation is determined by continuously measuring the amount of radiation incident above the crop and subtracting the amount that penetrates below the canopy (e.g., 24, 101). Light levels are highly variable both spatially and temporally at the base of the canopy. Line radiation sensors provide a means to average across this heterogeneity. At any one point in time, the fraction of light intercepted by the canopy (α_c) is given by

$$\alpha_c = 1 - \tau_c \qquad 2a.$$

where τ_c is the fraction of incident radiation transmitted by the canopy. Because α_c will vary with sun angle and day of year, cumulative absorbed radiation is typically calculated by summing measurements made at short intervals (i), e.g., every hour, across the growing season.

$$I' = \Sigma I_i.\alpha_{c,i} \qquad 2b.$$

Radiation interception might be overestimated at the end of the growing season as a result of presence of necrotic shoot tissue in the upper canopy and senescing floral parts, an issue that can be overcome by estimating the proportion of the dead or senescing parts using imaging methods (14). Radiation capture can also be estimated mathematically if leaf area index (leaf area per unit ground area) and leaf angular distribution are known (see **Supplemental text;** follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). To obtain a true measure of ε_c for the full growing season, the total biomass, comprising leaves, stem, root, and seeds, and including those shed before crop maturation, need to be taken into account (24, 84). The total energy content is then calculated based on the biomass quantity and the energy content of each biomass component (14, 24). Despite the simplicity and importance of this measurement in providing a link between crop production and photosynthesis, such complete data sets are rare.

Surprisingly often, accumulation of biomass (W') versus cumulative intercepted radiation (I') describes a linear relationship (e.g., **Figure 3**), implying that ε_c is relatively constant. This has been interpreted to imply that

crops respond to stress by altering their canopy size; i.e., ε_i rather than ε_c (83). This has important implications, since it suggests that success in genetically improving ε_c may be just as valuable under suboptimal growth conditions as under optimal.

Variations of ε_c in the Field

Monteith (83), upon reassessing maximum growth rates for C3 and C4 crops, found maximum short-term ε_c of 0.029 and 0.042, respectively, on the basis of photosynthetically active radiation. While the advantage of C4 photosynthesis diminishes as temperature decreases, there is still a theoretical advantage to the simulated daily integral of canopy CO_2 uptake even down to 5 °C (72) at current [CO_2], although other physiological and biochemical factors conspire to limit this advantage to temperatures above ~14 °C in maize (e.g., 96) and other C4 grain crops. However, certain C4 species have been shown to maintain their advantage at lower temperatures (70, 131). Increased nitrogen fertilizer applications dramatically increase ε_c of major crop species, such as barley, oat, rice, and wheat (43, 86), as does irrigation (21, 30). ε_c can differ with developmental stage. For example, the ε_c of oat is higher before heading compared to postheading; in contrast, barley and wheat showed higher ε_c after heading (86). One of the highest annual measured ε_c is 0.078 for the equatorial Amazonian C4 grass *Echinochloa polystachya* (67, 101). However, the temperate C4 grass *Miscanthus* x *giganteus* growing at 52°N also achieved 0.078 averaged across the growing season (15). Compared to C4 species, C3 species usually have smaller ε_c across the growing season.

Why the Maximum Observed ε_c Is Lower Than the Maximum Theoretical ε_c

The observed maximal ε_c with few exceptions is approximately one-third of the theoretical (13). This section examines the inherent mechanisms within photosynthesis that underlie the lower ε_c achieved in field crops relative to the theoretical ε_c of **Figure 2**.

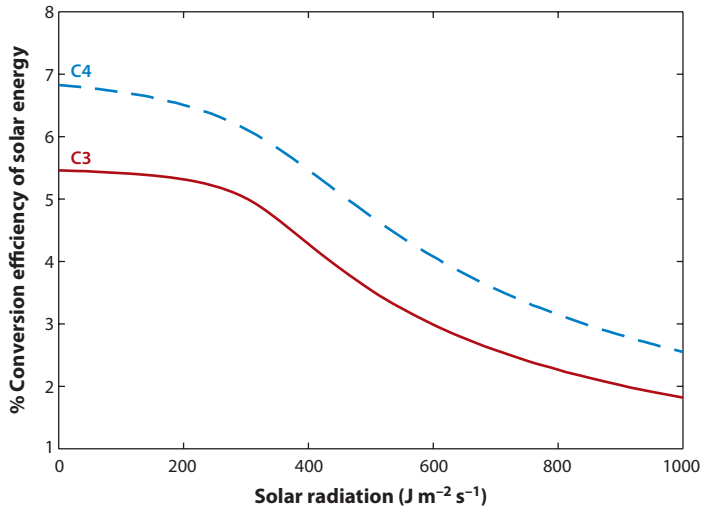

Figure 3

Decline in conversion efficiency of photosynthesis at the leaf level with increasing incident solar radiation. The lines are calculated using maximum observed quantum efficiencies and maximum leaf photosynthetic rates for C4 and C3 species.

Light Saturation

The response of the rate of leaf photosynthetic CO_2 uptake per unit leaf area (A) to sunlight intensity is commonly described in terms of the response to the number of photons rather than energy. This is because the response is largely independent of wavelength and therefore independent of energy content of the photons within the photosynthetically active waveband (400–700 nm). This response can be effectively described by a nonrectangular hyperbola (32, 65, 74):

$$A = \frac{\phi_{CO_2} I + A_{sat} - \sqrt{(\phi_{CO_2} I + A_{sat})^2 - 4\theta\phi_{CO_2} I A_{sat}}}{2\theta} \quad \ldots \ldots (10)3.$$

where Φ_{CO_2} is the maximal quantum efficiency of CO_2 fixation; θ is the convexity of the hyperbola; A_{sat} is the light-saturated rate of photosynthetic CO_2 uptake; and I is the photon flux density. With an increase in I, A increases rapidly

A: rate of leaf photosynthetic CO_2 uptake per unit leaf area

Φ_{CO_2}: maximum quantum efficiency of CO_2 fixation, or the maximal fractional number of CO_2 molecules that can be fixed with the absorption of one photon

θ: convexity of the nonrectangular hyperbola that describes the dependence of photosynthesis on light intensity (I)

