



ANNUAL
REVIEWS **Further**

Click [here](#) to view this article's online features:

- Download figures as PPT slides
- Navigate linked references
- Download citations
- Explore related articles
- Search keywords

The Costs of Photorespiration to Food Production Now and in the Future

Berkley J. Walker,^{1,2} Andy VanLoocke,⁴
Carl J. Bernacchi,^{1,2,3} and Donald R. Ort^{1,2,3,*}

¹Global Change and Photosynthesis Research Unit, US Department of Agriculture Agricultural Research Service (USDA/ARS), Urbana, Illinois 61801; email: d-ort@illinois.edu

²Carl R. Woese Institute for Genomic Biology and ³Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801

⁴Department of Agronomy, Iowa State University, Ames, Iowa 50011

Annu. Rev. Plant Biol. 2016. 67:107–29

First published online as a Review in Advance on February 8, 2016

The *Annual Review of Plant Biology* is online at plant.annualreviews.org

This article's doi:
10.1146/annurev-arplant-043015-111709

Copyright © 2016 by Annual Reviews.
All rights reserved

*Corresponding author

Keywords

climate change, food security, modeling

Abstract

Photorespiration is essential for C₃ plants but operates at the massive expense of fixed carbon dioxide and energy. Photorespiration is initiated when the initial enzyme of photosynthesis, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), reacts with oxygen instead of carbon dioxide and produces a toxic compound that is then recycled by photorespiration. Photorespiration can be modeled at the canopy and regional scales to determine its cost under current and future atmospheres. A regional-scale model reveals that photorespiration currently decreases US soybean and wheat yields by 36% and 20%, respectively, and a 5% decrease in the losses due to photorespiration would be worth approximately \$500 million annually in the United States. Furthermore, photorespiration will continue to impact yield under future climates despite increases in carbon dioxide, with models suggesting a 12–55% improvement in gross photosynthesis in the absence of photorespiration, even under climate change scenarios predicting the largest increases in atmospheric carbon dioxide concentration. Although photorespiration is tied to other important metabolic functions, the benefit of improving its efficiency appears to outweigh any potential secondary disadvantages.

Contents

INTRODUCTION	108
THE RATES AND ENERGETICS OF PHOTORESPIRATION	109
Biochemical Models of Leaf Photosynthesis	109
The Costs of Photorespiration	111
THE RESPONSE OF PHOTORESPIRATION TO THE ENVIRONMENT	113
The Response of Photorespiration to Carbon Dioxide	113
The Response of Photorespiration to Temperature	115
CANOPY-SCALE MODELS OF PHOTORESPIRATION	116
THE FUTURE OF PHOTORESPIRATION	116
What Future Conditions Can We Expect?	116
A Mechanistic Leaf Photosynthesis Model to Predict Rates of Photorespiration ...	117
A Multilayer Canopy Model of Photorespiration	117
The Impact of Future Climates on Photorespiration Predicted	
from Multilayer Canopy Modeling	117
The Impact of Temperature on Carbon Dioxide Conductances	120
The Impact of Photorespiration on Current and Future Yields	
at Regional Scales	120
PHOTORESPIRATION AND NITRATE ASSIMILATION	124
DOES PHOTORESPIRATION HAVE OTHER ESSENTIAL	
METABOLIC ROLES?	125

INTRODUCTION

Out of a current world population of 7 billion, there are almost 800 million who do not have enough food to lead a productive life (27). Population growth, increasing global affluence, and the expanding bioeconomy all require increased agricultural productivity, perhaps by as much as 60–120% over 2005 levels (3, 75). The problem of insufficient food seems unlikely to improve, because the current rate of crop productivity improvement is not sufficient to meet the need to double food production by 2050, as estimated by the Food and Agricultural Organization of the United Nations (62). The prospect that historically highly successful breeding and agronomic strategies will not be enough to keep pace with the acceleration of growth in agricultural demand indicates that additional approaches are needed to mitigate current and future hunger. Although there are many promising approaches to improving crop yield, increasing photosynthetic efficiency offers a unique solution that could be applied to a wide range of staple food crops (49, 58).

The efficiency of the photosynthetic conversion of light energy into biomass is surprisingly low compared with technologies such as photovoltaic solar cells (11). The commonly used silicon-based solar cell converts 11% of the sun's energy into electricity, with some multijunction-type cells converting close to 40% (33). By comparison, photosynthetic conversion efficiency reaches a theoretical maximum of 4.6% in plants that use C_3 photosynthesis, and the highest realized solar energy conversion efficiencies in the field are less than half this value (88). Although this comparison is admittedly biased—photosynthetic energy is stored as stable carbohydrates, and the entire photosynthetic apparatus is self-assembled with significantly less inputs than are required for solar cell production—this comparison raises an interesting question: Why is the core conversion efficiency of photosynthesis so low?

Photosynthetic conversion efficiency:

the percentage of total light energy intercepted by a leaf that is present in biomass produced by photosynthesis

C_3 photosynthesis:

one of three metabolic pathways for carbon fixation in photosynthesis, along with C_4 and crassulacean acid metabolism; its defining first step is catalyzed by Rubisco converting CO_2 and RuBP into 3-phosphoglycerate

The theoretical photosynthetic conversion efficiency is limited by a variety of factors, including the fraction of solar radiation that is photosynthetically active; the fact that photosynthesis is driven by the energy of red photons despite absorbing mostly higher-energy photons; and, for C_3 plants, photorespiration. Photorespiration is estimated to reduce the theoretically attainable efficiency of gross C_3 photosynthesis by 48% (assuming a carbon dioxide concentration of 380 ppm and a temperature of 30°C) (88). However, the actual costs of photorespiration in agricultural fields in different localities have never been systematically evaluated, nor have the counteracting effects of increasing atmospheric carbon dioxide concentrations and increasing growing-season temperatures on photorespiration and their projected effects on C_3 crop yield been quantitatively assessed. The response of photorespiration to climate depends on a host of factors, ranging from the biochemical to the ecophysiological. In this review, we examine the most relevant drivers for photorespiration, starting with fundamental enzyme kinetics and ending with regional-scale modeling. We examine these drivers to determine the impact of photorespiration on crop yields under current and future atmospheres. The costs of photorespiration can then be weighed against possible mitigation strategies to determine whether such efforts are worth the associated time and expense.

THE RATES AND ENERGETICS OF PHOTORESPIRATION

Photorespiration begins after the reaction of ribulose-1,5-bisphosphate (RuBP) with oxygen instead of carbon dioxide, which is catalyzed by the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary carboxylating enzyme of C_3 photosynthesis. This reaction produces one molecule of 3-phosphoglycerate and one molecule of phosphoglycolate, the latter of which is converted to glycolate, which is toxic in the chloroplast and represents a waste of fixed carbon. Photorespiration detoxifies glycolate and recycles 75% of the carbon into phosphoglycerate, which can reenter the C_3 cycle. This recycling releases carbon dioxide and requires ATP and NADPH, thereby significantly reducing the efficiency of C_3 photosynthesis. Rates of oxygenation and therefore of photorespiration are governed by the reaction kinetics of Rubisco and ambient atmospheric conditions. The atmosphere has a complex relationship with photorespiration because Rubisco loses specificity for carbon dioxide relative to oxygen as temperatures increase, thus increasing the rates of oxygenation, whereas oxygenation decreases as carbon dioxide increases. Because the specific pathway and genes of photorespiration have been covered extensively in previous reviews, we highlight only the steps most important to understanding what governs the net rates and energy demands of photorespiration (32, 56, 68) (**Figure 1**).

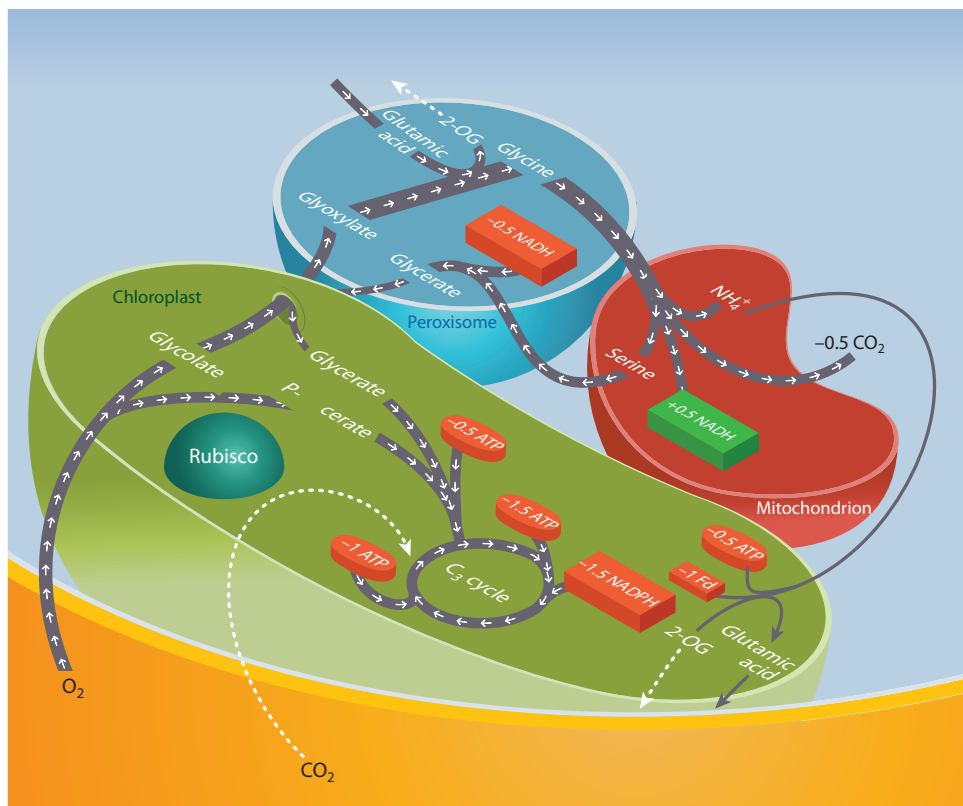
Biochemical Models of Leaf Photosynthesis

Rates of net carbon dioxide assimilation and energy use can be modeled with remarkable accuracy based on the reaction kinetics of Rubisco for either carbon dioxide or oxygen. The reaction with oxygen to produce phosphoglycolate is the first step of photorespiration, which ultimately converts one phosphoglycolate molecule into 0.5 phosphoglycerate molecules at the cost of 0.5 carbon dioxide molecules liberated and 2 NADH equivalents and 3.5 ATP consumed (**Figure 1**). The Rubisco kinetics have been combined with the stoichiometry of photorespiratory carbon dioxide release per Rubisco oxygenation and energy demand to produce a powerful model of leaf carbon dioxide exchange (76, 79; reviewed in 7). This model represents net carbon dioxide assimilation (A) according to

$$A = V_c - 0.5V_o - R_d, \quad (1)$$

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco): the enzyme that carries out the first step of CO_2 fixation; it also catalyzes the reaction with oxygen and initiates photorespiration

