PLANTS FACING THE HEAT

REVIEW

Safeguarding crop photosynthesis in a rapidly warming world

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Continued greenhouse gas emissions will accelerate global warming and intensity of heat waves, which already harm crop productivity. From the stability of key enzymes to canopy processes, photosynthesis is affected by temperature. All crops suffer declines in photosynthetic rate when temperatures cross critical thresholds, with irreversible losses typically occurring above 40° to 45°C. Protective measures within plants can be induced by growth at elevated temperatures but not from the sudden temperature elevation of heat waves. Strategies to improve the heat resilience of photosynthesis include modifying surface energy balance, optimizing canopy architecture, improving enzymatic heat tolerance, and (re)engineering key metabolic pathways for greater efficiency or to remove bottlenecks. This Review summarizes present knowledge on the major mechanisms that underlie high-temperature inhibition of photosynthesis and explores opportunities for breeding and biotechnological interventions to overcome them.

Greenhouse gas emissions from anthropogenic activities are driving an upward shift in global mean temperatures, which have already surpassed the preindustrial baseline by 1.5°C in 2024 (*1*) and are projected to rise a further 1.2°C by 2050 under the "business-as-usual" scenario SSP5-8.5 of the Intergovernmental Panel on Climate Change (IPCC) (*2*). This reflects a global average that does not account for spatial and temporal variability. Terrestrial surfaces are warming faster than ocean surfaces, and temporal variability is driving a large increase in short-duration extreme temperature events (heat waves) (*3*). For example, Coordinated Regional Downscaling Experiment (CORDEX) model ensembles (*2*) predict that for Southeast Asia, the number of days per year with a heat index exceeding 41°C will increase from around 50 in the period 1995–2014 to 160 for 2041–2060 and 300 by 2081–2100. By mid-century, the southern United States can expect around 50 more days at these temperatures per year and central and northern Brazil some 100 more days. All crop-growing regions of the world will see an increased number of days with such extreme temperatures (*2*). Rising average global temperatures, coupled with these increasingly frequent heat waves, already pose a major threat to agricultural productivity worldwide (*4*).

Temperature plays a dominant role in all facets of crop physiology, and photosynthesis, the primary means by which carbon is assimilated for growth and yield, is of particular importance (*5*). Many years of field experiments studying elevated atmospheric [CO_2] (*6*) have shown the close link between net photosynthesis and crop productivity. Any decline in photosynthetic efficiency with temperature increase has the potential to substantially affect yields. High temperatures affect photosynthesis at multiple levels, from altering energy balance and gas exchange to impairing enzyme function and altering gene expression (*7*). Crops may be divided into two photosynthetic types: C_3 and C_4 (see Box 1 for an explanation of these and other terms). Because it uses a different metabolic process, C_4 photosynthesis has a greater degree of resilience to warmer temperatures (*8*) than C_3 photosynthesis (Fig. 1). Substantial declines in the net rate of CO_2 uptake per unit of leaf area (A) occur when temperatures surpass the relatively low thermal optimum (T_{opt}) of around 25°C in most C_3 crops, whereas C_4 crops typically show a T_{opt} of about 35°C (*9*, *10*). Beyond a critical leaf temperature threshold, typically in the range of 40° to 45°C, photosynthetic rate drops sharply in both C_3 and C_4 crops (Fig. 1). Yet as outlined above, days with these air temperatures will become far more common over the next two to three decades. This underscores the urgent need to develop heat-resilient crops through a combination of physiological insights and breeding or bioengineering strategies to meet present and growing global demands for food, feed, fiber, bioenergy, and other bioproducts (*11*). Recent advancements provide promising avenues that could mitigate the impacts of high temperatures on photosynthesis, at least to some extent, in order to avoid substantial yield losses.

Plant energy balance and heating

Plants are efficient at absorbing solar radiation, which is foundational for supplying the energy needed for photosynthesis. However, in full sunlight, the energy absorbed by leaf chlorophylls is in excess of that needed to drive photochemistry (*12*), and this excess must be dissipated to minimize temperature elevation and photoinhibition (*13*, *14*). The major fates of absorbed energy (*15*) are loss through evaporation of water (latent heat loss), convection (sensible heat loss), and radiation (thermal heat loss) (Fig. 2). Latent heat transfer from transpiration serves to lower leaf temperature. If the rate of latent cooling is inadequate to balance the absorbed radiant and thermal energy, leaves will warm. Convective and radiative heat losses from the leaf to the surrounding environment will also lower leaf temperature, but unlike transpiration, these cannot, during conditions when photosynthesis occurs, lower leaf temperature below that of the ambient air.

Plants experience extreme heat stress when both air temperature and solar radiation are high. This is exacerbated by drought, which limits transpiration and latent heat cooling. Even when soil moisture is not limiting, stomatal opening is negatively correlated with atmospheric vapor pressure deficit (VPD). VPD is a measure of how "dry" the air is relative to its maximum capacity for holding moisture. As temperature increases, the moisture-holding capacity of air rises exponentially, which can be predicted from the thermodynamic properties of air. The large increase in VPD that can result from a temperature increase is illustrated in the following example. At a leaf temperature of 25°C and 60% relative humidity in the surrounding air, the water vapor pressure of that air (e_a) will be 1.90 kPa and the saturation vapor pressure (e_s) 3.17 kPa. The difference between the two is VPD ($e_s - e_a$), in this case, 1.27 kPa, which quantifies the drying power of the air. If leaf temperature is now increased to 35°C and e_a remains constant at 1.90 kPa, VPD nearly triples (3.72 kPa). In practice, warming also elevates the humidity of the air (e_a) such that relative humidity might remain constant. Even so, the VPD at 35°C would still be 2.25 kPa and almost double its value at 25°C. This sharp rise in VPD doubles evaporative demand and simultaneously reduces stomatal conductance (g_s) (*16*). Prolonged exposure to high VPD stress slows cell expansion, reduces leaf area, and decreases stomatal aperture and density, compounding limitations on CO_2 uptake and lowering water-use efficiency (WUE) and overall plant productivity (*17*, *18*). These are therefore indirect effects of rising temperature that limit photosynthesis and potentially yield.