A_{sat}: light-saturated rate of photosynthetic CO_2 uptake

I: photon flux density

$V_{c,max}$: maximum capacity for Rubisco catalyzed carboxylation of RuBP

J_{max}: maximum capacity for regeneration of RuBP

C_c: CO_2 concentration at the site of carboxylation in the chloroplast

C_a: CO_2 concentration in the ambient atmosphere surrounding the leaf

C_i: CO_2 concentration in inner cellular airspaces within the leaf

initially, but following an inflection (typically, approximately one-quarter of full sunlight), A approaches a plateau. The initial slope of the A versus I represents the maximum quantum yield of CO_2 uptake, i.e., the fractional number of CO_2 molecules that can be fixed with absorption of 1 photon. At low light, more than 80% of the absorbed photosynthetically active quanta can be used (18), but at one-half of the full sunlight (~1000 μmol m^{-2} s^{-1}), as little as 25% of the absorbed quanta are used; at full sunlight this value falls to <10% (69). Full-spectrum sunlight at Earth's surface will typically contain ~2 μmol of photons (400–700 nm) per J. Based on this conversion and assuming that every g of CH_2O synthesized represents 17.5 kJ of stored energy, **Figure 3** shows how, at the leaf level, efficiency of radiation use declines with increase in radiation received by the leaf. Under optimal conditions, efficiency is high and close to theory in low light. Extensive measurements of the actual efficiency of photosynthesis in low light have shown that for unstressed leaves: (*a*) while C3 and C4 are distinct within these groups, there is remarkably little variation, even between young and old leaves, and (*b*) the value is often close to the theoretical maximum (18, 71). For healthy leaves acclimated to high sunlight, this high efficiency may be maintained until approximately one-tenth of full sunlight. Beyond this point efficiency declines, as depicted in **Figure 3**. A higher ε_c could therefore be achieved by selecting canopy structures or photosynthetic pigment concentrations that spread light within the canopy to minimize occurrence of light levels above one-tenth full sunlight (as discussed below) or by increasing capacity for photosynthesis at light saturation. What limits photosynthesis at light saturation?

Despite the complexity of the overall process, C3 photosynthesis has been successfully summarized in a relatively simple and widely validated steady-state biochemical model developed by Farquhar et al. (35), with subsequent minor modifications (44, 127). In these models, the steady-state light-saturated leaf photosynthetic CO_2 uptake rate (A_{sat}) is determined by three processes: (*a*) Rubisco catalyzed RuBP carboxylation, (*b*) RuBP regeneration, and (*c*) triose phosphate utilization. Under given light, CO_2, and O_2 conditions, A is determined by the slowest of these three processes. Under the optimal conditions that will determine maximum yield, potential for triose phosphate utilization, which typically reflects inability to utilize photosynthate, would not be expected to be limiting. At low [CO_2], photosynthesis is limited by capacity for Rubisco catalyzed carboxylation ($V_{c,max}$), and at high [CO_2], by the capacity for regeneration of RuBP (J_{max}). J_{max} may be limited both by the rate of whole chain electron transport and/or by the activity of enzymes involved in regeneration of RuBP within the C3 carbon reduction cycle. In well-fertilized C3 crops under current ambient atmospheric [CO_2], control appears to be shared between $V_{c,max}$ and J_{max}. Light-saturated photosynthesis could therefore be increased by increasing $V_{c,max}$, J_{max} or/and [CO_2] at the site of carboxylation. The following sections examine these issues and, finally, consider photoinhibition: one factor that can lower the maximum efficiency even under low-light conditions.

The CO_2 concentration at the site of carboxylation (C_c) is determined by both the ambient CO_2 concentration (C_a) and the conductance of the diffusion path from the bulk atmosphere to the chloroplast stroma. The diffusion path includes the leaf boundary layer, stomatal aperture, substomatal cavity, and the cell wall, cell membrane, and cytosol of the mesophyll (9, 38). At light-saturation, [CO_2] in the intercellular space (C_i) is typically 0.7 of C_a in C3 plants. This fraction appears remarkably constant across species, even when C_a is elevated (2, 62). The decline between C_i and C_c is similar to that between C_a and C_i. At the current (i.e., 2009) atmospheric CO_2 concentration of 387 ppm (77), the typical [CO_2] at Rubisco at light-saturation would therefore be ~194 ppm. The remarkably constant ratio of C_i/C_a appears to result from coordination between the rate of CO_2 assimilation and stomatal conductance. A higher conductance and C_i/C_a would deliver a higher photosynthetic CO_2 uptake rate (A).

However, because the response of A to C_i is nonlinear, an increase in stomatal conductance (g_s) results in diminishing returns but a linearly proportional increase in transpiration. Higher A through increased g_s would therefore come at the expense of decreased efficiency of water use and a disproportionate increase in transpiration. Diffusion of CO_2 from the intercellular airspace through the liquid phase to the site of carboxylation is governed by the mesophyll conductance (g_m). Factors controlling g_m are poorly understood and have been associated with the mesophyll surface area exposed to the intercellular air space, carbonic anhydrase, and aquaporins. A higher g_m could be an important approach to increasing [CO_2] at the site of carboxylation and, in turn, photosynthetic rate. For example, if typical C3 crop g_m values could be doubled, then light-saturated A could be increased nearly 20% and, since g_m has no known effect on transpiration, it would also result in a 20% improvement in water use efficiency (see **Supplemental Material** for details of the simulation; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). Unlike increased g_s, there is no evidence of a penalty for increased g_m (16, 91). Light-saturated photosynthesis in C3 species has been shown to be closely related to the amount of Rubisco in a leaf. However, there is substantial evidence that in well-fertilized C3 grain crops, there may be no physical capacity for more Rubisco and other soluble proteins in the mesophyll. In this case, is partitioning of this fixed quantity of total soluble protein among enzymes of carbon metabolism optimized (104)? This question is addressed below, under Carbon Metabolism Engineering.