Glycolate: the toxic molecule that is formed as a result of the oxygenation of RuBP catalyzed by Rubisco and subsequently recycled by photorespiration



Erratum

Figure 1

The biochemical pathway of photorespiration along with the energy and gas stoichiometry. Photorespiration is initiated when oxygen is fixed by Rubisco to form P-glycerate and P-glycolate from RuBP. The P-glycerate enters C₃ carbon fixation, but the P-glycolate is dephosphorylated to produce glycolate. The glycolate is transported to the peroxisome, where it is converted to glycine using an amino group from glutamate. Ultimately, this glycine is converted to serine, but only one serine is produced for every two glycines, so the remaining stoichiometry is fractional. The glycine is transported to the mitochondria, where it is deaminated and decarboxylated before being combined with another glycine to form serine. This reaction releases 0.5 mol CO₂ and 0.5 NADH per Rubisco oxygenation. The serine is transported into the peroxisome, where it is reduced to glycerate by 0.5 NADH. This glycerate is phosphorylated in the chloroplast at the cost of 0.5 ATP and can then enter the C₃ cycle. The conversion of the 1.5 P-glycerates produced following Rubisco oxygenation consumes an additional 2.5 ATP and 1.5 NADPH. An additional 0.5 ATP and 1 Fd (equivalent to 0.5 NADH) is consumed to refix the deaminated amino group back to glutamate in the chloroplast. In total, each Rubisco oxygenation consumes 3.5 ATP and 2 NADH equivalents. Abbreviations: Fd, ferredoxin; 2-OG, 2-oxoglutarate; P-glycerate, phosphoglycerate; P-glycolate, phosphoglycolate; RuBP, ribulose-1,5-bisphosphate; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase.

where R_d represents the carbon dioxide release from mitochondrial day respiration and V_c and V_o represent the rates of Rubisco carboxylation and oxygenation, respectively. Because this model is mechanistic in basis, it can be applied to leaves exposed to changing temperature and carbon dioxide, making it an ideal tool for quantitatively understanding the impact of climate on plant productivity.

This model also enables the calculation of rates of Rubisco oxygenation (V_o) and carboxylation (V_c) in a given atmosphere from measurements of net carbon dioxide gas exchange. V_o and V_c help

quantify the absolute and relative rates of photorespiration under a given condition. For example, photorespiration is argued to play an essential role in photoprotection when stomata are closed during drought by providing an alternative sink for electrons when sufficient atmospheric carbon dioxide is unable to diffuse into the chloroplast (57, 84). Although photorespiration's role as an alternative electron sink has been established in many situations, it is still unclear how large of a role it plays in protecting the photosynthetic apparatus from overreduction during drought and when it does so. The electron sink size of photorespiration can be surmised quickly from leaf-level gas exchange under a given condition. Modeled rates of photorespiration can also aid comparisons among different species under different environmental stress conditions.

Modeling of V_o and V_c uses the basic equation of leaf carbon dioxide gas exchange and Rubisco specificity for carboxylation relative to oxygenation to determine rates of A (67, 79) (Equation 1). A key relationship between V_c and A is represented by

$$V_c = \frac{A + R_d}{1 - (\Gamma^*/C_c)}, \quad (2)$$

where Γ^* represents the carbon dioxide photocompensation point and C_c represents the concentration of carbon dioxide at the chloroplast. Equation 2 can be combined with Equation 1 to solve for V_o according to

$$V_o = \frac{A + R_d}{(C_c/2\Gamma^*) - 0.5}. \quad (3)$$

This modeling requires an assumption of conductance between the intercellular air space and the chloroplast (i.e., the mesophyll conductance, g_m) to calculate C_c from the measured intercellular carbon dioxide concentration (C_i) according to

$$C_c = C_i - \frac{A}{g_m}. \quad (4)$$

Assumptions concerning the diffusion path of carbon dioxide are important not only for determining the concentration of carbon dioxide in the chloroplast, but also for understanding the fate of photorespired carbon. Although carbon dioxide transfer to the chloroplast has generally been considered to be a single diffusive path, as shown by Equation 4, evidence from photosynthetic isotope discrimination and subambient carbon dioxide concentrations has suggested that photorespiratory release from the mitochondria could justify a more complicated model (17, 71, 72, 77) (**Figure 2**). This extended model partitions photorespired carbon loss between reentry into the chloroplast and release into the intercellular air space. It is still not certain whether such an extended model is necessary to interpret net carbon dioxide exchange around ambient carbon dioxide levels, and a recent advance in interpreting measurements of Γ^* indicates that the simple model presented in Equation 4 may explain most of the carbon dioxide transfer to the chloroplast, at least in soybean and wheat (81). Because the present model of mesophyll conductance appears to adequately describe leaf-level gas exchange, it seems reasonable to continue using it for higher-scale modeling until additional evidence is presented to the contrary.

The Costs of Photorespiration

The biochemistry of photorespiration indicates that it negatively affects net carbon dioxide assimilation by losing fixed carbon and consuming energy in recycling glycolate, but by how much does photorespiration reduce photosynthesis under field growth conditions? The cost of photorespiration depends on its rate. Early attempts to measure photorespiratory loss directly from carbon dioxide efflux had experimental limitations, but fortunately rates of oxygenation can be reasonably inferred using leaf models of photosynthesis, as outlined above (67). This modeling revealed that

Carbon dioxide photocompensation point (Γ^*): the CO_2 concentration at which net CO_2 fixation offsets CO_2 loss from photorespiration; this is an essential parameter in leaf models of photosynthesis

Mesophyll conductance: CO_2 transfer conductance from the intercellular air spaces of the leaf into the chloroplast

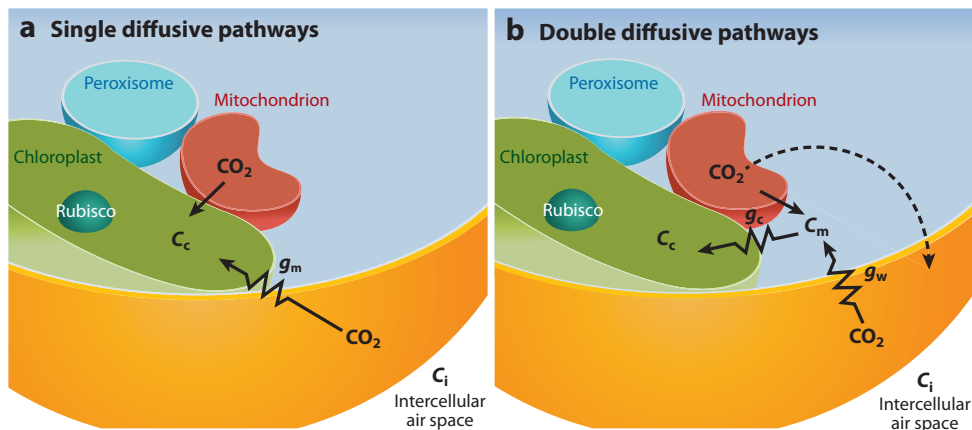


Figure 2

Single and multiple diffusive pathways for CO₂ in a plant cell. The path of CO₂ diffusion through the cell can have a significant impact on net CO₂ gas exchange, particularly when considering the fate of CO₂ released during photorespiration. CO₂ diffusion is important for determining the concentration of CO₂ around Rubisco in the chloroplast (C_c). This concentration is in turn important because it drives the activity of Rubisco, and Rubisco kinetics underpin biochemical models of leaf photosynthesis. C_c must be determined from the CO₂ concentration in the intercellular air space (C_i) because this is what is determined during measurements of leaf gas exchange. Determining C_c from C_i requires considering the diffusive pathway of CO₂ to the chloroplast stroma. In commonly used models of leaf CO₂ exchange, only one diffusive conductance is used (mesophyll conductance, g_m), and the CO₂ release from photorespiration implicitly occurs in the same compartment as Rubisco (panel *a*). This assumption creates a simpler model for gas exchange but does not take into account that photorespired CO₂ may leak directly from the mitochondria to the intercellular air space. This possibility is considered in recent models that include two diffusive conductances: one across the cell wall (g_w) and one across the chloroplast (g_c) (panel *b*). These models better represent leaf anatomy, but whether the increased completeness is worth the added complexity is still under debate. Abbreviation: Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase. Figure adapted from Reference 77; see also References 17, 71, and 72.

at 25°C and under the then-current ambient carbon dioxide concentration of 350 ppm, photorespiration loses carbon at ~26% the rate of net carbon dioxide assimilation. This corresponds to ~2 Rubisco oxygenations for every 5 carboxylations.

This proportion of carboxylations and oxygenations largely determines the total energy demand of an illuminated leaf because the activity of Rubisco dominates metabolism in terms of gross flux. As outlined above and in **Figure 1**, every Rubisco oxygenation consumes 3.5 ATP and 2 NADH equivalents to process the phosphoglycolate and phosphoglycerate into the Rubisco substrate RuBP. Alternatively, Rubisco carboxylation consumes 3 ATP and 2 NADH equivalents to regenerate the RuBP needed to maintain Rubisco substrate (26). The stoichiometry outlined above can thus be used to approximate the total energy demand for photorespiration. This stoichiometry dictates that there are 5 carboxylations for every 7 Rubisco reactions, requiring a total of 15 ATP and 10 NADH equivalents. These 5 carboxylations are accompanied by 2 oxygenations, which require a total of 7 ATP and 4 NADH equivalents. When the total ATP and NADH equivalent demands are tallied for photorespiration and carbon dioxide fixation, this suggests that photorespiration consumes 32% of total ATP and 28% of total NADH equivalents in an illuminated C₃ leaf under current atmospheric conditions at 25°C, although this will vary extensively based on changing environmental conditions, particularly temperature and the relative concentrations of oxygen and carbon dioxide surrounding Rubisco. The partitioning of

energy between photosynthesis and photorespiration occurs in very predictable ways, allowing for the partitioning of electrons, NADPH, and ATP to be modeled under a wide range of environmental conditions. A Mathematica (85) model visualizing the partitioning of energy into photosynthesis and photorespiration is available as a **Supplemental Material** CDF file download (follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>) and at the Wolfram Demonstrations website (<http://demonstrations.wolfram.com/FluxesAndEnergeticsOfPhotosynthesisAndPhotorespiration>).