The strong coupling between VPD and temperature makes it difficult to isolate their individual effects on stomatal conductance as temperatures rise. As VPD increases, a continued lowering of g_s would potentially lead to complete stomatal closure. However, studies in which temperature is increased under constant VPD show that the

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VPD-g_s relationship can uncouple at extreme high temperatures (*19*), allowing increased transpiration that may prevent temperatures lethal to photosynthesis. However, if soil water is scarce or if plant hydraulic conductivity is insufficient, this potential for evaporative cooling diminishes. Field and controlled-environment studies indicate that many major crops fail to sufficiently enhance hydraulic conductivity at high temperatures, limiting their ability to meet rising evaporative demand (*20*). Variability in hydraulic conductance within the germplasm of major crops has not been extensively evaluated but could provide an important avenue to improving capacity for latent heat cooling.

Rather than dissipate absorbed energy, adaptation in some plants has involved decreasing the amount of solar energy absorbed. Because leaves receive more energy in full sunlight than they can use in photosynthesis, reflecting more light does not affect carbon gain yet will both cool the leaf and lower photoinhibiton and photodamage to photosynthetic capacity. Several leaf properties can increase reflectivity, including surface hairs (*21*), surface waxes (*22*), and leaf chlorophyll content. Given variability in each within crop germplasm, these properties could all be used in breeding crops with more reflective leaves. Altered leaf angles may also decrease radiation interception around solar noon. Leaves that are more vertical intercept less direct radiation when solar elevation is high, decreasing thermal load around the warmest time of the day (*23*) (Fig. 2). A more vertically oriented canopy decreases the total direct solar radiation incident upon leaf surfaces (*24*). A further mechanism for achieving reduced light absorption, particularly during water shortage, is paraheliotropism, which lowers light interception by dynamic changes in leaf orientation. This change in leaf orientation occurs through the action of the pulvinus, an enlarged section at the base of a leaf petiole (stalk) that causes the leaf to move as it swells or shrinks according to its water content. For example, soybean leaflets move under the control of such pulvini. In a soybean cultivar, strong paraheliotropic movement during mild drought and high sunlight was shown to significantly lower leaf temperature, transpiration, and water stress (*25*).

Photosynthetic gas-exchange responses to high temperature

Measured net leaf CO_2 uptake (A) reflects the balance between photosynthetic CO_2 uptake and CO_2 released from mitochondrial respiration and photorespiration. There is some plasticity in temperature tolerance resulting from crop growth temperature. Both the T_{opt} and thermal maximum (T_{max}) for A can increase with a period of growth at higher temperatures. This can be substantial for T_{opt} (>10°C) in evergreen perennials but is small in C_4 species and in C_3 annuals, which includes most food crops (*9*). What underlies reduction in A at temperatures above T_{opt}?

Within the chloroplast, there is a wide array of photosynthetic processes that are temperature sensitive (*26*, *27*). In addition to increases in membrane fluidity, the photosynthetic apparatus and pigments are affected by the increased generation of reactive oxygen species above T_{opt}. Inhibition of oxygen evolution as well as photosystem I function can occur at high temperatures, but well above T_{opt}. However, field experiments and controlled environment studies (Fig. 3) implicate carbon metabolism as the most important and physiologically meaningful cause of high-temperature inhibition of photosynthesis, and this is therefore the focus of this and the following sections (*9*, *28*).

The probability of an oxygenation event at the active site for the enzyme Rubisco (see Box 1), and therefore of photorespiration, increases with temperature. Based on the conserved kinetics of Rubisco, it can be predicted that the loss of photosynthetic carbon gain to photorespiration is 28% at 25°C but 48% at 35°C in C_3 plants. The rate

Box 1. Explanation of major terms and abbreviations.

A The net rate of CO_2 uptake per unit of leaf area

CBB cycle Calvin-Bassham-Benson cycle. Carboxylation of the five-carbon RuBP results in two molecules of the C3 compound glycerate-3-phosphate (G3P), which are reduced to glyceraldehyde-3-phosphate. This triose phosphate is then cycled through a series of isomerase-, bisphosphatase-, transketolase-, and phosphorylase-catalyzed reactions to regenerate RuBP. The cycle is autocatalytic, potentially releasing one triose phosphate, for every three carboxylations, for onward synthesis of all organic constituents of the plant and substrates for respiratory metabolism.

C_3 Refers to plants in which Rubisco and the CBB cycle are in all green cells of the leaf and the first product of CO_2 assimilation is the C_3 compound G3P. Most crops are C_3 plants, including all woody crops, rice, wheat, brassicas, and legumes.

C_4 Refers to plants in which Rubisco and most of the CBB cycle is confined to chloroplasts within the bundle sheath—large cells that surround the vascular bundles. These in turn are surrounded by mesophyll cells with chloroplasts that lack Rubisco. CO_2 is first assimilated into the C_4 compound oxaloacetate, a dicarboxylate, within the mesophyll via the carboxylation of phospho-enol-pyruvate (PEP) catalyzed by PEP carboxylase. The resulting dicarboxylates diffuse to the Rubisco-containing bundle sheath cells, where they are decarboxylated to release CO_2 and pyruvate. An impermeable barrier minimizes CO_2 diffusion back to the mesophyll. The pyruvate diffuses back to the mesophyll via plasmodesmata, where it is phosphorylated to PEP, completing the C_4 photosynthetic cycle. Compared with C_3 photosynthesis, C_4 requires an extra two ATPs per CO_2 assimilated. However, this cost is typically offset by the fact that CO_2 is concentrated in the bundle sheath to a level that competitively inhibits the oxygenase reaction of Rubisco, all but eliminating photorespiration. Only a few crops are C_4, notably maize, pearl millet, sorghum, sugarcane, grain amaranths, most tropical pasture grasses, and miscanthus, a biomass feedstock.

Photorespiration Begins when Rubisco catalyzes the oxygenation of RuBP, which produces one molecule of G3P and one of 2-phosphoglycerate (2-PG). 2-PG is metabolized through a multiorganelle pathway to G3P, which reenters the CBB cycle. This is at the cost of one CO_2 emitted for every two 2-PG molecules with the consumption of four NADPH and seven ATP. The process from oxygenation to recovery of G3P is termed photorespiration, owing to its analogy to respiration in consuming oxygen and releasing CO_2; however, unlike respiration, it consumes rather than produces ATP and NADPH. It imposes a substantial penalty on *A*.