In C4 species, an analogous steady-state model of photosynthesis has been developed. Here, light-saturated photosynthesis is limited by the activity of the primary carboxylase of C4 photosynthesis, phosphoenol pyruvate carboxylase (PEPcase) at low C_i. At high C_i, photosynthesis is colimited by the activity of Rubisco, which in C4 plants is limited to the photosynthetic bundle sheath, and by pyruvate Pi dikinase (PPDK), which regenerates PEP in the mesophyll (127). Unlike C3 photosynthesis, light-saturated C4 photosynthesis in healthy leaves is generally CO_2-saturated. This is because the C4 pathway is in effect a mechanism for concentrating CO_2 and elevating C_i in the bundle sheath so that Rubisco is CO_2 saturated. As a result, increasing g_s or g_m will not increase photosynthesis.

Rising CO_2 Concentration

Atmospheric [CO_2] over the past 400,000 years, and probably several million years, averaged 220 ppm. It is only since the beginning of the Industrial Revolution that it has begun to rise. This has provided little time in which plants could adapt to this increase and, in the absence of natural adaptation, what opportunity is there for engineering adaptation?

Rubisco is especially pertinent since its activity, among carboxylases, is unusually sensitive to variation in [CO_2] in the range of current atmospheric levels. Rubisco catalyzes the competitive reactions of RuBP carboxylation and RuBP oxygenation. It has long been recognized that genetic modification of Rubisco to enhance its specificity for CO_2 relative to O_2 (λ) would decrease photorespiration and potentially increase C3 photosynthesis and correspondingly crop productivity. However, analysis of the natural genetic variation in the kinetic properties of Rubisco from divergent photosynthetic organisms reveals that forms with higher λ have lower maximum catalytic rates of carboxylation per active site (k^c_c), and vice versa (7, 144). This inverse relationship implies that higher λ would increase light-limited photosynthesis, while the associated decrease in k^c_c would lower the light-saturated rate of photosynthesis (144). The daily integral of CO_2 uptake by a crop canopy is determined by a dynamic combination of light-limited and light-saturated photosynthesis, so the benefit of increasing λ at the expense of k^c_c is not intuitive. Using a model of canopy photosynthesis that determined the daily course of light level on both the sunlit and shaded leaves in the canopy,

g_m: mesophyll conductance; numerical measure of the rate of diffusion of CO_2 from the intercellular airspace through the liquid phase to the site of carboxylation in the chloroplast

g_s: stomatal conductance; numerical measure of the rate of diffusion of water vapor, carbon dioxide, or other gases through the stomatal pore

PEPcase: phosphoenol pyruvate (PEP) carboxylase; the primary carboxylase of C4 photosynthesis, which catalyzes the fixation of CO_2 to phosphoenol pyruvate

PPDK: pyruvate Pi dikinase regenerates PEP in the mesophyll cells during C4 photosynthesis

PEP: phosphoenol pyruvate; the three-carbon carboxylation substrate for PEPcase in C4 plants

k^c_c: maximum catalytic rate of Rubisco carboxylation per active site

Supplemental Material

LSU: large subunit of Rubisco; eukaryotic Rubisco has eight large chloroplast-encoded and eight small nuclear-encoded protein subunits

Zhu et al. (144) showed that the average λ found in current C3 crops exceeds the level that would be optimal for the present atmospheric [CO_2] of >380 ppm but would be optimal for ~220 ppm, which is close to the average of the last 400,000 years prior to the Industrial Revolution (10). The simulation showed that for the same amount of Rubisco, 10% more carbon could be assimilated if λ were optimized for the current atmospheric [CO_2]. An even greater improvement could be achieved for the same total quantity of Rubisco if a low λ and high k^c_c (as found in some algae and C4 plants) could be expressed in the upper canopy and then be replaced by the current C3 Rubisco as these leaves become shaded by new leaves as the canopy grows upward. The possibility that increased [CO_2] favors the evolutionary selection of forms of Rubisco with increased k^c_c and decreased λ is also consistent with the observation that Rubisco from C4 plants, where the enzyme that originated in C3 ancestors, now functions in a high [CO_2]. Some C4 Rubiscos have been shown to have the predicted higher k^c_c and lower λ than that of C3 land plants (110, 113).

Substantial variations in Rubisco catalytic rate and specificity do exist in nature; e.g., Rubisco from red algae has a specificity three times that of C3 crop species (120, 125). Even in higher plants, Rubisco with higher λ values has been reported in plants adapted to dryer environments and in species that are hemideciduous or evergreen (41). But, as noted above, there is a trade-off between specificity and catalytic rate; i.e., the tighter binding required for specificity results in slower catalytic turnover rate. Therefore improving catalytic rate could be at the expense of specificity (144). If Rubisco from the red alga *Griffithsia monilis* could be expressed in place of the present C3 crop Rubisco, then daily canopy carbon gain would be predicted to increase by 27% (72, 144). Large gains could also be made by expressing Rubisco from the C4 dicot *Amaranthus*. As noted above, the ideal situation would be for a crop to express a high-k^c_c Rubisco in the upper canopy leaves exposed to full sunlight and a high-λ Rubisco in the shaded lower canopy leaves thereby resulting in even greater gains (72).

Eukaryotic Rubisco has eight large chloroplast-encoded and eight small nuclear-encoded protein subunits. The large subunit (LSU) contains the structure needed for the catalysis, so most of the current Rubisco genetic screening and mutagenesis research focuses on the LSU, with the aim of improving the catalytic efficiency and specificity of Rubisco to CO_2 versus O_2. Unfortunately, although amino acid substitutions to different areas of LSU have been attempted with guidance from the holoenzyme crystal structure, no more efficient enzymes have been produced so far; in fact, only less effecient enzymes have been produced (5, 75, 97, 117). Comparison of the three-dimensional X-ray structure of Rubisco from multiple prokaryotic and eukaryotic sources suggest a notable difference in one region of small subunit, indicating that small subunit engineering holds some potential to increase Rubisco efficiency and specificity (5, 57). Replacing the loop of the green alga *Chlamydomonas reinhardtii* enzyme with the sequences of the *Synechococcus* loop caused decreases in V_{max}, affinity for oxygen, and specificity, whereas substitution with sequences from the spinach loop caused decreases in V_{max}, affinity for both CO_2 and oxygen but without a change in specificity.