This massive cost of photorespiration in terms of carbon dioxide and energy use highlights the importance of understanding how it is affected by environmental conditions and the expected consequences of continuing climate change. Modeling may help to determine whether the costs of photorespiration will increase or decrease under future climates and the extent to which changes might occur, and may help to identify and quantify the major uncertainties in the response of photorespiration to the changing environment.

The large cost of photorespiration has also justified major efforts to increase net photosynthesis by reengineering photorespiration. One approach to minimize photorespiratory loss is to reduce the number of initial Rubisco oxygenation reactions. This is being attempted both by optimizing the Rubisco reaction kinetics and by increasing the carbon dioxide concentration around Rubisco by introducing C₄ photosynthesis in rice (36, 83). Another approach is to reengineer photorespiration itself by introducing novel metabolic pathways that use less energy and release photorespired carbon dioxide in the chloroplast, where it can be refixed more efficiently by Rubisco (40, 50, 51, 60). Despite reports of improvements to photosynthetic performance, these photorespiratory bypasses have not been thoroughly validated or tested under field conditions, and recent modeling work indicates that their expected benefit may be limited (86).

Given the amount of time it will take to reengineer crop plants to reduce the costs of photorespiration as well as the rising atmospheric concentrations of carbon dioxide, which mitigate photorespiration, is doing so even worth the investment of time and resources? The answer depends on a variety of factors, including actual future carbon dioxide concentrations and temperatures. This question also must be addressed in a way that accounts for field-scale processes, which are highly dynamic and can include a multitude of microenvironments within a single canopy that affect photorespiration. Fortunately, biochemical models of leaf photosynthesis can be placed in a complex environmental context to estimate both the current and future costs of photorespiration at field and regional levels.

THE RESPONSE OF PHOTORESPIRATION TO THE ENVIRONMENT

To quantify and scale the response of photorespiration to field conditions, it is important to quantify how plants respond to rapidly changing environmental factors. Three interconnected environmental factors that affect photorespiration are carbon dioxide concentration, temperature, and water relations. The following sections examine carbon dioxide concentration and temperature, with water relations discussed throughout in the context of these two factors.

The Response of Photorespiration to Carbon Dioxide

Rates of photorespiration respond to changes to the carbon dioxide concentration in the chloroplast around Rubisco (C_c), which can be quite dynamic during a day and across a season and which has been rising since the beginning of the Industrial Revolution owing to increases in atmospheric carbon dioxide. Although photorespiration is also sensitive to changes of oxygen concentration, these concentrations change only over geological time, whereas carbon dioxide concentrations

C₄ photosynthesis: a form of photosynthesis in which CO₂ is concentrated around Rubisco, which then enables more efficient C₃ photosynthesis by drastically minimizing oxygenation and subsequent photorespiration

Photorespiratory bypasses: novel introduced pathways to detoxify glycolate that require less energy or have some other advantage over native photorespiration

Boundary layer:

the layer of still air surrounding a leaf that forms a resistance to CO₂ and water flux into and out of the intercellular air space

Stomatal conductance:

the resistance to CO₂ diffusion from the leaf surface to the intercellular air space imposed by diffusion through the stomata

fluctuate rapidly (10, 70). Assuming oxygen concentrations are constant, changes in C_c directly affect the ratio of V_c to V_o , resulting in direct changes in A (Equations 2 and 3). Because C_c is defined as the carbon dioxide concentration in the chloroplast, determining the substrate availability for photosynthesis requires knowing the diffusion path of carbon dioxide from the atmosphere to inside the chloroplast.

There are three major barriers to carbon dioxide flux from the air outside the leaf into the chloroplast: (a) the boundary layer of air that surrounds the leaf, (b) stomatal conductance, and (c) mesophyll conductance. Because the boundary layer of air around the leaf is relatively still compared with the turbulent mixing that dominates the rest of the atmosphere, carbon dioxide must diffuse through this boundary (18). Carbon dioxide diffusion through an unmixed boundary layer of air is much slower than transport through air that is mixed, resulting in lower conductances for carbon dioxide through the boundary layer. The carbon dioxide conductance is lower when the boundary layer is thick, and its thickness depends primarily on wind speed and leaf morphology. The boundary layer is an important limitation in canopy photosynthesis but has often been ignored in leaf-level models used to determine carbon dioxide exchange between the leaf and the atmosphere (20). The boundary layer can decrease the carbon dioxide available to Rubisco by as much as 50% and thereby increase photorespiration while decreasing Rubisco carboxylation, resulting in a 30% decrease in net photosynthesis (16).

Once carbon dioxide has reached the leaf surface, it must then enter the leaf via the stomata. Stomatal conductance depends on a host of physiological and environmental factors and imposes significant limitations on carbon dioxide transport into the leaf intercellular air space and subsequent rates of photosynthesis (2). When plants are grown under elevated carbon dioxide, stomatal conductance decreases, somewhat buffering the expected increases in net photosynthesis by impeding carbon dioxide transfer into the intercellular air space. However, despite this response, the limitation imposed by the stomata is generally lower in elevated carbon dioxide (8). Nevertheless, a consequence of this carbon dioxide-induced reduction in stomatal conductance, concomitant with an increase in A , is improved water use efficiency (1, 2, 45). Stomatal conductance is similarly sensitive to short-term changes (minutes) in carbon dioxide, as demonstrated by numerous empirical observations (6, 52). The sensitivity of stomatal conductance does not appear to be linked directly to photorespiration, because conductances are unaffected when photorespiration is altered by the oxygen concentration under a range of carbon dioxide concentrations and light intensities (15). This suggests that future changes in photorespiration brought about by environmental changes or transgenic manipulations would probably not affect the relationship between stomatal conductance and carbon dioxide concentration in the short term, but the prospects for longer-term acclimation are unclear because the modeling cannot represent longer-term acclimations that have not yet been characterized physiologically.

Mesophyll conductance represents the third resistance to carbon dioxide diffusion to the chloroplast, increasing photorespiration by lowering C_c compared with a hypothetical situation in which the mesophyll conductances were infinite (30). Whereas an increased stomatal conductance also increases carbon dioxide delivery to the chloroplast and subsequent photosynthesis, an increased stomatal conductance does so at the cost of increased water loss through the stomata. This trade-off between photosynthesis and water loss is evident, for example, across eight wheat cultivars in which higher yield and photosynthetic rates correlated with increased stomatal conductance and water loss (29). Water loss through the stomata is driven by the large difference in water potential between a dry atmosphere and the intercellular air space, which is generally assumed to be saturated. Water loss is thought not to occur to the same degree across the cell wall, because there would be no water potential gradient between saturated air in the intercellular air space and within the cell. Therefore, increases in mesophyll conductance may be able to increase carbon

dioxide delivery without resulting in increased water loss, thereby increasing water use efficiency (30).

The carbon dioxide concentration also has a direct effect on Rubisco function and quantity. Rubisco content and expression in major C_3 crops decreases when plants are grown under elevated carbon dioxide (8, 23, 54, 63). Additionally, the carbon dioxide level can affect how much of the Rubisco is active: The activation state of Rubisco decreased with carbon dioxide concentration in sweet potato (19). The activation state also decreased with temperature above the thermal optimum at each measurement of carbon dioxide concentration in these experiments, likely because of the limited thermotolerance of Rubisco activase, a vital chaperone for Rubisco activity (66). Despite this relationship between Rubisco activation state and temperature, it is still debated whether this results directly in the decrease in photosynthetic rate at elevated temperature or leads to other limitations becoming more dominant (65, 66). Changes in Rubisco quantity or activation state affect absolute rates of V_o but have only a slight impact on the V_o/V_c ratio under identical atmospheric carbon dioxide concentrations. These small differences in V_o/V_c arise not from direct changes to the reaction kinetics of Rubisco, but rather because different rates of A produce different drawdowns between the atmospheric carbon dioxide concentration, C_i , and C_c but do not significantly affect oxygen concentrations.

The Response of Photorespiration to Temperature

Temperature affects photorespiration by directly changing the kinetics and activity of Rubisco. As temperature increases, the Rubisco specificity for carbon dioxide relative to oxygen decreases (4, 9, 80), resulting in a higher V_o/V_c ratio for a given carbon dioxide concentration. Additionally, the maximum rate of Rubisco oxygenation and carboxylation ($V_{o\max}$ and $V_{c\max}$, respectively) increases with temperature, meaning that both the absolute rates of $V_{o\max}$ and $V_{c\max}$ and the $V_{o\max}/V_{c\max}$ ratio increase with temperature until Rubisco or Rubisco activase becomes thermosensitive.

Stomatal conductance is also sensitive to the vapor pressure deficit of water between the leaf and the atmosphere. Because this deficit increases exponentially with temperature, stomatal conductance is also sensitive to temperature. Such decreases of stomatal conductance further increase the impact of temperature on photorespiration. The relationship between stomatal conductance and temperature through changes in vapor pressure deficit is often quantified through a semi-empirical relationship (6). This relationship also considers leaf water balance in modeling the impact of environmental factors on stomatal conductance, and predicts that increasing temperature and decreasing water availability serve to decrease stomatal conductance. A reduced stomatal conductance impedes carbon dioxide transfer to Rubisco, thereby increasing V_o and V_o/V_c .

Mesophyll conductance has a less well-defined and validated response to temperature. Mesophyll conductance was originally shown to increase with temperature in tobacco (9), but subsequent studies found that the temperature response of mesophyll conductance is not consistent among species (78, 80). These experiments suggest that mesophyll conductance generally increases with temperature in warm-adapted plants but remains fairly constant in more temperate-adapted species. This means that mesophyll conductance becomes less of an impedance to carbon dioxide transfer and subsequent rates of photosynthesis with increasing temperature in some species as compared with others. Of the agronomically important species described so far, mesophyll conductance increases with temperature in rice (2% per degree Celsius increase between 20°C and 35°C) and soybean (3% per degree Celsius) but remains fairly constant in wheat (<1% per degree Celsius). Earth system models of photosynthesis have recently reemphasized the importance of mesophyll conductance in leaf models of photosynthesis (69). Although there is a growing recognition of the need to consider mesophyll conductance in models of photosynthesis, it remains difficult

Vapor pressure deficit: the difference in water partial pressures between the atmosphere and the intercellular air space that drives water loss in leaves

MLCan: a multilayer canopy model that integrates above- and belowground ecophysiology and biochemistry to simulate photosynthetic CO₂ assimilation

Intergovernmental Panel on Climate Change (IPCC): a scientific organization created to assess “the scientific, technical and socio-economic information relevant to understanding the scientific basis of the risk of human-induced climate change” (37)

to measure, and there are few data broadly characterizing the temperature responses of different species and the acclimation of mesophyll conductance to growth carbon dioxide and temperature.

