

Perspectives on improving light distribution and light use efficiency in crop canopies

Rebecca A. Slattery¹ and Donald R. Ort ^{1,2,*†}

1 Carl R. Woese Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA

2 Departments of Plant Biology & Crop Sciences, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, USA

*Author for communication: d-ort@illinois.edu

†Senior author.

R.A.S. and D.R.O. prepared the figures and wrote the article.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (<https://academic.oup.com/plphys>) is: Donald R. Ort (d-ort@illinois.edu).

Abstract

Plant stands in nature differ markedly from most seen in modern agriculture. In a dense mixed stand, plants must vie for resources, including light, for greater survival and fitness. Competitive advantages over surrounding plants improve fitness of the individual, thus maintaining the competitive traits in the gene pool. In contrast, monoculture crop production strives to increase output at the stand level and thus benefits from cooperation to increase yield of the community. In choosing plants with higher yields to propagate and grow for food, humans may have inadvertently selected the best competitors rather than the best cooperators. Here, we discuss how this selection for competitiveness has led to overinvestment in characteristics that increase light interception and, consequently, sub-optimal light use efficiency in crop fields that constrains yield improvement. Decades of crop canopy modeling research have provided potential strategies for improving light distribution in crop canopies, and we review the current progress of these strategies, including balancing light distribution through reducing pigment concentration. Based on recent research revealing red-shifted photosynthetic pigments in algae and photosynthetic bacteria, we also discuss potential strategies for optimizing light interception and use through introducing alternative pigment types in crops. These strategies for improving light distribution and expanding the wavelengths of light beyond those traditionally defined for photosynthesis in plant canopies may have large implications for improving crop yield and closing the yield gap.

Introduction

There is a growing need for sustainably increasing crop production per land area. With the global human population expected to reach nine billion by the year 2050 and a growing affluence in some countries that increases the consumption of grain-fed livestock, crop yield per land area may need to double by the middle of the century to keep pace (based on 2005 levels; [Tilman et al., 2011](#)). Crop yields increased by 162% between 1961 and 2005 due to agricultural land expansion and intensification during the Green Revolution ([Burney et al., 2010](#)). However, the rate of yield increase in several major food crops is stagnating ([Long and](#)

[Ort, 2010](#); [Ray et al., 2013](#)), and the detrimental effects of climate change may further challenge agricultural yield improvements ([Lobell et al., 2011](#); [Lobell and Gourdji, 2012](#)). Thus, new methods for advancing crop productivity in a sustainable manner are of increasing importance to meet the challenge of feeding the human population.

Closing the gap between actual and potential crop yields

Increasing realized yields per area requires both increasing the maximum possible regional yield for a given crop in the absence of biotic or abiotic stress (yield potential [Y_p];

Evans and Fischer, 1999) and closing the gap between realized yields and Y_p (Lobell et al., 2009). The Y_p of a crop stand over the growing season was originally described by Monteith (1977) and has been modified by Zhu et al. (2010) to $Y_p = 0.487 S_t \times \varepsilon_i \times \varepsilon_c \times \varepsilon_p$, where approximately half (0.487) of incoming solar radiation (S_t) is available for photosynthesis (defined as 400–700 nm; photosynthetically active radiation [PAR]), available PAR is intercepted with an efficiency of ε_p , intercepted radiation is converted to biomass with an efficiency of ε_c (i.e. net canopy photosynthesis or radiation use efficiency), and biomass is partitioned to harvestable product with an efficiency of ε_p (i.e. harvest index). S_t for field-grown crops largely depends on location and time of year, and although S_t varies inter-annually due to atmospheric conditions, strategies to increase S_t depend on lengthening the growing season or making crops more resilient to conditions that can shorten the season. Although artificial lighting can extend growth duration in controlled environments, such as greenhouses and indoor growth facilities, we focus here on field-grown crops, given the limited feasibility with which many staple crops may be grown in controlled environments. The proportion of S_t used for photosynthesis in plants could potentially increase through introduction of different pigments and their associated proteins in plants (see “Opportunities” below). Of the efficiency terms, which are genetically determined, ε_p and ε_i were largely targeted for improvement during the Green Revolution and are approaching the theoretical limit in most crops (Evans, 1993; Hay, 1995; Sinclair, 1998); therefore, these hold little further potential for improving Y_p in major crop species.

Unlike ε_i and ε_p , ε_c was not increased through genetic improvements in photosynthesis during the Green Revolution and therefore provides potential for increasing Y_p . Studies by Monteith (1965, 1972, 1977) established the concept of ε_c to define crop growth and efficiency based on intercepted light, rather than using rates of growth based on time that could be confounded by light conditions. Despite a clear relationship between intercepted light for photosynthesis and crop growth, initial studies indicated no correlation between increasing photosynthesis and yield (Evans, 1993). However, field studies using free-air CO₂ enrichment technology and the statistical meta-analyses of the data obtained from these types of experiments (Kimball, 1983; Ainsworth et al., 2002; Long et al., 2004; Ainsworth and Long, 2005; Long et al., 2006a) have shown a clear association between sustained increases in photosynthetic efficiency and increased yields across various crops, thus providing motivation for improving photosynthesis to increase yields.