A great deal of progress is still needed in order to efficiently transform foreign Rubisco into crop species. Replacing Rubisco in one plant species with Rubisco from a different species is challenging because of the different coding locations of the subunits of Rubisco and the intricate mechanism coordinating the expression, posttranslational modifications, and assembly of the subunits into the functional hexadecamer (L_8S_8) enzyme within the chloroplast stroma (54, 132)—to say nothing of the issue of silencing the native genes. Replacing Rubisco in tobacco with the simple homodimeric form of the enzyme from the α-proteobacterium *Rhodospirillum rubrum*, which has no small subunits and no special assembly requirements, produced plants that were autotrophic

and reproductive, although they required CO_2 supplementation, thereby establishing that Rubisco from a very different phylogeny can be integrated into chloroplast photosynthetic metabolism without prohibitive obstacles (134). The tobacco chloroplast genome has been transformed with plastid DNA containing the Rubisco large subunit (*rbcL*) gene from both sunflower (*Helianthus annuus*) and the cyanobacterium *Synechococcus* PCC6301, although the catalytic activities of the recombinant enzymes were only 25% of the native tobacco enzyme (56). Compared to the genetic manipulation of the large subunit, engineering the small subunit is very difficult because a gene family of multiple closely related genes codes for the small subunit, making targeted mutagenic or placement strategies problematic. A potential alternative route is simultaneous expression of both the large and small subunits as a fusion protein, as demonstrated recently by the success of linking the subunits of *Synechococcus* PCC6301 Rubisco to generate correctly assembled Rubisco in *E. coli*, with catalytic capacity similar to wild-type *Synechococcus* (133). Studies to assess the applicability of this linking strategy to assemble functional Rubisco complexes of higher plant Rubisco large and small subunits in chloroplasts are warranted. Thus, while the rewards, in terms of improved ε_c, of introducing Rubiscos better adapted for current and future conditions are fully evident, technical obstacles are preventing implementation.

A second instance in which acclimation and adaptation have been insufficient to ensure maximal ε_c in the face of rapid environmental change has been the inability of plants to optimally deploy nitrogen resources within the photosynthetic apparatus. In the Farquhar (35) model, the maximal rate of RuBP carboxylation catalyzed by Rubisco (V_{cmax}) is determined by the catalytic rate and the amount of active Rubisco in a leaf, while the maximal rate of RuBP regeneration (J_{max}) is determined by not only proteins in the photosynthetic electron transport chain but also enzymes in the C3 cycle other than Rubisco (46, 64, 127). To attain the maximal ε_c under a given level of nitrogen availability, V_{cmax} and J_{max} need to be balanced so that neither Rubisco nor enzymes controlling J_{max} are overly limiting.

Theoretical analysis suggests that the current ratio of V_{cmax} to J_{max} is not optimal for maximizing ε_c for a given level of available nitrogen. Under the ambient CO_2 concentration of 387 ppm, the intercellular C_i is ~270 ppm consistent with a C_i/C_a of 0.7 (139). Given the average V_{cmax} (75 mmol $m^{-2}s^{-1}$)and J_{max} (154 mmol m^{-2} s^{-1}) (140), and the fact that the transition C_i from Rubisco-limited to RuBP-limited photosynthesis is ~287 ppm, it follows that C3 photosynthesis currently operates as Rubisco-limited photosynthesis since C_i is lower than the transition C_i; i.e., there is not balanced control by V_{cmax} and J_{max}. If atmospheric [CO_2] reaches 550 ppm by the middle of this century, then this would require a 30% increase in the J_{max}/V_{max} ratio to optimize investment between Rubisco and apparatus for the regeneration of RuBP. Plants are well known to show acclimation to growth at elevated [CO_2], but is this sufficient to achieve this projected requirement? A meta-analysis of Free Air Concentration Enrichment (FACE) of CO_2 experiments showed an average decrease in V_{cmax} of 13% in C3 plants (68). On the one hand, this result suggests an active acclimation of photosynthesis to high [CO_2], since according to the Farquhar et al. (35) model, less Rubisco is needed to keep the same photosynthetic CO_2 uptake rate under elevated [CO_2]. On the other hand, J_{max} decreases on average by 5% under elevated [CO_2] of 550 ppm (68), leading to a transition C_i of approximately 356 ppm, which is substantially lower than the operating C_i of 385 ppm at an elevated [CO_2] of 550 ppm (68). This again suggests that the available acclimatory mechanisms inherent in current C3 plants are not able to keep V_{cmax} and J_{max} balanced to maximize photosynthesis and ε_c under today's or future [CO_2]. The necessary decrease in Rubisco activity to optimize V_{cmax}/J_{max} could be achieved easily through antisense or RNAi; however, which genes might need to be overexpressed to achieve the parallel increase in J_{max}

FACE: Free Air Concentration Enrichment is employed under field conditions to raise the concentration of CO_2 to mimic future atmospheric conditions without disturbing other interactions

is far less clear. The following section examines a potential approach that might guide such manipulations.

Carbon Metabolism Engineering

Although Rubisco has been the primary focus of research to improve photosynthetic efficiency (117), other enzymes in the C3 cycle have been manipulated in different plants and their impacts on photosynthesis evaluated (105, 106). Results from these experiments clearly demonstrate that metabolic control of CO_2 fixation rate is shared among different enzymes (105). The control coefficient is defined as the ratio of the proportional increase in A to the proportional change in the activity of an individual enzyme underlying A. For example, if the activity of enzyme x is increased twofold, and A increases 1.5-fold, then the control coefficient for enzyme x would be 0.5. The sum of all control coefficients in the pathway leading to CO_2 assimilation is unity. If any one enzyme had a control coefficient of 1, it would be the only rate-limiting step under the conditions of measurement. At low CO_2 and high light, as implicit in the model of Farquhar et al. (35), the control coefficient for Rubisco must approach 1. Under other conditions, no single step in the process has a control coefficient of 1, implying that control is shared. As expected, enzymes show different control coefficients under different conditions. For example, Rubisco has a low control coefficient under low light conditions (118). Even enzymes usually regarded as catalyzing reversible reactions, such as transketolase, can have a control coefficient higher than 0 (48). This suggests that the choice of enzyme to be engineered differs depending on different growth environments, and thus identifying the optimal engineering option requires a systemwise approach.