CANOPY-SCALE MODELS OF PHOTORESPIRATION

The mechanistic leaf model of photosynthesis discussed above can accurately predict the rates of photosynthesis and photorespiration for a given set of environmental conditions. However, numerous challenges are associated with trying to predict the environmental conditions that exist within a complex plant canopy. Light, carbon dioxide, temperature, vapor pressure deficit, and a range of other micrometeorological variables change from the air space immediately above a plant canopy to each point within a plant canopy (39). As most of these variables influence photorespiration directly or indirectly, the accuracy of canopy models for predicting rates of photorespiration is limited to the biophysical models that account for within-canopy gradients of these meteorological factors. The most recent canopy and ecosystem models are based on well-established biophysical relationships between plants and their environment. For the simulations described below, we used a well-validated multilayer canopy model, MLCan, to scale photorespiration to the canopy (24, 25). We then scaled photorespiration regionally using an alternative well-validated model to estimate current and future potential costs of photorespiration to the most important C₃ agronomic species grown in the United States. We consider these costs in terms of both the energy required for photorespiration (ATP and NADH equivalents) and the actual monetary costs, measured as a function of yield loss.

THE FUTURE OF PHOTORESPIRATION

What Future Conditions Can We Expect?

The composition of trace gases in the atmosphere, most notably carbon dioxide, and concomitant changes in the atmosphere have already occurred and are expected to accelerate in the future owing to anthropogenic greenhouse gas emission (38). The future climate scenarios are based on a range of social and political predictions. We input the least and most aggressive climate change scenarios from the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (38) to determine the potential impact of atmospheric and climatic changes on photorespiration into leaf-, canopy-, and regional-scale models (**Table 1**). The most aggressive climate change scenario [representative concentration pathway (RCP) 8.5] has a mean prediction of a 600-ppm increase in carbon dioxide concentration accompanied by a 3.7°C increase in temperature by 2114, and the least aggressive scenario (RCP 2.6) has a mean prediction of a 50-ppm increase in carbon dioxide concentration accompanied by a 1.0°C increase in temperature by that same year. These two scenarios provide the upper and lower predictions, respectively, for potential changes in photorespiration.


Table 1 Current and future predictions of mean global CO₂ and temperatures according to the IPCC Fifth Assessment Report (38)

Scenario	Ambient CO ₂	Temperature increase	Average model temperature
Current conditions	400 ppm	0.0°C	22.4°C
RCP 2.6	450 ppm	1.0°C	23.4°C
RCP 8.5	1,000 ppm	3.7°C	26.1°C

RCP values are for the year 2114. Abbreviations: IPCC, Intergovernmental Panel on Climate Change; RCP, representative concentration pathway.

A Mechanistic Leaf Photosynthesis Model to Predict Rates of Photorespiration

The leaf photosynthesis model used for this review computes A as a function of photosynthetic carbon uptake, photorespiratory carbon loss, and respiratory carbon loss. This model is the backbone for most models of photosynthesis and productivity, ranging from the plant to the ecosystem and beyond. Even with a generic parameterization, it can reasonably predict net assimilation, making it a useful tool for demonstrating the potential energetic costs of photorespiration. As a way to demonstrate the role of atmospheric and climatic changes in net carbon assimilation and the partitioning of absorbed energy to photorespiration, we also developed a Mathematica-based tool (85) to allow direct manipulation of key environmental factors associated with leaf-level carbon assimilation (available as a **Supplemental Material** CDF file download and at the Wolfram Demonstrations website; <http://demonstrations.wolfram.com/ModelingLeafPhotosynthesisAndPhotorespirationInCurrentAndFut>). This demonstration illustrates one way that models in general can be packaged into an accessible format, a critical need as models play a growing role in understanding and scaling plant biology. More critically, it provides a direct way to understand how key environmental variables can drive significant changes in net carbon assimilation, which is important when considering the role that this leaf-level mechanistic model plays in predicting changes at the canopy and regional scales presented below.

 Supplemental Material

A Multilayer Canopy Model of Photorespiration

We used the IPCC-based climate change scenarios and field data from the Bondville, Illinois, AmeriFlux eddy covariance site measured during the 2002, 2004, and 2006 growing seasons (available from the AmeriFlux Database; <http://ameriflux.lbl.gov/data/download-data>) to parameterize a multilayer canopy-soil-root systems model (MLCan) (24). This model couples the biochemical descriptions of leaf photosynthesis with canopy- and soil-level environmental biophysics to enable a robust mechanistic understanding of field-scale processes (24). We applied this model to a canopy of soybean as a representative C_3 species in order to illustrate season-long and diurnal changes in photorespiration in response to the scenario-dependent changes in ambient carbon dioxide and temperature.

We made several minor amendments to MLCan to better focus on the impact of changes in carbon dioxide and temperature on photorespiration, and included a component to describe the effects of temperature on mesophyll conductance, given the recent demonstrations of the importance of these effects (69). We assumed that mesophyll conductance increased with temperature according to the tobacco temperature response (9). To remove the modeled impact of photorespiration on net photosynthesis, we changed the atmospheric oxygen concentration from 21% to 0%. The model, run with and without photorespiration, provided an approximation of how much photorespiration will affect net carbon dioxide assimilation and, by extension, final crop yield within the above-described IPCC scenarios. (For the model code, please contact the corresponding author.)

The Impact of Future Climates on Photorespiration Predicted from Multilayer Canopy Modeling

Parameterizing MLCan with three years of soybean field data produced a typical diurnal response of photosynthesis (**Figure 3a**). Integrating the diurnal response over the whole day resulted in a total diurnal assimilation at the current atmospheric carbon dioxide concentration and temperature of ~ 160 mmol CO_2 m^{-2} day^{-1} (**Figure 3a**). This integral of photosynthesis increased to 168 and 241 mmol CO_2 m^{-2} day^{-1} under the RCP 2.6 and 8.5 scenarios, respectively. These

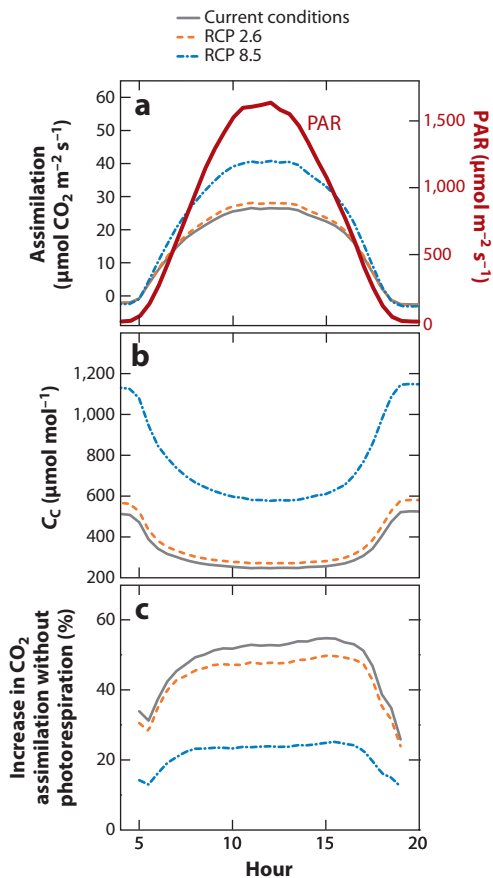


Figure 3

Current and future modeling of (a) diurnal net CO₂ assimilation and average PAR (red line), (b) diurnal chloroplastic CO₂ concentration (C_c), and (c) the percent increase of gross CO₂ assimilation predicted to occur with a complete suppression of Rubisco oxygenation, resulting in no photorespired CO₂ or energy consumption. Shown are averaged diurnal canopy-level responses from models parameterized with field data from Bondville, Illinois, during the 2002, 2004, and 2006 growing seasons, assuming CO₂ concentrations and temperatures under current conditions (400 ppm, no change in air temperature), IPCC scenario RCP 2.6 (450 ppm, +1°C), and IPCC scenario RCP 8.5 (1,000 ppm, +3.7°C). Abbreviations: IPCC, Intergovernmental Panel on Climate Change; PAR, photosynthetically available radiation; RCP, representative concentration pathway; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase.

modeled results suggest that the RCP 2.6 and 8.5 scenarios will result in a total stimulation of net photosynthesis by 5% and 50%, respectively. As photosynthetic rates increased from current conditions to the RCP 8.5 scenario, drawdown of chloroplastic carbon dioxide concentrations relative to the simulated atmospheric carbon dioxide concentration also increased (Figure 3b). This drawdown shows a diurnal trend that follows the availability of light energy provided by the sun (Figure 3a,b) and is exaggerated as photosynthetic rates increase.

Removing photorespiration from the model led to a substantial improvement in gross carbon dioxide assimilation that ranged from 12% to 55% depending on the time of day and climate change scenario (Figure 3c). This improvement was greatest when assuming current atmospheric conditions and least when assuming the aggressive changes predicted by RCP 8.5. The extent

of the improvement showed a diurnal trend as well, with the maximum benefit found during midday, when net photosynthesis is at its highest rate. This higher benefit arises from the increased photorespiration that results from the large drawdown in carbon dioxide in the chloroplast when plants are maximally photosynthetic and the ratio of carbon dioxide to oxygen is lowest. The largest net benefit of removing photorespiration was found under current climates, with an ~50% increase in net photosynthesis during peak photosynthetic rates (**Figure 3**). The benefit of fully suppressing photorespiration was only slightly decreased under RCP 2.6 (a 48% improvement) and was the least assuming RCP 8.5 (a 23% improvement). This demonstrates that even though future climates will progressively lessen the energy loss from photorespiration, it will continue to be an inefficient process in C_3 species.