Assessing ε_c in crops under various growth conditions began in the 1970s following the definition of ε_c . More recently, the theoretical maximum ε_c of PAR into biomass was estimated as 12.3% in C4 and 9.4% in C3 plants (Zhu et al., 2010). A quantitative assessment of ε_c in crops from the literature shows realized ε_c in relatively non-stressed conditions is less than half the calculated maxima in several

important C3 and C4 food crops and often less than a third in legumes (Slattery and Ort, 2015). In addition, ε_c significantly declines with abiotic and biotic stresses (Slattery et al., 2013). Importantly, ε_c often declines as S_t increases (Sinclair and Muchow, 1999; Slattery et al., 2013; Slattery and Ort, 2015), indicating major crop canopies overinvest in light capture and underinvest in light utilization, thus leading to inefficient light use.

Numerous strategies have recently been proposed to improve overall photosynthetic efficiency in crops under different growth conditions (Bar-Even, 2018; Slattery et al., 2018; Bailey-Serres et al., 2019; Simkin et al., 2019; Slattery and Ort, 2019; Weber and Bar-Even, 2019). Here, we focus specifically on light use efficiency of crops: how selection for high-yielding individual plants in mixed stands leads to inefficient light use in crop monocultures, the major sources of light use inefficiency, and strategies directly related to light capture and use for improving photosynthesis within leaves and canopies.

Strategies for dealing with heterogeneous light in a mixed stand

Light conditions in a dense canopy are heterogeneous in time, space, quantity, and quality. Light intensity on average is the highest at the top of the canopy but varies with location, time of year, and time of day. Atmospheric aerosols and intermittent clouds also change the incident intensity and ratio of diffuse to direct light. Some light passes through the upper canopy unaltered, as with sunflecks reaching leaves lower in the canopy. However, most light is intercepted by leaves in the upper canopy. As leaves intercept light, the light is either absorbed or scattered, the latter resulting in transmission and reflection. The strong absorption of red and blue light by chlorophylls *a* and *b* in plant chloroplasts results in a decline in both light intensity and ratios of red to far-red, blue to green, and red to green light with canopy depth (Fig. 1). As light quantity and quality decline, plants sense the changes via photoreceptors, such as cryptochromes and phytochromes, which then trigger one of two responses: shade tolerance or shade avoidance (Valladares and Niinemets, 2008; Gommers et al., 2013; Pierik and De Wit, 2014; Fiorucci and Fankhauser, 2017).

The type of shade response typically depends on the overall characteristics of the stand. Upon shading, both shade-tolerant and shade-intolerant plants will maximize light absorption and light use efficiency for carbon gain through increasing specific leaf area, decreasing chlorophyll *a:b* ratios through increased antenna size, and repartitioning nitrogen among the photosynthetic machinery components, namely, to pigment–protein complexes (Givnish, 1988; Evans and Poorter, 2001). However, responses specific to shade tolerance usually occur in forest understories where shaded plants cannot outcompete the surrounding trees. Under these conditions, shade-tolerant species employ strategies to minimize carbon lost through respiration under low-light conditions, often resulting in reduced phenotypic plasticity