Given some 60+ metabolic reactions in photosynthetic carbon metabolism and associated cellular metabolism in sucrose synthesis and photorespiration, there are thousands of potential permutations of change, which could not be addressed practically without some means of directing the effort. Zhu et al. (141) extended existing dynamic metabolic models of the C3 cycle by including the photorespiratory pathway and cellular metabolism to starch and sucrose to develop a complete dynamic model of photosynthetic carbon metabolism. The model consisted of a series of linked differential equations, with each differential equation representing the concentration change of one metabolite. Initial concentrations of metabolites and maximal activities of enzymes were extracted from the literature. The dynamics of CO_2 fixation and metabolite concentrations were simulated by numerical integration, such that the model could mimic well-established physiological phenomena. Using an evolutionary optimization algorithm, in which partitioning of a fixed quantity of protein-nitrogen among enzymes was allowed to vary, and selecting on photosynthetic rate, resulted after several generations in individuals with a light-saturated photosynthetic rate that was 60% higher. This suggests that the "typical" partitioning of resources among enzymes of photosynthetic carbon metabolism in C3 crop leaves is not optimal for maximizing the light-saturated rate of photosynthesis under current or future conditions. In particular, there appears to be an overinvestment in enzymes of the photorespiratory pathway and marked underinvestment in ADP glucose pyrophosphorylase and SBPase (sedoheptulose-1:7-bisphosphatase), enzymes which occupy key control points in carbon metabolism. Under the elevated [CO_2] conditions predicted for the future, this pattern of under- and overinvestment is amplified, suggesting that manipulation of partitioning of resources among enzymes could greatly increase carbon gain without any increase in the total protein-nitrogen investment in the apparatus for photosynthetic carbon metabolism. Direct support for this prediction comes from the fact that overexpression of SBPase was shown to increase photosynthesis and biomass production of tobacco (64), whereas small decreases in SBPase were shown to decrease photosynthesis and biomass production (45, 46).

Decreasing Photorespiratory Losses

At 25°C and current atmospheric [CO_2], ~30% of the carbohydrate formed in C3 photosynthesis is lost via photorespiration and the size of this loss increases with temperature. But blocking photorespiratory C2 metabolism downstream of Rubisco, e.g., by deletion or downregulation of an enzyme in the C2 pathway prevents recycling of carbon back to the C3 cycle, while carbon accumulates at the point of blockage. Such mutations and transformations are lethal, unless the plant is rescued with high [CO_2], which will inhibit oxygenation of RuBP and entry of carbon into the C2 pathway.

Synthetic biology, however, is now opening new opportunities of altering C2 metabolism downstream of oxygenation (39). Kebeish et al. (58) produced plants in which chloroplastic glycolate can be converted directly to glycerate in the chloroplast by introducing five genes of the *E. coli* glycolate catabolic pathway into *Arabidopsis thaliana* chloroplasts. This created a bypass of the energy-intensive conversion that otherwise involves the cytosol, peroxisomes, and mitochondria. The bypass decreased the energy required to recycle glycoate back to the C3 pathway as glycerate and correspondingly increased photosynthesis and biomass production (58). This increase in photosynthetic rate is attributed to the increase in [CO_2] around Rubisco, since CO_2 is released in the chloroplast rather than the mitochondrion, and because the bypass decreased the ATP required by avoiding ammonium refixation. If this engineering could completely bypass the normal photorespiratory pathway, then it would raise maximum efficiency in C3 photosynthesis at 25 °C and current atmospheric [CO_2] by 13% (142).

Another approach to decrease photorespiratory loss is to engineer the C4 photosynthetic processes into C3 plants. As shown in **Figure 2**, C4 photosynthesis has significantly higher ε_c under current atmospheric [CO_2] than C3 photosynthesis, although this efficiency advantage will decline as atmospheric [CO_2] continues to rise, reaching parity by the end of this century, except at very high leaf temperatures (142). Is the conversion of C3 species to C4 photosynthetic metabolism a feasible goal? The polyphyletic evolution of the C4 pathway (111), characteristics of the C4 pathway in some cell types of C3 species (50), the C3 pattern of cell differentiation in some tissues of C4 species (60), and the switch between C3 and C4 photosynthesis in some plants (20, 126) all suggest that the transition from C3 to C4 species may be controlled by relatively few genes and that the mechanisms controlling the C3 and C4 photosynthesis differentiation are flexible (51). Efforts to transform C3 plants to express the C4 pathway enzymes to create C4 photosynthesis in a single cell (82, 119) have had very little success so far (76, 82). A single-cell type C4 might not be able to support a high ε_c, even though single-cell C4 photosynthesis in multicellular plants exists in nature, with PEPcase and Rubisco spatially separated by distance in elongated cells (129, 130). Indeed, these plants are slow growing and usually exist in hot, semiarid environments, consistent with the theoretical prediction that a single-cell C4 system would allow a positive carbon balance only under high light and drought conditions, but not with high efficiency of light use due to the increased ATP demand for CO_2 fixation caused by the CO_2 leakage and refixation (128). Considering that for all domesticated and high-yielding C4 crops, Kranz anatomy and the compartmentation of photosynthetic enzymes are closely linked, conversion of a C3 to a C4 crop will inevitably require the elucidation of the interaction between leaf morphology and photosynthesis. A full understanding of the factors determining and controlling the divergent development of mesophyll and bundle sheath cells in C4 leaves will be critical (49, 51).