The change in the energetic cost of photorespiration as atmospheric and climatic changes progress is further reflected in the amount of total cellular ATP and NADH equivalents consumed by photorespiration under each IPCC scenario. Under the current 400-ppm carbon dioxide concentration and the temperatures input from the model validation site, ~40% of ATP produced during peak canopy photosynthesis was consumed by photorespiration (**Figure 4a**). This percentage of ATP loss to photorespiration is larger than that inferred from the leaf-level gas exchange alone described above (32%), illustrating the importance of placing leaf-scale processes into an ecophysiological context to determine the impact on crop growth. The differences between rates

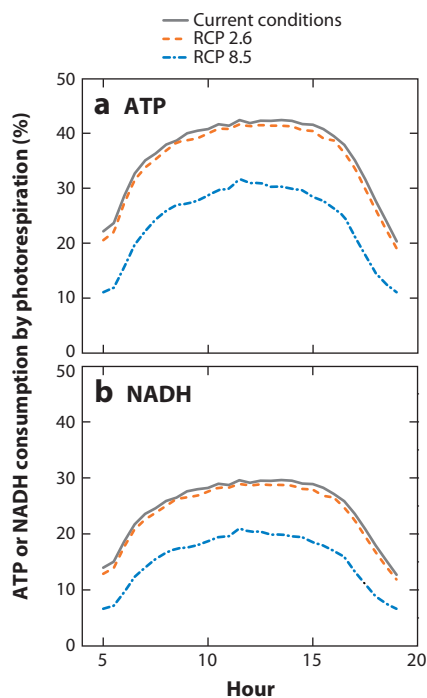


Figure 4

Current and future modeling of (a) diurnal ATP and (b) diurnal NADPH costs of photorespiration expressed as percentages of total demand. Shown are averaged diurnal responses from models parameterized with field data from Bondville, Illinois, during the 2002, 2004, and 2006 growing seasons, assuming CO_2 concentrations and temperatures under current conditions (400 ppm, no change in field temperature), IPCC scenario RCP 2.6 (450 ppm, $+1^\circ C$), and IPCC scenario RCP 8.5 (1,000 ppm, $+3.7^\circ C$). Abbreviations: IPCC, Intergovernmental Panel on Climate Change; RCP, representative concentration pathway.

**Agro-IBIS
(Integrated
BIosphere
Simulator,
agricultural version):**

a comprehensive model that integrates land and ecosystem processes and can be used to understand the impact of climate on crop yield

of simulated energy use in laboratory and field-scale experiments arise from the generally higher temperatures experienced in the field as well as decreased C_i driven by lower stomatal conductance under water-limiting conditions. The percentage of the ATP demand of photorespiration decreased only slightly with the assumptions of RCP 2.6, and even under the assumptions of RCP 8.5, photorespiration consumed ~30% of ATP produced. NADH-equivalent consumption was similarly affected, with ~30% of NADH-equivalent production supporting photorespiration under current conditions and the RCP 2.6 assumptions and ~20% under the RCP 8.5 assumptions. The massive photorespiratory demand for ATP and NADH equivalents in C_3 plants illustrates the scale of the energy requirement of photorespiration. The energy demand for photorespiration is high even under the most aggressive assumptions of increased carbon dioxide, in part because of the attendant increase in temperature, again indicating that photorespiration will continue to be an important process reducing photosynthetic efficiency in C_3 species for at least the next 100 years.


The Impact of Temperature on Carbon Dioxide Conductances

The multilayer canopy modeling also illustrates a notable interaction between temperature and carbon dioxide conductance through the stomata and mesophyll, which affects rates of photorespiration. Although stomatal conductance decreases with scenario temperature, mesophyll conductance increases (**Figure 5**). This means that stomatal limitations on photosynthesis should increase more with temperature than mesophyll limitations on photosynthesis. This trend will be prominent in warm-adapted crops such as rice and soybean, which show increases in mesophyll conductance with temperature, but will also occur in other crops even if mesophyll conductance remains constant with temperature (78). Additionally, decreases in stomatal conductance reduce water loss at a given temperature at the expense of carbon dioxide transfer to the intercellular air space, but changes in mesophyll conductance are not expected to have the same relationship with water loss (30). This means that, all other factors being the same, plants with a mesophyll conductance that increases with temperature should have a greater water use efficiency under warmer climates than plants in which mesophyll conductance does not change or decreases with increasing temperature.

The Impact of Photorespiration on Current and Future Yields at Regional Scales

Estimating current and future yields accurately from meteorological data and climate predictions involves many uncertainties and is an evolving science. However, even simple environmental factors—especially growing-season temperature—can account for much of the variation in crop yield (46–48). In this context, it is valuable to evaluate how photorespiration will affect future yields in light of the counteracting influences of rising temperature and rising carbon dioxide even while recognizing that other factors, such as water availability, would alter the quantitative outcome.

We conducted simulations in a process-based agroecosystem model, Agro-IBIS (Integrated BIosphere Simulator, agricultural version) (31, 44), with and without oxygen to estimate the impact of photorespiration on major C_3 crops in the United States (for a description of our Agro-IBIS simulation methodology, see the online **Supplemental Appendix**). Agro-IBIS simulates the biogeochemical cycles and biophysical processes associated with the production and management of most major US crops (42). Carbon and water exchange are simulated on an hourly time step based on a biophysical/biochemical approach that includes the C_3 and C_4 photosynthetic pathways and leaf physiology (20, 28) as well as canopy scaling (73, 74). Limitations are imposed on photosynthesis by modifying the carboxylation efficiency when the nitrogen availability is suboptimal (22, 43).

 **Supplemental Material**

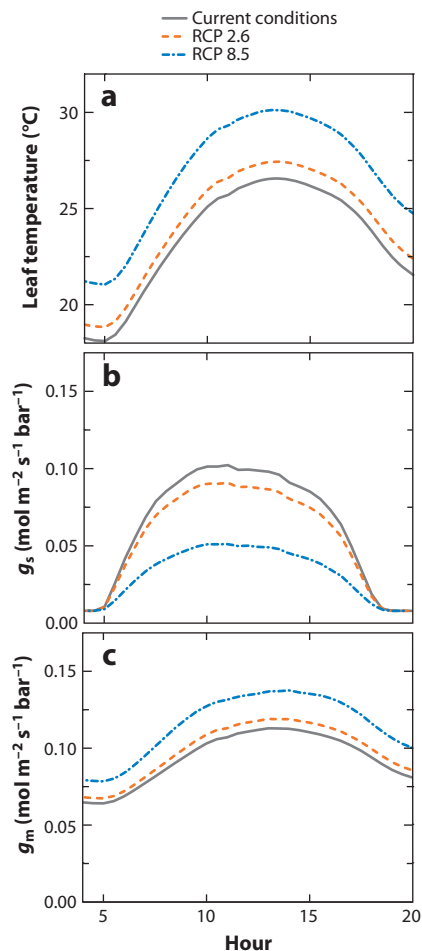


Figure 5

Current and future modeling of (a) diurnal canopy temperature, (b) diurnal stomatal conductance (g_s), and (c) diurnal mesophyll conductance (g_m). Shown are averaged diurnal responses from models parameterized with field data from Bondville, Illinois, during the 2002, 2004, and 2006 growing seasons, assuming CO_2 concentrations and temperatures under current conditions (400 ppm, no change in field temperature), IPCC scenario RCP 2.6 (450 ppm, $+1^\circ\text{C}$), and IPCC scenario RCP 8.5 (1,000 ppm, $+3.7^\circ\text{C}$). Abbreviations: IPCC, Intergovernmental Panel on Climate Change; RCP, representative concentration pathway.

This regional modeling reveals the cost of photorespiration to major midwestern US C_3 crops in terms of average yield and total production. Photorespiration decreased US soybean and wheat production by 36% and 20%, respectively, under current climates (**Table 2**). This decrease in production translates to a total loss of 148 trillion calories, or enough to meet the daily dietary requirements of an additional 203 million people for a year. The consequences of photorespiration are predicted to remain high under the IPCC climate change scenarios: Under RCP 2.6, photorespiration reduced total calories from soybean and wheat by 27% and 19%, respectively, and RCP 8.5 led to reductions of 16% and 8%, respectively. To isolate the effects of photorespiration and minimize agronomic factors such as soil fertility, we also conducted simulations assuming optimal nitrogen fertilizer application (i.e., no nitrogen limitation on photosynthetic capacity)

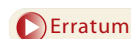


Table 2 Modeled production gain to eliminate photorespiration under current and future climates for the top US C₃ crops

Crop	With PR			Without PR		
	Current conditions	RCP 2.6	RCP 8.5	Current conditions	RCP 2.6	RCP 8.5
Average yield (bu/ac)						
Soybean	37.8	44.6	63.4	65.7	66.3	78.0
Wheat	39.1	42.8	60.0	48.8	52.7	65.3
Total production (Gbu)						
Soybean	2.35	2.71	3.78	3.70	3.74	4.50
Wheat	1.87	2.02	2.81	2.33	2.49	3.07
Total calories (TC)						
Soybean	211	243	339	332	335	404
Wheat	111	120	167	138	148	182
Total	322	363	506	470	483	586
Loss to PR	31%	25%	14%	NA		

Calculations are based on the expected increase in gross CO₂ assimilation if there were no O₂ fixation by Rubisco. Shown are the results using 100 years of climate input (from 1900 to 2000), giving the average yield in mean bushels per acre (bu/ac), the total production in billions of bushels (Gbu), and the total dietary calories produced in trillions of calories (TC). Additional abbreviations: NA, not applicable; PR, photorespiration; RCP, representative concentration pathway.

(**Figure 6**). Under these conditions, photorespiration may have a larger cost, especially in wheat, although that is predicted to be of diminishing importance under the RCP 2.6 and 8.5 scenarios.

The reduction in crop production caused by photorespiration was not constant across the major crop-producing areas of the United States (**Figure 6**). Photorespiration caused larger relative yield decreases in the warmer, southern portions of the US soybean production areas, with relative yield reductions of 50% or more (e.g., 40 as opposed to 80 bushels per acre), and smaller decreases in the higher-latitude portions (**Figure 6**). This pattern aligns well with the temperature dependence of Rubisco oxygenation versus carboxylation discussed above. This simulation also illustrates that the future impact of photorespiration is highly specific to region and atmospheric conditions. For example, under RCP 2.6, North Dakota has yield reductions due to photorespiration of 30–40%, whereas under RCP 8.5, this reduction is approximately 20%.

Although it is unrealistic to expect an engineering solution to entirely eliminate the wastes of photorespiration indicated above, the scale of these wastes indicates that even a marginal improvement could translate to significant gains in productivity and crop value. For example, if we assume that the efficiency of photorespiration could be improved in a way that reduces total loss by only 5%, the result would be an additional 68 million bushels of soybean and 23 million bushels of wheat annually under current atmospheric conditions. These additional bushels of soybean and wheat would have a value of almost \$540 million in international dollars, assuming 2012 global prices and production and the price elasticities of major commodity grain crops (53). Current work indicates that engineered photorespiratory pathways could lead to similar modest improvements to photosynthesis. For example, modeling indicates that a photorespiratory bypass utilizing the chloroplastic conversion of glycolate to glycerate could lead to an 8% increase in net carbon dioxide assimilation by reducing the energy demands of photorespiration and increasing internal refixation of released carbon dioxide (86).