Rca Rubisco activase is essential to maintaining the activity of Rubisco. In the dark, inhibitory sugar phosphates inactivate Rubisco by occupying the enzyme active site. On illumination, Rca in a multimeric form uses energy from ATP hydrolysis to structurally remodel Rubisco to release the inhibitory sugar phosphates. This activity is also important throughout the course of the day to prevent the inhibition of Rubisco activity.

RuBP Ribulose-1:5-bisphosphate

Rubisco RuBP carboxylase/oxygenase. All CO_2 assimilated by plants is through the carboxylation of RuBP, which is catalyzed by this enzyme and forms the first step of the CBB cycle. However, the enzyme also catalyzes the oxygenation of RuBP, leading to photorespiration.

T_{opt} The leaf temperature at which light-saturated *A* is maximal

T_{max} The leaf temperature at which irreversible damage to photosynthesis begins to occur

of carboxylation is not a direct factor affecting A if ribulose-1:5-bisphosphate (RuBP) regeneration is limiting. However, there is still a reduction in A, albeit smaller, when RuBP regeneration is limiting, because increased photorespiration consumes adenosine triphosphate (ATP) and NADPH (reduced form of nicotinamide adenine dinucleotide phosphate) that would otherwise power RuBP regeneration. The probability of oxygenation of RuBP increases with temperature because the solubility of CO_2 in water (relative to that of O_2) decreases, and the activation energy requirement of the oxygenation reaction is greater than that of carboxylation, both of which cause increased photorespiration (*7*). This largely explains the higher temperature optimum of C_4 photosynthesis, in which photorespiration is minimal. The optimum temperature of A in C_3 plants increases from 25°C in normal air, of about 400 parts per million (ppm) [CO_2], to 35°C at 800 ppm [CO_2], a similar optimum to that of C_4 photosynthesis resulting from suppression of photorespiration (*7*).

Growth at elevated temperature can produce both damaging and protective effects on photosynthesis. Increasing exposure time to heat stress exacerbates the negative effects of instantaneous heat stress. High temperatures deactivate enzymes, but with continued exposure, these can become irreversibly denatured. Membrane fluidity increases with temperature, and with prolonged exposure, leakage of metabolites and inorganic ions will occur, as well as disruption of membrane organization. As the time at elevated temperature is prolonged, these changes result in a steady decline in photosynthesis and, in turn, productivity while limiting the potential for any recovery. Secondary effects also result. Because high temperatures typically coincide with high light, impairment of photosynthetic capacity and its protective mechanisms makes the apparatus more vulnerable to photodamage, particularly a loss of the labile D1 protein in the photosystem II core (*29*). If the temperature increase is gradual, then protective mechanisms can allow photosynthesis to continue at higher temperatures. In general, these mechanisms raise the temperature tolerance of photosynthesis by an extra 2° to 3°C. There are three major mechanisms by which photosynthesis can acclimate to high temperature. (i) Several photosynthetic proteins are coded by gene families or result from alternative splicing, where more thermotolerant isoforms are expressed at elevated temperatures. Rubisco activase (Rca) is one of the best-known examples (*30*). Altered patterns of gene expression can result in increased amounts of proteins that would otherwise limit photosynthesis at high temperature (*31*). This may include a rebalancing of investment in Rubisco versus RuBP regeneration, because RuBP regeneration limitation increases with temperature (*28*). (ii) Heat shock proteins (HSPs), which facilitate the correct folding of photosynthetic proteins, can also prevent enzyme inactivation, denaturation, and aggregation. The heat shock transcription factor (HSF), recognized by a conserved region on the promoters of HSP genes, is elevated with growth at high temperature, resulting in increased protection (*32*). (iii) Remodeling of the lipid composition of the thylakoid membranes by increasing diglyceride content counteracts increased fluidity that would otherwise allow ion leakage and disruption of membrane processes (*33*).

The temperature sensitivity of Rubisco catalytic efficiency and specificity

In addition to photorespiration in C_3 crops increasing with rising temperature, the Rubisco activation state declines, further contributing to decreased A and underlying the sharp drop in photosynthesis observed at about >40°C (*34*, *35*) (Fig. 1). Rubisco is deactivated by the binding of inhibitory sugar phosphates, which cannot dissociate from its catalytic sites without intervention by Rca (*36*). Temperatures above T_{opt} increase the rate of Rubisco inactivation owing to higher concentrations of inhibitory compounds. In addition, Rca is often the most thermolabile photosynthetic protein, leading to inactivation at temperatures often at or slightly above T_{opt} (*37*) and below temperatures that affect other