Plant Architecture Modification

Plant architecture, such as dwarf stature in cereal crops, which has been associated with large improvements in harvest index (ε_p), contributed substantially to the success of the green

LAI: leaf area index; defined as the one-sided green leaf area per unit ground area in broadleaf canopies, or as the projected needle leaf area per unit ground area in needle canopies

revolution. Beyond maximizing harvest index, ideal crop plant architecture should minimize the highest photon flux density at an individual leaf level while at the same time maximize the total solar energy absorbed by the canopy per unit ground area. Ideally, the plant architecture and leaf biochemical properties should be designed so that the light levels match the photosynthetic capacity at different layers within the canopy (52, 90). It is not fully clear how well nitrogen distribution within a canopy tracks light distribution, although the photosynthetic apparatus show clear differentiation under different light conditions (121–123). What is the optimal plant architecture? When leaf area index (LAI) is lower than 2, canopies with horizontal leaves will enable the greatest interception of daily incident solar irradiance (73). For a canopy with a higher LAI, however, an ideal plant architecture will have a more vertical leaf angle at the top of the canopy that gradually decreases with depth into the canopy (72). This will ensure that light is spread more evenly through the canopy and that a high proportion of leaves will fall on the high-efficiency left-hand side of **Figure 3**. Theoretical analysis suggested that compared to a canopy with horizontal leaves, a canopy with a gradual decreased leaf angle can increase the daily intergral of carbon uptake as much as 40% on a sunny day at midlatitude (72). A season-long improvement of ε_c of ~20% could result from the avoidance of severe light saturation at the top of the canopy and severe light limitation within the canopy due to the improved canopy architecture.

Substantial progress has been made in elucidating the genetic basis of plant architecture determination (85, 112). In rice, the dwarf stature is caused by loss of function of brassinosteroid insensitive1 ortholog, OsBRI1 (85). One allele of OsBRI1, *d61–7*, confers important agronomic traits—semidwarf stature and erect leaves—and led to 30% more grain yield than wild type at high planting densities (85). Genes for the erect leaves likely exist in most current crops (107, 108); if so, searching for *d61–7* like alleles may be an important way forward in improving ε_c. Additionally, engineering or selecting plants with gradually decreasing leaf angles at different layers of canopy has the potential to further increase ε_c compared to either a uniform horizontal leaf angle or a uniform erect leaf angle (72). Theoretically, optimal architecture in plant monocultures will differ among species that vary in plant stature, leaf chlorophyll content, canopy albedo, and other species-specific features. Additionally, geographic location and time of the year matter because canopies with higher LAI and more erect leaves show the greatest advantage with high solar elevation, such as during summer or at low latitude (26).

Fine-Tuning Antenna Size

Engineering a smaller antenna size is another possible opportunity to optimize light energy distribution within a canopy to improve ε_c (80). Glick and Melis (42) estimated that the minimal number of chlorophyll molecules needed for the assembly of the photosystem core complexes was 37 chlorophyll *a* molecules for photosystem II and 95 chlorophyll *a* molecules for photosystem I, which is approximately 25% of the number of chlorophylls normally associated with a typical plant photosystem (78, 89, 135). In bright light, high chlorophyll content results in overexcitation, the induction of nonphotochemical quenching (NPQ; see below under Fine-Tuning Photoprotection), and greater potential for photodamage (69, 79, 87, 103). At the same time, a high chlorophyll concentration also directly deprives cells at lower layers of a canopy or even lower cells within the leaf of light, which lowers ε_c (78, 87, 88). Therefore, a smaller antenna size would not only mitigate efficiency losses associated with NPQ but also allow a greater transmittance of light into lower layers of the crop canopy or cells towards the lower surface of the leaf (81, 88), correspondingly increasing ε_c. Given these seeming advantages of a smaller antenna size and the scarcity of nitrogen in the field, why has a lower chlorophyll content not shown a selective advantage? It is perhaps because low chlorophyll may be a disadvantage

in a competitive natural habitat with other species; the circumstance in which most plant evolutionary selection has occurred. That is, if a plant intercepts light that it cannot itself use, it still disadvantages a competitor that might otherwise have received that light. The ideal for crop plants would seemingly be a minimum antenna size in upper canopy leaves, which increases as leaves become progressively more shaded. In theory, this could lead to increased ε_c in crop canopies (80), but even in a crop monoculture there are counteracting issues. Most notably, early in the season when canopy density is insufficient to absorb nearly all of the photosynthetically active radiation, a reduced antenna will be a disadvantage due to lower ε_i. The hypothesis that smaller antennae size may improve ε_c has not yet been tested rigorously in crops, but there does appear to be proof of concept. Mutants of soybean cultivar Clark Y_9 and Y_{11} contain about half the chlorophyll of the wild type, yet mature canopies of these low-chlorophyl mutants show a substantially higher daily integral of photosynthesis than do wild type (>30% in some cases) (100). On the other hand, a rice mutant (*Oryza sativa* L. var. Zhenhui 249Y) with a low content of chlorophyll *b* and a high chl *a/b* ratio of 4.7 (19) was reported to have slightly decreased *A*, but with improved resistance to photoinhibition (23), perhaps indicating that when canopy light penetration is improved by more erect leaf deployment, the benefits of reduced antennae size are less. The way in which the antenna is reduced may also be important to determining the extent to which ε_c is improved. For example, lowering chlorophyll content by dramatically reducing chlorophyll *b* synthesis, which was the case with both the soybean and rice mutants, might be expected to imbalance the antennae size (i.e., absorption cross-section) of photosystem I and photosystem II, create a respiratory drag (as LHCII will continue to be synthesized but cannot be stabilized in the absence of chlorophyll *b*), and reduce exciton transfer among photosystem II centers—all factors that would be expected to constrain improvements to ε_c. Downregulating chlorophyll synthesis early in the pathway might be a better option. The complicated interactions of lowering leaf chlorophyll on canopy light dynamics, which will vary with location and time of year, suggest an important role for modeling in optimizing chlorophyll content to improve ε_c.