These simulations are intended to give mechanistically based estimates of the cost of photorespiration over a major crop production area. In doing so, we made some simplifying assumptions about agronomic factors (e.g., in the case of **Figure 6**, we assumed that cultivar selection did not

International dollar:

a hypothetical currency with the same purchasing power as a US dollar between the years 1990 and 2000; it is commonly used to benchmark global economic impacts

Price elasticity:

a measure used in economics to quantify how much the price of something will change with a given change in supply

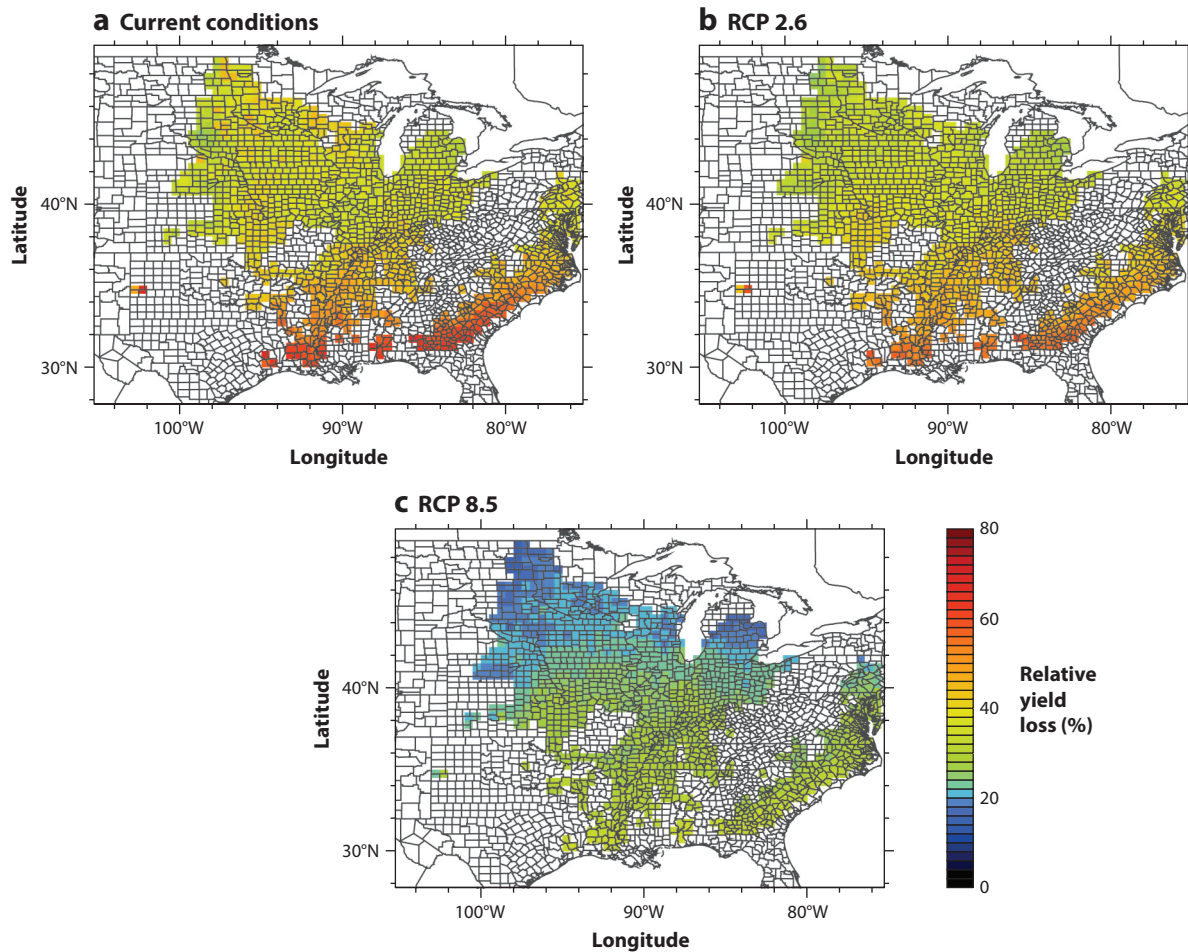


Figure 6

Simulated soybean relative yield loss [(no photorespiration – photorespiration)/photorespiration] caused by photorespiration assuming CO_2 concentrations and temperatures under (a) current conditions (400 ppm, no change to field temperature), (b) IPCC scenario RCP 2.6 (450 ppm, +1°C), and (c) IPCC scenario RCP 8.5 (1,000 ppm, +3.7°C). Abbreviations: IPCC, Intergovernmental Panel on Climate Change; RCP, representative concentration pathway.

change with changes in growing-season growing degree days and that fertilizer application was optimal). We also made physiologically relevant assumptions about acclimation of photosynthesis (5), with no acclimation assumed in either set of simulations. Process-based models such as the one used here are also not yet as capable of simulating stresses on sink-related processes (i.e., seed abortion) as they are in terms of source processes (i.e., photosynthesis). An additional set of simulations using the conditions imposed in an outdoor, free-air carbon dioxide and temperature enrichment (550 ppm and 3.5°C, respectively) predicted an ~15% increase in US soybean yields, whereas observational studies indicated that a reduction in yield is more likely under these conditions owing to the effects of temperature on other, primarily reproductive, processes (e.g., 64). Nevertheless, regardless of actual future yields, the proportion of photorespiratory loss should be similar because factors such as seed abortion do not affect the ratio of photorespiration to photosynthesis.

PHOTORESPIRATION AND NITRATE ASSIMILATION

The regional-scale simulations presented above predict a decrease in photosynthesis when nitrogen fertilization is suboptimal. The problem of nitrogen availability may increase as photorespiration decreases in future climates because photorespiration and nitrate assimilation appear to be related at the leaf level. This relationship is most firmly established in *Arabidopsis* and wheat, where increases in carbon dioxide or decreases in oxygen decrease rates of both nitrate uptake and assimilation (13, 61). This decrease in nitrate assimilation may affect growth and explain why many C₃ crops and tree species grow more slowly under elevated carbon dioxide when supplied only with nitrate (12). The inhibition of nitrate assimilation by elevated carbon dioxide is not seen in maize, which lacks significant rates of photorespiration owing to the C₄ carbon-concentrating mechanisms, further suggesting that this relationship is related to photorespiration and not a secondary effect of carbon dioxide or oxygen (21). These observations at the plant level suggest that rates of nitrate assimilation are correlated with the ratio of photorespiration to carbon dioxide assimilation.

Recently, evidence for this relationship between photorespiration and nitrate assimilation was observed on a field scale from archived samples of wheat grown under free-air carbon dioxide enrichment (14). These experiments revealed that wheat grown under high carbon dioxide levels has increased amounts of free nitrate and decreased ratios of organic ¹⁵N and ¹⁵NO₃⁻. Both of these observations can be explained by decreased nitrate assimilation relative to uptake when photorespiration is reduced. Interestingly, the percentage of total nitrogen is not significantly affected by this apparent reduction in nitrate assimilation.

The mechanism linking nitrate assimilation to photorespiration is unknown. Studies have suggested that nitrate reduction in the cytosol is limited by reductant availability and that photorespiration provides reductant for nitrate assimilation by shuttling malate through the cytosol (32, 34). Similarly, nitrate reduction could serve to consume excess electrons when the ATP:NADPH demand from the primary metabolism is higher than what is produced from the light reactions of photosynthesis (82). Such energy balancing between supply and demand is important to prevent photoinhibition of the light reactions, although other means of balancing the ATP/NADPH production ratio, such as photosystem I cyclic electron transport and the water-water cycle, are well established (41, 59, 87).

Irrespective of the mechanism, studies have suggested that the primary relationship between nitrate assimilation and photorespiration explains the growth acclimation of C₃ plants to high carbon dioxide (14, 32). This acclimation results in long-term growth and reduced photosynthetic rates relative to the initial response to elevated carbon dioxide. Under this hypothesis, reductions in nitrate assimilation inhibit plant growth and photosynthesis owing to the decrease of available organic nitrogen. It has been established that nitrate assimilation decreases with photorespiration, but whether this decrease is large enough to affect growth under field conditions remains unclear. Although the reduction in nitrate assimilation in wheat was a pronounced 20–56% under elevated carbon dioxide concentrations (720 ppm, compared with 380 ppm in the baseline conditions), these measurements were performed under low-nitrogen hydroponic conditions that were presumably optimized to measure the response of nitrate assimilation to carbon dioxide and oxygen (13). It is not clear that wheat grown in the field experienced a similar decrease in nitrate assimilation, especially because total nitrogen concentrations were unaffected by an elevated carbon dioxide concentration (548 ppm, compared with 363 ppm in the baseline conditions) (14). This area of research clearly merits additional work because of its potential relationship to primary plant growth and seed nutritional content under changing climates and atmospheres (55).

DOES PHOTORESPIRATION HAVE OTHER ESSENTIAL METABOLIC ROLES?

The relationship between photorespiration and nitrate assimilation and the role of photorespiration in photoprotection have led some to question whether photorespiration is necessary for healthy plant growth. In addition to playing a role in nitrate assimilation and photoprotection, photorespiration is likely the primary source of one-carbon metabolites (such as formate) in C_3 plants (35). Although photorespiration appears to have been co-opted into several important aspects of primary metabolism, it does not appear to be essential. For example, C_4 plants are able to both assimilate nitrate and maintain photoprotection in field conditions of high light and variable water availability. Aside from experiments under low oxygen, the necessity of photorespiration in a C_3 plant could only be probed by the generation of a Rubisco with identical kinetics for carbon dioxide and no affinity for oxygen, as suggested previously (84). Although such a Rubisco would doubtlessly improve our understanding of the importance of photorespiration to photoprotection and nitrate assimilation, the modeling presented here indicates that the larger benefit would be the increase in food supply. This highlights the conclusion that although photorespiration may be co-opted into other aspects of metabolism, the process as a whole consumes many plant resources, and the benefits of efforts to optimize it will likely outweigh the disadvantages.

SUMMARY POINTS

1. Photorespiration is an essential component of plant primary metabolism, but it consumes energy and releases carbon dioxide as it detoxifies glycolate following oxygenation by Rubisco.
2. Photorespiration increases with temperature and decreases with carbon dioxide in a way that can be quantified by mechanistic models.
3. These models reveal that photorespiration is currently decreasing US production of soybean and wheat by 148 trillion calories per year.
4. Additionally, a 5% decrease in photorespiratory loss would be worth almost \$540 million in international dollars per year.
5. As the atmospheric carbon dioxide concentration and temperature increase with the continued progression of climate change, crop yield losses due to photorespiration will decrease but remain significant.
6. Although photorespiration is intimately intertwined with plant metabolism, the benefits of engineering strategies to improve the efficiency of photorespiration likely outweigh any disadvantages.