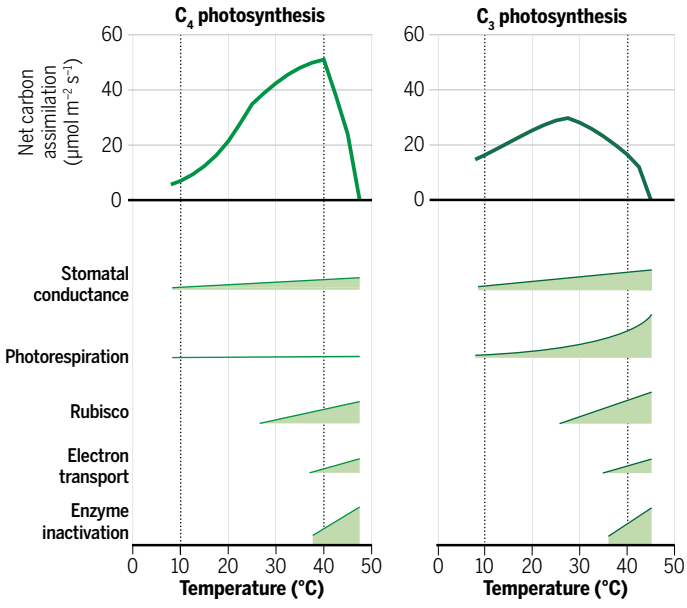

Fig. 1. Modeled temperature responses of leaf-level net carbon assimilation for C_4 and C_3 photosynthetic pathways. Graphs were created using a C_4 (*8*) and a C_3 (*76*) gas-exchange model but modified to include a rapid loss of enzymatic function above 42°C—an effect usually omitted from leaf gas-exchange models. For C_3 species, as leaf temperature increases beyond T_{opt}, photosynthesis declines while photorespiration and dark respiration increase, whereas for C_4 species, there is no photorespiration, resulting in a high T_{opt}. The average T_{opt} for net CO_2 uptake (A) is around 35°C for C_4 and 25°C for C_3 plants. Average high-temperature tolerance of photosynthesis (T_{max}), that is, the temperature at which complete irreversible damage occurs, is about 50°C for tropical plants and 42°C for plants from high latitudes (*77*). However, these vary with adaptation to the area of origin. For example, the C_4 grass *Spartina anglica* in Britain has a T_{opt} of 30°C compared with a T_{opt} of 47°C for the C_4 shrub *T. oblongifolia* in Death Valley, California (*78*,*79*). Below each graph, semiquantitative schematics depict the temperature sensitivity of key processes—stomatal conductance, photorespiration, Rubisco activity, electron transport, and enzyme inactivation. The width of each shape is aligned to the temperature axis and denotes the relative contribution of that process to limiting photosynthesis as temperature increases.

enzymes and chloroplast membrane processes. The thermolability of Rca causes the proportion of inactive Rubisco to rise with temperature.

Most plants express two Rca isoforms: a smaller β isoform (41 to 43 kDa) and a larger α isoform (43 to 47 kDa), which has a C-terminal extension containing two redox-regulated cysteine residues (*38*). Redox regulation of the Rca-α isoform by chloroplast-localized thioredoxin connects regulation of Rubisco activity to the dynamic chloroplast redox potential that changes with environmental conditions, including light intensity and temperature. Solanaceae species are distinctive in that they express only the redox-insensitive β isoform. In the absence of redox regulation in Solanaceae, light regulation via Rca appears to be mediated by changes in the adenosine diphophaste (ADP)/ATP ratio of the chloroplast (*34*, *36*).

Beyond differences in the number of Rca genes and the isoforms they produce, there is notable variation across species in the expression and relative abundance of Rca isoforms and their response to temperature (*39*, *40*). In *Arabidopsis* (*Arabidopsis thaliana*), the Rca-α and -β isoforms originate from alternative splicing of a single gene and are present at the transcript and protein levels in approximately equal amounts; their ratio is not affected by temperature. In rice (*Oryza sativa* L.), the two Rca isoforms are also produced by alternative splicing in which Rca-β is at higher levels at permissive growth temperatures but heat stress results in increased expression of Rca-α (*41*).