LHCII: the light-harvesting complex; an array of protein-chlorophyll molecules within the thylakoid membrane containing both chlorophylls a and b, which transfer light energy to the photosystem II reaction center

Fine-Tuning Photoprotection

When there is light in excess of that used by photosynthesis, the normally efficient light-harvesting system of PS II switches to a photoprotective state in which there is thermal dissipation of the potentially harmful excess energy (66). This photoprotective heat dissipation is measured as and often called nonphotochemical quenching (NPQ) (1, 28, 53, 95) referring to the fact that this thermal dissipation of chlorophyll-excited states competes with photosystem II fluorescence emission as well as with photochemistrty. Dissipating more energy as heat instead of driving primary charge separation decreases the quantum yield of PS II (92). The downregulation of efficiency in PS II drives a commensurate quenching in PSI, in this case due to quenching by elevated amounts of P_{700}^+ (95). Together the lowered efficiencies of the photosystems drive corresponding decreases in Φ_{CO_2} and in the convexity (θ) of the nonrectangular hyperbolic response of *A* to light (Equation 3) and decreases in efficiency at low light as depicted in **Figure 3**. At high light, decrease in Φ_{CO_2} itself has minimal impact on carbon gain, while the increased thermal energy dissipation protects the photosynthetic apparatus against photooxidative damage. On the other hand, the decrease in θ coupled to a decrease in Φ_{CO_2} is significant in the context of ε_c because it extends the influence of a decrease in Φ_{CO_2} to much higher light levels. For example, at A_{sat} of 25 μmol m^{-2} s^{-1}, decreasing Φ_{CO_2} from a normal value of 0.055 by 50% will result in only a 2% decrease in *A* under full sunlight. However, if this 50% decrease in Φ_{CO_2} is coupled with a 10% decrease in θ (from 0.095 to 0.0855), then *A* at full sunlight will decrease by

NPQ: nonphotochemical quenching of chlorophyll fluorescence due to the thermal dissipation of chlorophyll excited states, which competes with photosystem II fluorescence emission as well as with photochemistry

A_c': integrated daily canopy carbon uptake

D1: a protein of the photosystem II reaction center involved in charge separation and vulnerable to oxidative damage, resulting in a high repair turnover

PsbS: a protein of photosystem II that is involved in nonphotochemical quenching (NPQ) and heat dissipation of excess absorbed energy

26% (69). The coupled decrease of θ and Φ_{CO_2} is commonly encountered in the field (94), indicating the importance of NPQ in suppressing daily canopy carbon gain in the field even under high light. Under low light conditions, low Φ_{CO_2} and θ strongly limit A until they revert to their dark-adapted values, restoring the high-efficiency state. Light in plant canopies continually fluctuates, resulting in corresponding fluctuations of Φ_{CO_2} and θ. Given that the recovery of Φ_{CO_2} and θ from the photoprotected state to the high-efficiency state is sluggish in comparison to the rate of light fluctuations, NPQ inevitably leads to a substantial decreased canopy CO_2 uptake (143).

What is the cost of this delayed recovery to potential CO_2 uptake by a canopy in the field? Answering this question is experimentally challenging because of the difficulty of obtaining detailed measurements of the heterogeneous light environments inside the canopy. To overcome this issue, a reverse ray-tracing algorithm was used for predicting light dynamics of randomly selected individual points in a model canopy to describe the discontinuity and heterogeneity of light flux within the canopy (143). The predicted light dynamics were combined with empirical equations simulating the dynamics of the light-dependent decrease and recovery of Φ_{CO_2} and θ, and their effects on the integrated daily canopy carbon uptake (A_c'). The simulation predicts that the inability of leaves to rapidly recover efficiency upon a decrease in solar radiation causes average losses in daily canopy carbon gain at typical temperatures for temperate crops on the order of 15% due just to the continually changing sun-leaf geometry within a canopy over the course of a day, which results in sudden decreases in photon flux that are not met with immediate recoveries of Φ_{CO_2} and θ. These losses are greater at low temperatures at which recovery is slower (143).

If excess light cannot be dissipated safely, photodamage can occur and lead to oxidative damage to photosystem II, especially to D1 protein (69), which in itself would lower photosynthetic efficiency and would require repair and replacement of the protein before efficiency could be restored. The detailed energetic cost of photodamage, repair, and protective mechanisms has not been analyzed thoroughly; such costs are possibly smaller than the lost carbon uptake due to photoprotection since not many proteins are involved (69). This suggests that plants with increased capacity of photoprotection and repair will gain competitive advantage in high-light stress conditions. Are there such plants? Algae associated with the coral *Stylophora pistillata* can withstand 1.5x full sunlight without evidence of loss of maximum photosynthetic efficiency or photoinhibition, showing that photoprotection and the associated loss of efficiency are possibly not intrinsic requirements of the photosynthetic apparatus (33).

Can photoprotection be engineered to decrease losses in ε_c? Overexpressing betacarotene hydroxylase in *Arabidopsis thaliana*, which controls the biosynthesis of the xanthophylls cycle carotenoids, changed the rate of formation and relaxation of NPQ, though the final amplitude of NPQ was unaltered (55). In addition, the kinetics of NPQ correlate with the deep oxidation state of the xanthophyll cycle pool and not the amount of zeaxanthin, which suggests that zeaxanthin and violaxanthin antagonistically regulate the switch between the light harvesting and photoprotective modes of the light-harvesting system (55). This further suggests that fine-tuning of the xanthophyll cycle pool size might be a feasible approach to engineer optimal NPQ kinetics. Because the crystal structure of LHCII shows a single xanthophyll cycle carotenoid per monomer, it is somewhat puzzling how the over synthesis of xanthophyll cycle carotenoids acts to affect NPQ. Along similar lines, the overexpression of PsbS induces enhanced NPQ saturating at 5 PsbS/D1 (93), whereas the wild-type titer is a single PsbS/D1, again raising the question of how the extra copies interact to impact NPQ. Genetic variations within a single species or among species in susceptibility to photoinhibition, either by different decreases of Φ_{CO_2}

or by different rates of recovery of Φ_{CO_2} after photoinhibition (69, 102, 131), are another resource that can be used to identify and then engineer optimal NPQ kinetics.

Perspectives

The central challenge to improving photosynthetic efficiency is knowing how alterations made to the photosynthetic process at the level of the chloroplast will scale, because it is the impact on the integral of seasonal canopy photosynthesis, not the instantaneous rate of chloroplast or single leaf photosynthesis, that is related to biomass production and yield. In addition, photosynthesis is strongly influenced by external environmental factors as well as co-occurring internal processes such as respiration, nitrogen metabolism, and water transport (e.g., 6, 61). These considerations emphasize that selection of changes to the photosynthetic process intended to improve biomass production and crop yield must take into account a complex matrix of interacting elements. Using experimental approaches to test the impacts of individual engineering options for different crops under different conditions on canopy photosynthesis is clearly unrealistic. Developing systems models of photosynthesis—and eventually plant primary metabolism and plant growth and development—that can be combined with optimization algorithms to evaluate impacts on photosynthetic efficiency of large numbers of virtual genetic and trangenic manipulations in multiple combinations holds the greatest promise for improving photosynthetic efficiency. Indeed, the emergent efforts to use this approach reviewed above have already identified highly plausible targets for substantial improvements.