 Erratum

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Ainsworth EA, Long SP. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2 . *New Phytol.* 165:351–72

2. Ainsworth EA, Rogers A. 2007. The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant Cell Environ.* 30:258–70
3. Alexandratos N, Bruinsma J. 2012. *World agriculture towards 2030/2050: the 2012 revision*. ESA Work. Pap. 12-03, Agric. Dev. Econ. Div., Food Agric. Organ. UN, Rome
4. Badger MR, Collatz GJ. 1978. Studies on the kinetic mechanism of ribulose-1,5-bisphosphate carboxylase and oxygenase reactions, with particular reference to the effect of temperature on kinetic parameters. *Carnegie Inst. Wash. Yearb.* 76:355–61
5. Bagley J, Rosenthal DM, Ruiz-Vera UM, Siebers MH, Kumar P, et al. 2015. The influence of photosynthetic acclimation to rising CO₂ and warmer temperatures on leaf and canopy photosynthesis models. *Glob. Biogeochem. Cycles* 29:194–206
6. Ball JT, Woodrow I, Berry J. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In *Progress in Photosynthesis Research*, Vol. 4: *Proceedings of the VIIth International Congress on Photosynthesis Providence, Rhode Island, USA, August 10–15, 1986*, ed. J Biggins, pp. 221–24. Dordrecht, Neth.: Springer
7. Bernacchi CJ, Bagley JE, Serbin SP, Ruiz-Vera UM, Rosenthal DM, VanLoocke A. 2013. Modelling C₃ photosynthesis from the chloroplast to the ecosystem. *Plant Cell Environ.* 36:1641–57
8. Bernacchi CJ, Morgan PB, Ort DR, Long SP. 2005. The growth of soybean under free air CO₂ enrichment (FACE) stimulates photosynthesis while decreasing in vivo Rubisco capacity. *Planta* 220:434–46
9. Bernacchi CJ, Portis AR, Nakano H, von Caemmerer S, Long SP. 2002. Temperature response of mesophyll conductance. Implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthesis in vivo. *Plant Physiol.* 130:1992–98
10. Berner RA. 1999. Atmospheric oxygen over Phanerozoic time. *PNAS* 96:10955–57
11. Blankenship RE, Tiede DM, Barber J, Brudvig GW, Fleming G, et al. 2011. Comparing photosynthetic and photovoltaic efficiencies and recognizing the potential for improvement. *Science* 332:805–9
12. Bloom AJ, Asensio JSR, Randall L, Rachmilevitch S, Cousins AB, Carlisle EA. 2011. CO₂ enrichment inhibits shoot nitrate assimilation in C₃ but not C₄ plants and slows growth under nitrate in C₃ plants. *Ecology* 93:355–67
13. Bloom AJ, Burger M, Asensio JSR, Cousins AB. 2010. Carbon dioxide enrichment inhibits nitrate assimilation in wheat and *Arabidopsis*. *Science* 328:899–903
14. Bloom AJ, Burger M, Kimball BA, Pinter PJ Jr. 2014. Nitrate assimilation is inhibited by elevated CO₂ in field-grown wheat. *Nat. Clim. Change* 4:477–80
15. Buckley TN, Mott KA, Farquhar GD. 2003. A hydromechanical and biochemical model of stomatal conductance. *Plant Cell Environ.* 26:1767–85
16. Bunce JA. 1988. Effects of boundary layer conductance on substomatal pressures of carbon dioxide. *Plant Cell Environ.* 11:205–8
17. Busch FA, Sage TL, Cousins AB, Sage RF. 2013. C₃ plants enhance rates of photosynthesis by reassimilating photorespired and respired CO₂. *Plant Cell Environ.* 36:200–12
18. Campbell G, Norman J. 1998. *Introduction to Environmental Biophysics*. New York: Springer
19. Cen Y-P, Sage RF. 2005. The regulation of Rubisco activity in response to variation in temperature and atmospheric CO₂ partial pressure in sweet potato. *Plant Physiol.* 139:979–90
20. Collatz GJ, Ball JT, Griwet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. For. Meteorol.* 54:107–36
21. Cousins A, Bloom A. 2003. Influence of elevated CO₂ and nitrogen nutrition on photosynthesis and nitrate photo-assimilation in maize (*Zea mays* L.). *Plant Cell Environ.* 26:1525–30
22. Donner SD, Kucharik CJ. 2003. Evaluating the impacts of land management and climate variability on crop production and nitrate export across the Upper Mississippi Basin. *Glob. Biogeochem. Cycles* 17:1085
23. Drake BG, González-Meler MA, Long SP. 1997. More efficient plants: a consequence of rising atmospheric CO₂? *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 48:609–39
24. Drewry DT, Kumar P, Long S, Bernacchi CJ, Liang XZ, Sivapalan M. 2010. Ecohydrological responses of dense canopies to environmental variability: 1. Interplay between vertical structure and photosynthetic pathway. *J. Geophys. Res. Biogeosci.* 115:G04022

25. Drewry DT, Kumar P, Long S, Bernacchi CJ, Liang XZ, Sivapalan M. 2010. Ecohydrological responses of dense canopies to environmental variability: 2. Role of acclimation under elevated CO₂. *J. Geophys. Res. Biogeosci.* 115:G001341
26. Edwards GE, Walker DA. 1983. *C₃, C₄: Mechanisms, and Cellular and Environmental Regulation, of Photosynthesis*. Oxford, UK: Blackwell Sci.
27. FAO (Food Agric. Organ. UN), IFAD (Int. Fund Agric. Dev.), WFP (World Food Programme). 2015. *The state of food insecurity in the world 2015: strengthening the enabling environment for food security and nutrition*. Rep., FAO, Rome
28. Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78–90
29. Fischer RA, Rees D, Sayre KD, Lu Z-M, Condon AG, Saavedra AL. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Sci.* 38:1467–75
30. Flexas J, Ribas-Carbó M, Diaz-Espejo A, Galmés J, Medrano H. 2008. Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant Cell Environ.* 31:602–21
31. Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, et al. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Glob. Biogeochem. Cycles* 10:603–28
32. Foyer CH, Bloom AJ, Queval G, Noctor G. 2009. Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. *Annu. Rev. Plant Biol.* 60:455–84
33. Green MA, Emery K, Hishikawa Y, Warta W, Dunlop ED. 2015. Solar cell efficiency tables (version 45). *Prog. Photovolt. Res. Appl.* 23:1–9
34. Hanning I, Heldt HW. 1993. On the function of mitochondrial metabolism during photosynthesis in spinach (*Spinacia oleracea* L.) leaves: partitioning between respiration and export of redox equivalents and precursors for nitrate assimilation products. *Plant Physiol.* 103:1147–54
35. Hanson A, Roje S. 2001. One-carbon metabolism in higher plants. *Annu. Rev. Plant Biol.* 52:119–37
36. Hibberd JM, Sheehy JE, Langdale JA. 2008. Using C₄ photosynthesis to increase the yield of rice—rationale and feasibility. *Curr. Opin. Plant Biol.* 11:228–31
37. IPCC (Intergov. Panel Clim. Change). 2013. *Principles governing IPCC work*. <https://www.ipcc.ch/pdf/ipcc-principles/ipcc-principles.pdf>
38. IPCC (Intergov. Panel Clim. Change). 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switz.: IPCC
39. Jones HG. 2013. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*. Cambridge, UK: Cambridge Univ. Press
40. Kebeish R, Niessen M, Thiruveedhi K, Bari R, Hirsch H-J, et al. 2007. Chloroplastic photorespiratory bypass increases photosynthesis and biomass production in *Arabidopsis thaliana*. *Nat. Biotechnol.* 25:593–99
41. Kramer DM, Evans JR. 2011. The importance of energy balance in improving photosynthetic productivity. *Plant Physiol.* 155:70–78
42. Kucharik CJ. 2003. Evaluation of a process-based agro-ecosystem model (Agro-IBIS) across the U.S. Corn Belt: simulations of the interannual variability in maize yield. *Earth Interact.* 7:1–33
43. Kucharik CJ, Brye KR. 2003. Integrated BIOSphere Simulator (IBIS) yield and nitrate loss predictions for Wisconsin maize receiving varied amounts of nitrogen fertilizer. *J. Environ. Qual.* 32:247–68
44. Kucharik CJ, Foley JA, Delire C, Fisher VA, Coe MT, et al. 2000. Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. *Glob. Biogeochem. Cycles* 14:795–825
45. Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR. 2009. Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J. Exp. Bot.* 60:2859–76
46. Lobell DB, Asner GP. 2003. Climate and management contributions to recent trends in U.S. agricultural yields. *Science* 299:1032
47. Lobell DB, Burke MB. 2008. Why are agricultural impacts of climate change so uncertain? The importance of temperature relative to precipitation. *Environ. Res. Lett.* 3:034007
48. Lobell DB, Field CB. 2007. Global scale climate–crop yield relationships and the impacts of recent warming. *Environ. Res. Lett.* 2:014002