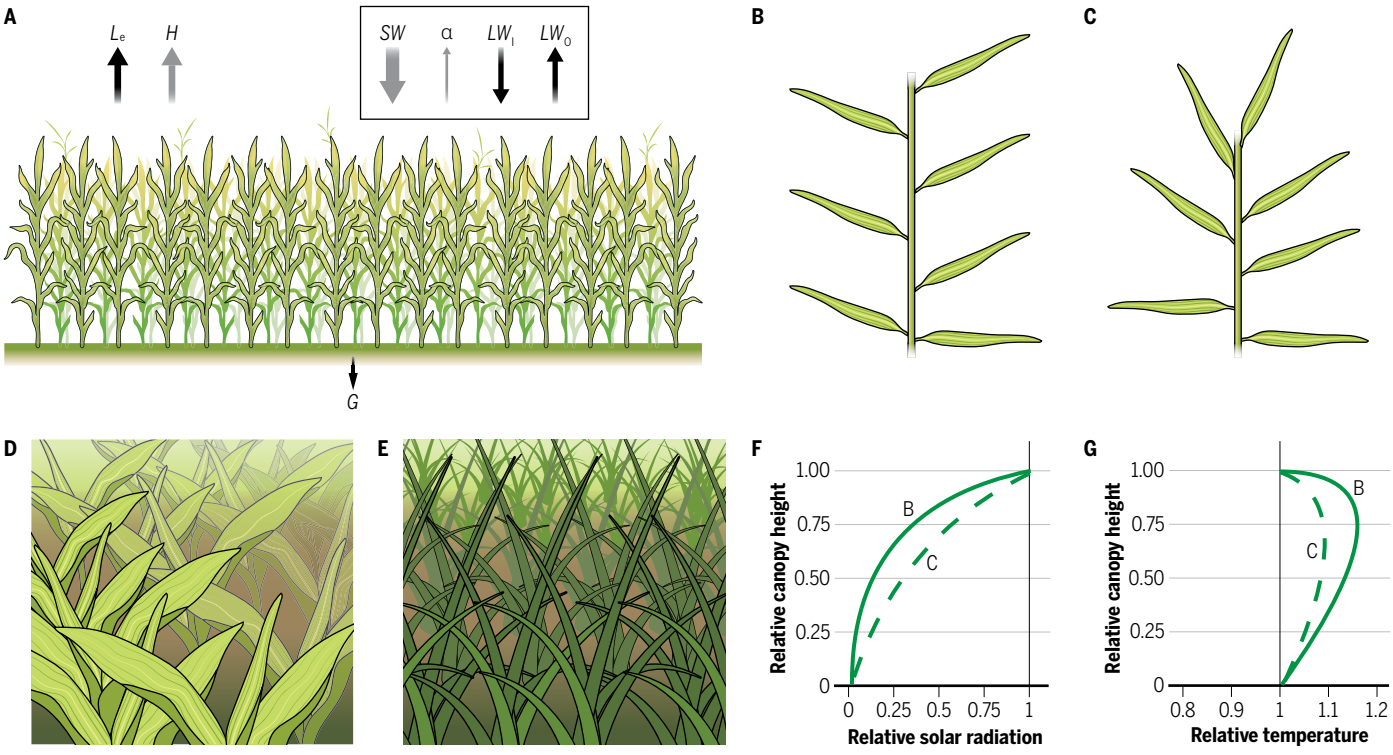

Fig. 2. Canopy energy balance and canopy architecture. (**A**) Energy budget representation of a plant canopy. The total available energy is determined by downwelling shortwave radiation from the sun (*SW*) minus the amount reflected (α) by the canopy, as well as by the difference between incoming (LW_I) and outgoing (LW_O) long-wave radiation. The balance of these radiative fluxes, outlined by a rectangular box in the figure, represents net radiation (R_n), which is the total potential energy available to a plant canopy (*15*). Most of this available energy is partitioned into latent (L_e) and sensible (*H*) heat fluxes, although a small amount of energy penetrates through the canopy into the soil (G) and a much smaller part is used in photosynthesis, typically <1%. The relative fluxes of *H* versus L_e are modulated by stomatal conductance—a higher conductance increases L_e and thus lowers *H*. Arrow widths represent the generalized magnitude of the fluxes for each component during midday, clear-sky conditions. (**B** to **G**) Idealized diagrams [(B) and (C)] and photographs [(D) and (E)] of horizontal [(B) and (D)] and vertical [(C) and (E)] plant architectures. Healthy (D) and heat and/or water-stressed (E) maize (*Z. mays*) plants at similar growth stages demonstrate adaptive responses that alter canopy energy balance under stress conditions. The relative solar radiation incident upon leaves (F) and the temperature of leaves (G) change from the canopy top (relative canopy height = 1) to the soil surface (relative canopy height = 0). The letters adjacent to the lines in (F) and (G) correspond to the respective canopy architecture panels [(B) and (C)]. Leaf rolling in stressed plants (E) creates a more vertical canopy orientation, changing the distribution of solar radiation within the canopy (F) and thereby lowering the heat load (G). In addition to modifying leaf orientation, plants use various strategies to influence their energy budgets, such as altering the leaf reflectivity using trichomes, waxes, or pigments and adjusting stomatal or boundary-layer conductances.

In the C_4 crops sorghum (*Sorghum bicolor*), sugarcane (*Saccharum officinarum*), and maize (*Zea mays* L.), two *Rca* genes are present, one each for Rca-α and Rca-β. Whereas the *Rca*-β gene is consistently expressed at normal growth temperatures, *Rca*-α expression is only induced at high temperatures (*40*). In maize, heat-induced expression of *Rca*-α occurs in seedlings but appears diminished or absent in mature plants (*42*, *43*). The induction profile of *Rca*-α expression mimics recovery of photosynthesis and the profile of Rubisco reactivation after high-temperature exposure. This association between Rca-α isoform expression and restoration of Rubisco activation at high temperature potentially supports a thermoprotective role of Rca-α in carbon fixation in C_4 grasses by sustaining Rubisco activation at high temperature. Wheat (*Triticum aestivum* L.) differs yet again. Although wheat has two *Rca* genes, one codes for the β isoform and the other produces both an α and β isoform by alternative splicing (*44*), again with α increasing with high-temperature exposure.

Developing photosynthetically thermotolerant crops

Crop architecture and energy balance

Optimizing crop canopies to achieve more even light distribution has long been hypothesized to increase net daily carbon gain. For example, selecting or engineering canopies with upright leaves in the upper canopy and more horizontal leaves in the lower canopy can increase carbon gain (*45*) and potentially enhance resilience to high temperatures (*7*) (Fig. 2). Reducing leaf chlorophyll content has also been shown to increase light penetration into the canopy without sacrificing overall photosynthetic rates (*45*, *46*). In these scenarios, upper leaves—which normally absorb more light than they can use—maintain high photosynthesis with reduced absorption while lower leaves benefit from receiving more solar radiation, thereby increasing total canopy photosynthesis (*45*). More evenly distributed solar radiation throughout the canopy will also distribute heat loads more uniformly, potentially moderating leaf temperatures. However, such traits may involve trade-offs; for instance, altering leaf reflectivity or absorptive properties could reduce total light capture and photosynthesis in milder conditions. This might be addressed using high-temperature inducible promoters. Consequently, breeders and biotechnologists must balance the benefits of temperature resilience with the risk of reduced net photosynthesis when growing conditions are not heat-stressed. Highly mechanistic modeling tools to quantitatively evaluate these trade-offs are available (*47*). Additionally, high-throughput field phenotyping of three-dimensional form and spectral properties (*48*) (Fig. 3) coupled with resequencing of hundreds of genotypes (*49*) of a crop can allow identification of advantageous alleles. Once identified, alleles underlying canopy and reflectance properties

that will improve protection of photosynthesis at high temperature could be introgressed into elite cultivars, aided by molecular marker or genomic selection.

Improving water-use efficiency

Anticipated increases in VPD due to rising temperature places added pressure on crop water resources. Presently, 40% of global crop production is irrigated, accounting for ~71% of freshwater extraction. With diminishing water resources (*50*), improved crop WUE will be vital. In principle, rising [CO_2] allows plants to maintain the same, or higher, photosynthetic carbon assimilation rate with lower stomatal conductance (g_s). Although plants naturally reduce g_s under elevated [CO_2], the reduction is typically insufficient to realize the full potential WUE gains—particularly in C_4 crops, where photosynthesis is already close to [CO_2] saturation (*51*, *52*). To address this, researchers are exploring ways to further decrease g_s through breeding and genetic engineering with little or no penalty to carbon gain (*53*). Overexpression of photosystem II subunit S, for instance, can lower g_s at all light intensities to levels that reduce transpiration without affecting photosynthesis or productivity, resulting in a 30% decrease in whole-plant water use (*54*). Another approach is reducing stomatal density, that is, the number of stomata per unit leaf area. In C_4 sorghum, a moderate reduction in stomatal density through the insertion of a synthetic epidermal patterning factor transgene lowered plant water use by ~15% with no adverse effect on photosynthesis (*55*). In addition to transgenic strategies, there is substantial natural variation in stomatal density within many crop germplasms (e.g., a 2.5-fold range across 235 rice accessions), suggesting that reduction could be achieved through breeding (*56*).

Although improving WUE through lower g_s may be useful in maximizing water availability (*55*), the lower transpirational cooling can also increase the likelihood of extreme leaf temperatures. This may be exacerbated in elevated [CO_2] through further decreases in g_s (*57*). However, the potential to lower water use with combined optimization of canopy structure and surface-energy balance can potentially overcome this hypothesized positive feedback (*47*). It will therefore be important to assess for each crop and region whether this promising approach to improving WUE risks temperature damage and how that might be alleviated by stacking traits. For example, combining altered canopy structure and reflectance with decreased transpiration has been predicted to improve WUE without elevating leaf temperature and impairing photosynthesis (*47*).