Meeting the increase in agricultural demand during this century is predicted to require a doubling of global production, although this projection assumes "business as usual" (116). Since the middle of the twentieth century, 95% of the production gains have come from yield increases, with the exception of Africa where 40% of the gains have come from expanding cultivated land. Currently, there is on the order of 1600 Mha under cultivation globally (37). Overall, the world has limited capacity to sustainably expand cropland; indeed, it is shrinking in many developed countries. Thus meeting future increases in demand will have to come from a near doubling of productivity on a land area basis. While important gains in productivity should be possible through reducing stress-induced and postharvest losses, and while some further improvement in interception efficiency (ε_i) and partitioning efficiency (ε_p) may also be possible, particularly in less developed crop species, a large contribution will have to come from improved photosynthetic conversion efficiency (ε_c), for which we estimate that at least a 50% improvement will be required to double global production. Combining systems modeling with modern breeding and transgenic technologies holds greatest promise to meet this grand challenge. Such an integrated modeling framework will also be critical to a synthetic biology research platform to design new pathways, such as improved CO_2 fixation and photorespiratory pathways (58), or new genetic regulatory networks (11) to improve photosynthetic efficiency.

The task of improving ε_c is therefore not a distant challenge but is already upon us, given that even when these improvements are achieved it may take an additional 10–20 years to bring such innovations to farms in commercial cultivars at adequate scale. In this context, it seems valuable to group the various alterations that have been discussed here by our best estimate of their relative time horizon and to identify the most important technical and/or scientific hurdles that must be overcome in order to be realized (**Table 2**). The time scenarios given here are the estimates of time to production of advantaged germplasm that could be incorporated into breeding programs. It is our contention that implementation of the four alterations to the photosynthetic process in the Near-term category of **Table 2** is limited primarily by the will to invest sufficiently to

Table 2 Timeline for improving photosynthetic efficiency

Time horizon	Change to be made	[a]Increase in ε_c (%)	Major obstacle(s) to implementation
Long-term[b]	Rubisco with dramatically decreased oxygenase activity	30	Determining which molecular features of Rubisco control specificity
	Increase mesophyll conductance	20	Determining which physiological factors control mesophyll conductance
	Conversion of C3 to C4	30	Identifying suite of genes that control morphological and biochemical conversion
Mid-term[c]	Increased rate of recovery from photoprotective state	15	Determining combination of components in PSII photoprotective pathway to be altered
	Introduction of Rubisco with increased carboxylation rate	25	Developing efficient transformation technologies
Near-term[d]	Photorespiration bypass	13	Maximizing bypass flux; introducing into crop plants
	Improved canopy structure	30	Identifying genetic variability
	Rebalancing of RuBP regeneration rate with increased carboxylation	30	Demonstrating proof of concept experiments in crop plants; developing efficient transformation technologies
	Optimize canopy chlorophyll content	30	Developing optimization models; determining metabolically most efficient mode of reducing chlorophyll content

[a]Percent increase in the daily integral of carbon uptake estimated for a sunny day at midlatitudes.

[b]Theoretical basis for what change to make to affect the increase is missing. Not enough is known to determine if answers can be bought.

[c]Important science regarding what components to change to affect the increase is missing. With substantial focused investment, possible in 20-year time frame.

[d]The basic science about what needs to be done is in place and the hurdles for implementation are technical. With adequate investment, possible in 10-year time frame.

make it happen; i.e., the solutions to the implementation hurdles could "be bought". This is perhaps also the case for the table's Mid-term goal of transferring C4 (high-k^c_c) Rubisco into the chloroplasts of C3 plants. The theory establishing the benefit of the alteration is well developed, but the technical obstacles to transforming both genomes, i.e., in ensuring proper import, posttranslational processing and assembly, silencing of native genes, and efficient interaction with regulatory partners (e.g., Rubisco activase), need to be overcome. Nevertheless, the solutions to implementation hurdles seem very plausible in a 20-year or shorter timeframe with sufficient investment. The same may be true for accelerating the rate of relaxation of photoprotection to restore fully efficient photosynthesis.

The Long-term category of **Table 2** includes proposed changes about which there exists too little science to judge feasibility; i.e., we don't know if the solutions can be bought. The molecular features of the Rubisco holoenzyme that control discrimination between oxygen and carbon dioxide are unknown, and it may be that the reaction mechanism of Rubisco precludes the possibility of engineering any significant decrease in oxygenation activity. In our view, the goal of converting C3 crops to C4 photosynthetic metabolism belongs in this Long-term category. Important science needed to judge feasibility remains critical; namely, discovering the genetic basis for Kranz anatomy and developmental compartmentation of the processes of C4 photosynthesis, which is still largely unknown. Another goal that remains long term is the engineering necessary to increase mesophyll conductance to CO_2, since critical information about the physiological and physical factors affecting mesophyll conductance, required to judge feasibility, is missing.

SUMMARY POINTS

1. While important gains in productivity should be possible through reducing stress-induced and postharvest losses, we estimate that at least a 50% improvement in photosynthetic conversion efficiency will also be critical to meet the doubled global productivity of grain crops that will likely be needed over this century.
2. Improving photosynthetic conversion efficiency will require a systems approach that is informed by coupled models able to correlate a change made in the chloroplast to yield in the field and that implements a full suite of tools including breeding, gene transfer, and synthetic biology in bringing about the designed alteration to photosynthesis.
3. Several changes to the photosynthetic process have been identified that are well supported by theory to increase canopy photosynthesis and production. For some, implementation is limited by technical issues that can be overcome by sufficient investment, whereas in other cases too little of the science has been undertaken to identify what needs to be altered to effect an increase in yield.

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Errata

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