49. Long SP, Ainsworth EA, Leakey ADB, Nösberger J, Ort DR. 2006. Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* 312:1918–21
50. Maier A, Fahnenstich H, von Caemmerer S, Engqvist MK, Weber APM, et al. 2012. Glycolate oxidation in *A. thaliana* chloroplasts improves biomass production. *Front. Plant Sci.* 3:38
51. Maurino VG, Peterhansel C. 2010. Photorespiration: current status and approaches for metabolic engineering. *Curr. Opin. Plant Biol.* 13:248–55
52. Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, et al. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Glob. Change Biol.* 17:2134–44
53. Michael JR, Wolfram S. 2013. Identifying supply and demand elasticities of agricultural commodities: implications for the US ethanol mandate. *Am. Econ. Rev.* 103:2265–95
54. Moore BD, Cheng SH, Rice J, Seemann JR. 1998. Sucrose cycling, Rubisco expression, and prediction of photosynthetic acclimation to elevated atmospheric CO₂. *Plant Cell Environ.* 21:905–15
55. Myers SS, Zanobetti A, Kloog I, Huybers P, Leakey ADB, et al. 2014. Increasing CO₂ threatens human nutrition. *Nature* 510:139–42
56. Ogren WL. 1984. Photorespiration: pathways, regulation, and modification. *Annu. Rev. Plant Physiol.* 35:415–42
57. Ort DR, Baker NR. 2002. A photoprotective role for O₂ as an alternative electron sink in photosynthesis? *Curr. Opin. Plant Biol.* 5:193–98
58. Ort DR, Merchant SS, Alric J, Barkan A, Blankenship RE, et al. 2015. Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *PNAS* 112:8529–36
59. Peltier G, Aro E-M, Shikanai T. 2016. NDH-1 and NDH-2 plastoquinone reductases in oxygenic photosynthesis. *Annu. Rev. Plant Biol.* 67:55–80
60. Peterhansel C, Blume C, Offermann S. 2013. Photorespiratory bypasses: How can they work? *J. Exp. Bot.* 64:709–15
61. Rachmilevitch S, Cousins AB, Bloom AJ. 2004. Nitrate assimilation in plant shoots depends on photorespiration. *PNAS* 101:11506–10
62. Ray DK, Mueller ND, West PC, Foley JA. 2013. Yield trends are insufficient to double global crop production by 2050. *PLOS ONE* 8:e66428
63. Rogers A, Humphries SW. 2000. A mechanistic evaluation of photosynthetic acclimation at elevated CO₂. *Glob. Change Biol.* 6:1005–11
64. Ruiz-Vera UM, Siebers M, Gray SB, Drag DW, Rosenthal DM, et al. 2013. Global warming can negate the expected CO₂ stimulation in photosynthesis and productivity for soybean grown in the midwestern United States. *Plant Physiol.* 162:410–23
65. Sage RF, Way DA, Kubien DS. 2008. Rubisco, Rubisco activase, and global climate change. *J. Exp. Bot.* 59:1581–95
66. Salvucci ME, Crafts-Brandner SJ. 2004. Mechanism for deactivation of Rubisco under moderate heat stress. *Physiol. Plant.* 122:513–19
67. Sharkey TD. 1988. Estimating the rate of photorespiration in leaves. *Physiol. Plant.* 73:147–52
68. Somerville C. 1986. Analysis of photosynthesis with mutants of higher plants and algae. *Annu. Rev. Plant Physiol.* 37:467–506
69. Sun Y, Gu L, Dickinson RE, Norby RJ, Pallardy SG, Hoffman FM. 2014. Impact of mesophyll diffusion on estimated global land CO₂ fertilization. *PNAS* 111:15774–79
70. Tans P. 2015. *Trends in atmospheric carbon dioxide*. Glob. Monit. Div., Earth Syst. Res. Lab., Natl. Ocean. Atmos. Adm., Boulder, CO. <http://www.esrl.noaa.gov/gmd/ccgg/trends>
71. Tholen D, Ethier G, Genty B, Pepin S, Zhu X-G. 2012. Variable mesophyll conductance revisited: theoretical background and experimental implications. *Plant Cell Environ.* 35:2087–103
72. Tholen D, Zhu X-G. 2011. The mechanistic basis of internal conductance: a theoretical analysis of mesophyll cell photosynthesis and CO₂ diffusion. *Plant Physiol.* 156:90–105
73. Thompson SL, Pollard D. 1995. A global climate model (GENESIS) with a land-surface transfer scheme (LSX). Part I: present climate simulation. *J. Clim.* 8:732–61
74. Thompson SL, Pollard D. 1995. A global climate model (GENESIS) with a land-surface transfer scheme (LSX). Part II: CO₂ sensitivity. *J. Clim.* 8:1104–21

75. Tilman D, Balzer C, Hill J, Befort BL. 2011. Global food demand and the sustainable intensification of agriculture. *PNAS* 108:20260–64
76. von Caemmerer S. 2000. *Biochemical Models of Leaf Photosynthesis*. Collingwood, Aust.: CSIRO
77. von Caemmerer S. 2013. Steady-state models of photosynthesis. *Plant Cell Environ.* 36:1617–30
78. von Caemmerer S, Evans JR. 2015. Temperature responses of mesophyll conductance differ greatly between species. *Plant Cell Environ.* 38:629–37
79. von Caemmerer S, Farquhar GD. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376–87
80. Walker BJ, Ariza LS, Kaines S, Badger MR, Cousins AB. 2013. Temperature response of in vivo Rubisco kinetics and mesophyll conductance in *Arabidopsis thaliana*: comparisons to *Nicotiana tabacum*. *Plant Cell Environ.* 36:2108–19
81. Walker BJ, Ort DR. 2015. Improved method for measuring the apparent CO₂ photocompensation point resolves the impact of multiple internal conductances to CO₂ to net gas exchange. *Plant Cell Environ.* 38:2462–74
82. Walker BJ, Strand DD, Kramer DM, Cousins AB. 2014. The response of cyclic electron flow around photosystem I to changes in photorespiration and nitrate assimilation. *Plant Physiol.* 165:453–62
83. Whitney SM, Houtz RL, Alonso H. 2011. Advancing our understanding and capacity to engineer nature's CO₂-sequestering enzyme, Rubisco. *Plant Physiol.* 155:27–35
84. Wingerl A, Lea PJ, Quick WP, Leegood RC. 2000. Photorespiration: metabolic pathways and their role in stress protection. *Philos. Trans. R. Soc. Lond. B* 355:1517–29
85. Wolfram Res. 2015. *Mathematica*. Wolfram Res., Champaign, IL. <http://www.wolfram.com/mathematica>
86. Xin C, Tholen D, Zhu X-G. 2014. The benefits of photorespiratory bypasses: How can they work? *Plant Physiol.* 167:574–85
87. Yamori W, Shikanai T. 2016. Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. *Annu. Rev. Plant Biol.* 67:81–106
88. Zhu X-G, Long SP, Ort DR. 2008. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Curr. Opin. Biotechnol.* 19:153–59



Contents

The Path to Thioredoxin and Redox Regulation in Chloroplasts <i>Bob B. Buchanan</i>	1
Learning the Languages of the Chloroplast: Retrograde Signaling and Beyond <i>Kai Xun Chan, Su Yin Phua, Peter Crisp, Ryan McQuinn, and Barry J. Pogson</i>	25
NDH-1 and NDH-2 Plastoquinone Reductases in Oxygenic Photosynthesis <i>Gilles Peltier, Eva-Mari Aro, and Toshibaru Shikanai</i>	55
Physiological Functions of Cyclic Electron Transport Around Photosystem I in Sustaining Photosynthesis and Plant Growth <i>Wataru Yamori and Toshibaru Shikanai</i>	81
The Costs of Photorespiration to Food Production Now and in the Future <i>Berkley J. Walker, Andy VanLooche, Carl J. Bernacchi, and Donald R. Ort</i>	107
Metabolite Damage and Metabolite Damage Control in Plants <i>Andrew D. Hanson, Christopher S. Henry, Oliver Fiehn, and Valérie de Crécy-Lagard</i>	131
The Regulation of Essential Amino Acid Synthesis and Accumulation in Plants <i>Gad Galili, Rachel Amir, and Alisdair R. Fernie</i>	153
Triacylglycerol Metabolism, Function, and Accumulation in Plant Vegetative Tissues <i>Changcheng Xu and John Shanklin</i>	179
The Plant Polyester Cutin: Biosynthesis, Structure, and Biological Roles <i>Eric A. Fich, Nicholas A. Segerson, and Jocelyn K.C. Rose</i>	207
Biosynthesis of the Plant Cell Wall Matrix Polysaccharide Xyloglucan <i>Markus Pauly and Kenneth Keegstra</i>	235
TOR Signaling and Nutrient Sensing <i>Thomas Dobrenel, Camila Caldana, Johannes Hanson, Christophe Robaglia, Michel Vincentz, Bruce Veit, and Christian Meyer</i>	261

Rapid, Long-Distance Electrical and Calcium Signaling in Plants <i>Won-Gyu Choi, Richard Hilleary, Sarah J. Swanson, Su-Hwa Kim, and Simon Gilroy</i>	287
Endocytosis and Endosomal Trafficking in Plants <i>Julio Paez Valencia, Kaija Goodman, and Marisa S. Otegui</i>	309
Staying Tight: Plasmodesmal Membrane Contact Sites and the Control of Cell-to-Cell Connectivity in Plants <i>Jens Tilsner, William Nicolas, Abel Rosado, and Emmanuelle M. Bayer</i>	337
Pre-Meiotic Anther Development: Cell Fate Specification and Differentiation <i>Virginia Walbot and Rachel L. Egger</i>	365
Plant Sex Chromosomes <i>Deborah Charlesworth</i>	397
Haploidization via Chromosome Elimination: Means and Mechanisms <i>Takayoshi Ishii, Rabeleh Karimi-Ashtiyani, and Andreas Houben</i>	421
Mechanisms Used by Plants to Cope with DNA Damage <i>Zhubing Hu, Toon Cools, and Lieven De Veylder</i>	439
The Conservation and Function of RNA Secondary Structure in Plants <i>Lee E. Vandivier, Stephen J. Anderson, Shawn W. Foley, and Brian D. Gregory</i>	463
Toxic Heavy Metal and Metalloid Accumulation in Crop Plants and Foods <i>Stephan Clemens and Jian Feng Ma</i>	489
Light-Mediated Hormonal Regulation of Plant Growth and Development <i>Mieke de Wit, Vinicius Costa Galvão, and Christian Fankhauser</i>	513
Transcriptional Responses to the Auxin Hormone <i>Dolf Weijers and Doris Wagner</i>	539
Mapping Transcriptional Networks in Plants: Data-Driven Discovery of Novel Biological Mechanisms <i>Allison Gaudinier and Siobhan M. Brady</i>	575
The Intracellular Dynamics of Circadian Clocks Reach for the Light of Ecology and Evolution <i>Andrew J. Millar</i>	595
Environmental Control of Root System Biology <i>Rubén Rellán-Álvarez, Guillaume Lobet, and José R. Dimmeny</i>	619
The Haustorium, a Specialized Invasive Organ in Parasitic Plants <i>Satoko Yoshida, Songkui Cui, Yasunori Ichihashi, and Ken Shirasu</i>	643

Antibody Production in Plants and Green Algae <i>Vidadi Yusibov, Natasha Kushnir, and Stephen J. Streatfield</i>	669
Perennial Grain and Oilseed Crops <i>Michael B. Kantar, Catrin E. Tyl, Kevin M. Dorn, Xiaofei Zhang, Jacob M. Jungers, Joe M. Kaser, Rachel R. Schendel, James O. Eckberg, Bryan C. Runck, Mirko Bunzel, Nick R. Jordan, Robert M. Stupar, M. David Marks, James A. Anderson, Gregg A. Johnson, Craig C. Sheaffer, Tonya C. Schoenfuss, Baraem Ismail, George E. Heimpel, and Donald L. Wyse</i>	703

Errata

An online log of corrections to *Annual Review of Plant Biology* articles may be found at <http://www.annualreviews.org/errata/arplant>