Leaf photosynthetic physiology

Natural variability in Rubisco specificity for CO_2 relative to O_2 and catalytic parameters also offer potential gains for photosynthetic efficiency and thermotolerance (*58*). High-throughput measurement of Rubisco kinetics has shown the potential to replace present crop Rubisco with faster or higher-specificity forms from other species that could boost photosynthetic rates under warm conditions and rising [CO_2] (*58*). Yet cross-species Rubisco substitution requires matching all necessary assembly and chaperone proteins—an ongoing challenge that has not yet been fully resolved (Table 1). Even though the many remaining mysteries and uncertainties concerning the regulation of Rubisco activity by Rca complicate the development of photosynthesis thermotolerance, the protection of Rubisco activity via more-thermotolerant Rca appears particularly promising (*59*).

As noted above, Rca is particularly thermolabile, and more so in crops adapted to cooler climates. Substituting Rca from a warm-climate species into a cooler-climate species has been shown to increase photosynthetic T_{opt} (*60*). An alternative approach involves manipulating Rca isoforms within a species. For instance, heat-induced expression of an Rca-α isoform in sorghum appears to confer a higher temperature tolerance of Rubisco activation (*41*). Because constitutive Rca-α expression might introduce a fitness cost at optimal temperatures, regulating its expression threshold or placing it under an inducible promoter may be advantageous. Overexpression of maize Rca in rice did not increase the Rubisco activation state or photosynthetic rate below 25°C but had a stimulatory effect at 40°C (*61*), suggesting a protective role of Rca overexpression on steady-state photosynthesis at high temperatures. Emerging evidence also suggests that a few amino acid changes can greatly improve Rca thermostability (*35*). However, the molecular basis for Rca thermolability varies across species and among isoforms. In some cases, thermolability may involve disruption of the multimeric Rca complex (*36*). Photosynthesis of *Tidestromia oblongifolia*, a native inhabitant of the floor of Death Valley, California, is clearly well adapted to high temperature (*62*), suggesting that understanding *Rca* sequence variations in this species and other desert plants may be especially informative. The diversity of Rca forms means that engineering robust, thermotolerant Rca will likely require species-specific or even cultivar-specific approaches.

Rising temperature and elevated [CO_2] can shift the primary limitation on C_3 photosynthesis from Rubisco activity to RuBP regeneration. Sedoheptulose-1,5-bisphosphatase (SBPase) is often a key bottleneck in RuBP regeneration via the CBBc (see Box 1). An open-air replicated field experiment (Fig. 3) tested soybeans with transgenic up-regulation of SBPase alongside wild-type controls under elevated temperature and [CO_2] singly and in combination (*63*). Although higher temperature reduced yield in both ambient and elevated [CO_2] conditions, the SBPase-transgenic lines maintained significantly higher yields than wild type under combined heat and elevated [CO_2], effectively matching wild-type yields in ambient conditions. Other transgenic approaches have also demonstrated potential in field settings. For example, heat stress–induced overexpression of the D1 protein significantly increased biomass and grain yield in field-grown rice (*29*).

Installing a photorespiratory "bypass" in C_3 crops provides another strategy to mitigate the effects of higher temperatures on photosynthetic efficiency (*59*, *64*). Several photorespiratory bypass designs have been proposed to recycle 2-phosphoglycolate (2-PG) with lower requirements for ATP and NADPH than in the native pathway (*65*). They generally rely on metabolizing 2-PG within the chloroplast and with fewer metabolic reactions. High-temperature field experiments (Fig. 3) using tobacco (*Nicotiana tabacum* L.) engineered with one such alternative photorespiratory pathway showed higher net photosynthetic CO_2 uptake and a 26% increase in biomass under season-long elevated temperatures (5°C above nonheated control plots) compared with wild-type plants (*66*). Similarly, genetically modified potato (*Solanum tuberosum*) expressing a bypass pathway showed increased photosynthetic capacity and daily carbon assimilation during naturally occurring heat waves and a 30% increase in tuber biomass relative to wild type (*67*). These findings support theoretical predictions that rising temperature amplifies photorespiratory losses and highlights the potential for bypass strategies to sustain or improve crop yields in a warming climate.

Photorespiration in C_3 crops could be largely eliminated by conversion to the C_4 form. A C_3-to-C_4 conversion would require C_4 compartmentation of photosynthetic enzymes and the formation of a diffusive barrier between the mesophyll and bundle sheath cells. Although this clearly requires multiple genetic changes, it is notable that nature has achieved this transition independently almost 70 times. The past two decades have seen great progress in understanding the molecular basis of what makes a C_4 leaf and in installing parts of the system into C_3 rice (*68*). This conversion would not only increase photosynthesis and WUE at all temperatures but also mean that carbon gain above 25°C would increase, rather than decrease, with temperature rise to a T_{opt} of 35°C (Fig. 1). A possibly more tractable alternative would be to convert C_3 crops to the C_2 form (*68*). C_2 photosynthesis is considered to represent evolutionary transition points between C_3 and C_4. In C_2 plants where photorespiratory CO_2 release is confined to the bundle sheath, there can be substantial recapture of this CO_2 in

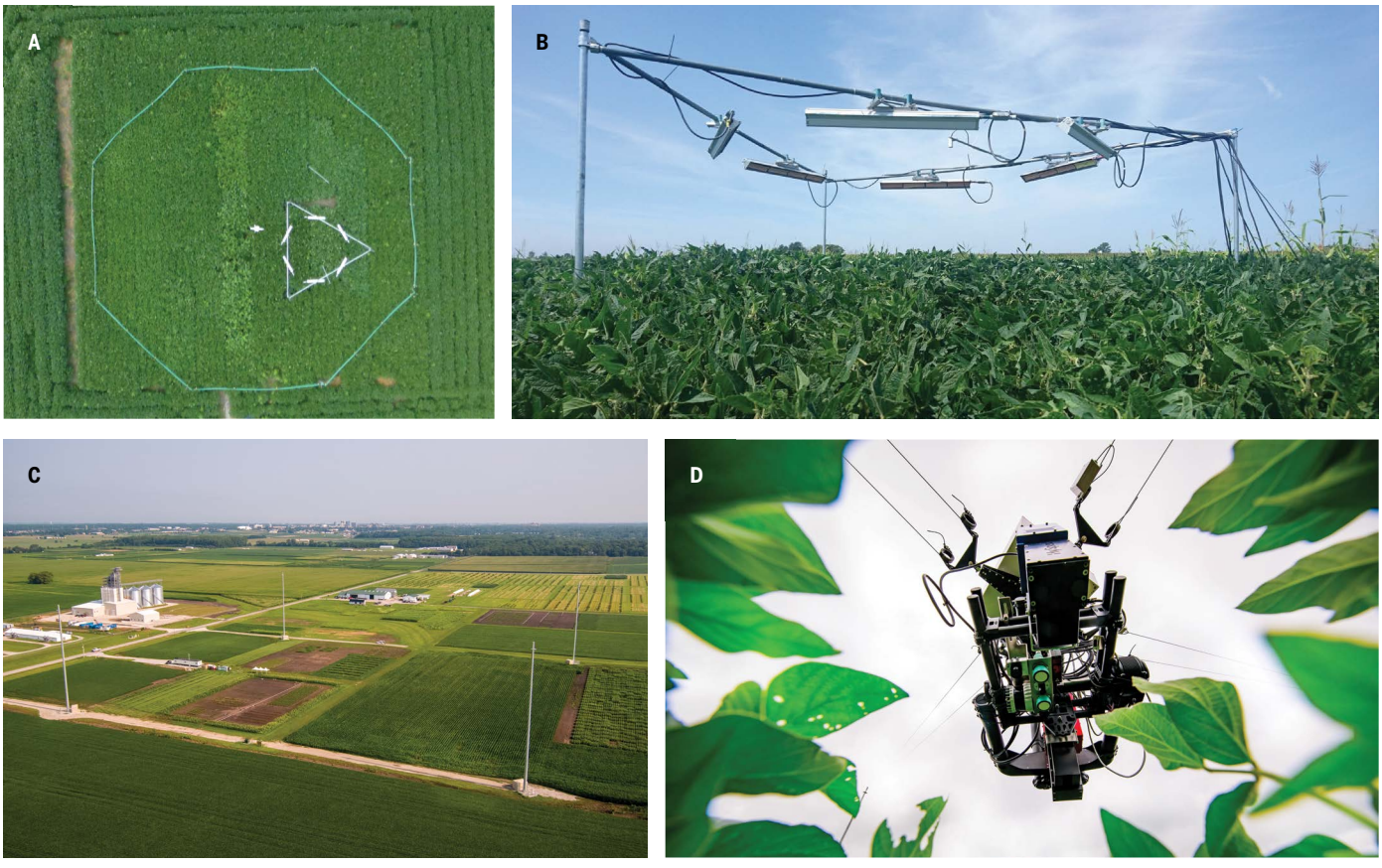

Fig. 3. Experimental techniques for understanding high-temperature impacts and tolerance in crop germplasm in farm fields. Aerial view within an elevated CO_2 plot (**A**) and lateral view (**B**) of an in-field infrared heating array used to simulate warmer growing conditions for crops at the Soybean Free Air Concentration Enrichment facility (SoyFACE) in Urbana, Illinois. The electrical current to six infrared heaters is modulated to maintain a set point canopy temperature above a nonheated reference area adjacent to the heated area, as determined from thermal imaging of the canopy. As temperatures fluctuate over the reference plot, output from the heaters is adjusted to match the target temperature increase for the heated plots. Various experiments have been undertaken to simulate global warming (*80*) and heat waves (*81*) and to test strategies to genetically improve crop resilience to temperatures (*63*,*66*). (**C**) Aerial view of the 4-Ha RIPE Aerial Plant Phenotyping System (RAPPS) located on the Energy Farm of the University of Illinois Urbana-Champaign and (**D**) a view of the sensor package, including hyperspectral imagers, light detecting and ranging (lidar), thermal photography, and RGB photography sensors, mounted on the dolly. RAPPS can move the sensor package over the 4 Ha of farmland to provide ultra-high-resolution, repeatable, semiautonomous, rapid, and high-accuracy information on more than 100,000 individual plants. RAPPS is highly versatile and can provide high-throughput information to advance breeding efforts for improved thermal resilience in crops using natural variation in temperatures or, alternatively, by integrating high-temperature treatments [(A) and (B)] into the measurement footprint.

the surrounding mesophyll as well as increased concentration around Rubisco. It would require fewer changes than conversion to C_4 but would have smaller benefits. Engineering microbial CO_2-concentrating mechanisms (CCMs) into crop chloroplasts is another strategy to improve the thermal resilience of C_3 crops. Like C_4 photosynthesis, these serve to concentrate CO_2 at Rubisco, thereby minimizing photorespiratory losses. Many cyanobacteria concentrate CO_2 in carboxysomes, which are microcompartments that contain Rubisco, Rca, and carbonic anhydrase. It is estimated that this system would increase both photosynthesis and WUE by about 60% and increase T_{opt} by about 10°C. Although carboxysomes have been assembled in C_3 crop chloroplasts (*69*), installing all the necessary ancillary components has not been achieved as of yet. Installing the pyrenoid system found in the chloroplasts of many eukaryotic algae would have similar benefits (*70*). For all these CCMs, success depends on the discovery of the set of components needed to make the system successful in C_3 crops, making the time horizon for attaining this difficult to know (Table 1).

Conclusions

The projected temperature increase between 2010 and 2050 is estimated to depress yields of the major grains by 6 to 16%, against a backdrop of a potential >50% increase in demand over this period (*11*). Table 1 shows a range of examples from cellular to whole-crop canopy changes that could safeguard photosynthesis in our warming world. Except for CCMs, all technological changes needed are known and therefore achievable. The time frames given assume that the resources and personnel are available, and this assumption has present real-world barriers. Whether advantageous alleles within the crop germplasm, edits, or transgenes are considered, all will require introgression by crop breeders into elite lines adapted and locally acceptable for different regions. This is at a time when capacity for public domain plant breeding has become substantially diminished (*11*). Several of the traits that have been shown to improve photosynthetic temperature resilience are transgenic. The time taken for a new plant biotechnology-derived genetic trait to reach commercialization during the period from 2017 to 2022 was 16.5 years at a cost of $115.0 million per transgene (*71*). Without changes in regulatory frameworks coupled with social acceptance of transgenic crops, this will remain a major impedance to progress. Many countries have accepted or are considering accepting DNA-edited crops, where no foreign DNA has been added, without regulation beyond that required of conventionally bred crops (*72*). The improvements demonstrated to date of the first

Table 1. Traits for, benefits of, timeline for, and risks of increasing the temperature resilience of crops. Estimated improvements in temperature tolerance and the time taken to achieve it. Where "years to proof of concept" are 0, the trait or invention has either been demonstrated in a single-site field trial or shown in a detailed mechanistic model, with reference number provided. Other time estimates are based on the authors' understanding of the state-of-the-art technology. "Years to farmers' fields" are minima and assume uninterrupted passage and use of winter nurseries for temperate crops. In the case of breeding, it assumes identification of the advantaged alleles and/or loci in year 1, hybridization with elites in year 2, and then three rounds of backcrossing per year and multiplication of resulting improved elite germplasm in years 4 and 5 for delivery to seed systems. Editing assumes that mutations that up-regulate (or, in the case of chlorophyll, down-regulate) expression are found and that these are then introgressed into elite cultivars, as is done for the use of natural variation. Time here will be strongly dependent on the evolving regulations around edited material. For transgenic plants, the time from discovery through development to authorization of a new plant biotechnology-derived trait for cultivation is estimated at 16 years, a number based on a survey of the major companies that produce transgenic food crops (*71*).

Trait or invention	Crop type	Predicted increase in photosynthetic thermotolerance (°C)	Years to proof of concept	Years to farmers' fields	Risks and notes
Up-regulation of SbPase	C_3	5	0 (*63*)	5*, 8†, 16‡	Sufficient variation within crop germplasm*; edit found that will up-regulate expression†
Up-regulation of Rca	$C_3(C_4)$§	3	0 (*61*)	5*, 8†, 16‡	As above
Up-regulation of HSPs	C_3 and C_4	3	0 (*32*)	5*, 8†, 16‡	As above
Increase leaf reflectivity	C_3 and C_4	5	0 (*47*)	5*, 8†, 16‡	As above
Decrease leaf chlorophyll	C_3 and C_4	3	0 (*47*)	5*, 8†, 16‡	As above
More vertical leaves	C_3 and C_4	3	0 (*47*)	5*, 8†, 16‡	As above; increased verticality has already been explored in cereals, which may leave little room for further change
Photorespiratory bypass	C_3	5	0 (*66*)	16‡	Already shown to protect yield at elevated temperature, without apparent detriment, despite decreased metabolic flux through the native photorespiratory pathway
Edited Rca	$C_3(C_4)$§	5	3	11†	Depends on advantageous edits being identified
Transplant thermally adapted Rca	$C_3(C_4)$§	10	5	20‡	Foreign Rca may not effectively bind native Rubisco
Transplant thermally adapted Rubisco	C_3 and C_4	10	15	30‡	Requires effective transformation of plastid and nucleus and effective binding to native Rca
Rubisco edited to obtain more thermostable forms	C_3 and C_4	10	3	11†	Depends on advantageous edits being identified
Add the carboxysome system	C_3	10	Uncertain¶	Uncertain¶	Would also substantially increase efficiency of light, water, and nitrogen use
Add the pyrenoid system	C_3	10	Uncertain¶	Uncertain¶	As above
Convert C_3 to C_4	C_3	10	Uncertain¶	Uncertain¶	As above; this transition has occurred in nature almost 70 times
Convert C_3 to C_2	C_3	5	Uncertain¶	Uncertain¶	As above, but likely to require fewer genes than conversion to C_4

*Alleles that improve thermotolerance identified and introgressed into elite cultivars. †DNA editing of the upstream region of a gene to increase expression. ‡Transgenic expression of a foreign gene or genes. §$C_3(C_4)$ indicates that the trait or invention is of benefit to C_3 and possibly of benefit to C_4. ¶Uncertain because more discovery is needed to determine the minimum set of genes required for this transition.

five entries in Table 1 have all concerned transgenic up-regulation or suppression of gene expression. These, however, concern genes already present in the crop. Increasingly, these changes could likely be achieved by editing the upstream noncoding region of genes, thereby producing the desired phenotype without the addition of foreign DNA (*57*). This could greatly decrease the time needed to move innovations to seed systems and farms (Table 1). New technologies, particularly those enabled by artificial intelligence, from high-throughput phenotyping to reconfiguration of key proteins coupled with DNA editing, offer hope that barriers can be reduced.

If alleles conferring improved thermal tolerance of photosynthesis are identified within the germplasm of a crop and its interfertile relatives, then these can be introduced into elite lines in a relatively short period of time (Table 1). The discovery of the rice *Sub1-1A* allele that allows rice to survive submergence with increasing flooding events and its introgression into a wide range of rice cultivars that were rapidly adopted by some of the world's poorest farmers shows how successful this approach can be in tackling climate change impacts (*73*). Until now, identifying alleles or loci that provide improved temperature tolerance of photosynthesis from hundreds or thousands of accessions or tilling populations of a crop would have been a huge undertaking, but new technologies offer a means to achieve this quickly. Full sequences of hundreds of genotypes of major crops are now becoming available at an ever-increasing pace. How might this be used in identifying alleles that could be used in adapting photosynthesis to higher temperatures? It would be challenging to screen large amounts of germplasm under a controlled elevation of temperature; however, high-throughput tools (Fig. 3) could be used to screen thousands of genotypes in the field under natural variations in temperatures, including under the increasingly frequent high-temperature events. High-throughput techniques of crops such as solar-induced fluorescence (*74*) and hyperspectral imaging to estimate different photosynthetic parameters, including Rubisco activity in vivo (*75*), facilitate the application of genome-wide association analyses to identify relevant loci and advantageous alleles that could then be introgressed into elite cultivars for improved photosynthetic temperature tolerance. Success here will depend on the existence of tolerance within the germplasm.

As highlighted here (Table 1), there are many opportunities to safeguard crop photosynthesis in a rapidly warming world. These are all technologically feasible. Whether they are achieved will depend, as with other adaptations in the food supply system, on public-domain commitment and investment.

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