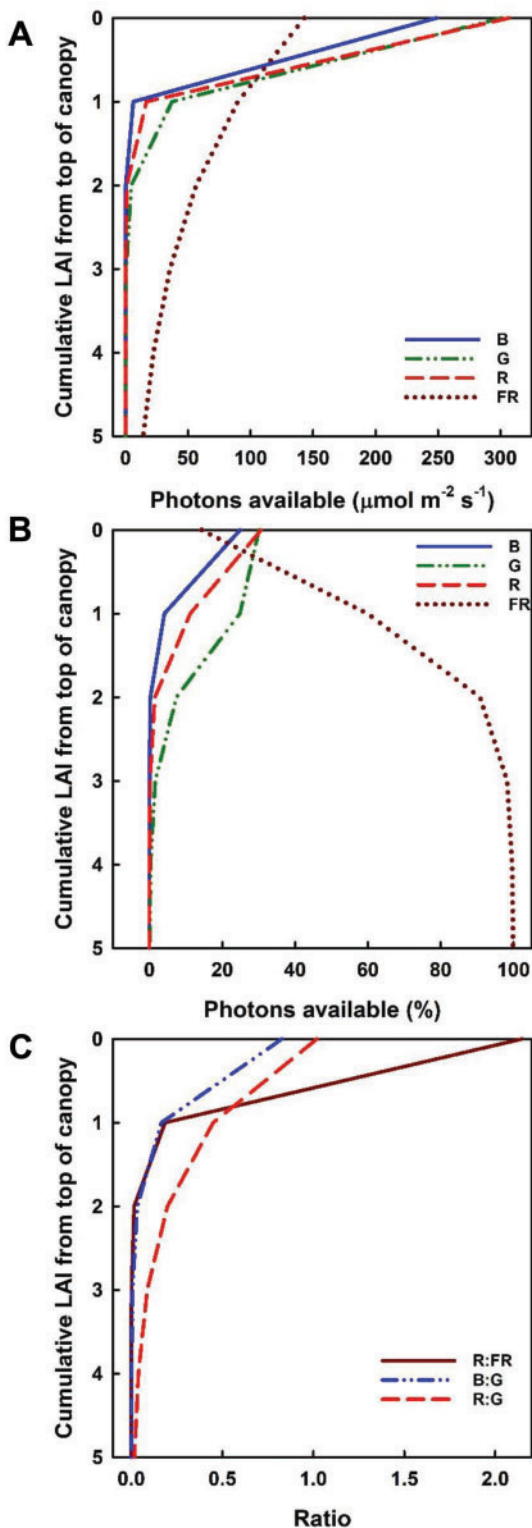


Figure 1 Wavelength-dependent light profiles in canopies. Modeled profiles of absolute photon availability (A), percent photon availability based on total photons within each layer (B), and photon ratios (C) in blue (B; 400–499 nm), green (G; 500–599 nm), red (R; 600–699 nm), and far-red (FR; 700–749 nm) wavelengths within a crop canopy illuminated by $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Absorbance of individual wavelengths in field-grown soybean leaves was used to determine light attenuation with cumulative leaf area index (LAI) from the top of the canopy using the Beer–Lambert equation ($I = I_0 e^{-k \times \text{LAI}}$).

(Valladares and Niinemets, 2008). In contrast, shade avoidance responses occur in canopies where a slight increase in height yields substantial gains in light interception (Fiorucci and Fankhauser, 2017). Rapid stem and petiole elongation, hyponasty, and reduced branching allow leaves to grow toward the light and escape shade conditions, whereas earlier flowering ensures completing reproduction before light levels are severely limited (Casal, 2012). Even when neighboring vegetation does not reduce incident light intensity, the increased reflection of far-red light from nearby plants or the developing canopy and the resulting decrease in the red to far-red ratio can trigger the shade avoidance response in anticipation of competition from neighboring plants (Ballaré et al., 1990; Casal, 2013), thus averting shading by potential competitors.

Shade avoidance responses are advantageous in mixed stands as long as the benefits outweigh the costs. As the costs start to outweigh the benefits, the stand reaches equilibrium and becomes evolutionarily stable. For example, a dense stand with shorter stems allocates relatively more biomass to leaves, thereby maximizing carbon gain at a given leaf area index (LAI) and leaf angle, but should a mutant arise that could grow taller, its leaves would grow above those of other plants, thereby capturing more light and shading competitors. The higher fitness of the mutant could allow it to take over the stand, and the process would repeat until the benefits of growing taller would no longer offset the costs, with the height of the stand becoming evolutionarily stable (Givnish, 1982). A similar phenomenon could occur with chlorophyll concentration, with higher leaf chlorophyll content conferring a competitive advantage until the increased light capture no longer outweighs the costs of chlorophyll and chlorophyll-binding protein production and possibly the efficiency costs of shading its own leaves. However, the characteristics that result in equilibrium or stabilization do not necessarily favor optimization in regards to maximum canopy carbon gain (Hikosaka and Hirose, 1997), especially in monoculture crop canopies (Anten, 2005).

Inefficient light use in monoculture crop canopies

Although investing resources for greater light capture in mixed stands increases fitness of the individual, the same strategy leads to imbalanced light capture and inefficient light use in a monoculture crop canopy. In a closed crop canopy (LAI = 5) at mid-day, only 40% is sunlit (Long, 1993) but may absorb up to 90% of incoming sunlight, whereas less than 10% reaches the lower layers that comprise the majority of the canopy leaf area (Long et al., 2006b). C3 leaf photosynthesis plateaus at light levels equal to approximately 25% of full sunlight. Therefore, competition among plants and/or leaves of a canopy for light results in upper leaves absorbing light in excess of their photosynthetic capacity, resulting in declines in photosynthetic efficiency proportional to the amount of excess light. Meanwhile, lower canopy leaves operate under limiting light that is

often insufficient to compensate for respiration, further reducing ε_c .

Because light levels in the field often oversaturate sun leaf photosynthesis, plants have evolved and employ several interrelated mechanisms within the photosynthetic membrane for coping with excess light absorption (Fig. 2). High light increases the ΔpH across the thylakoid membrane because of water oxidation at photosystem II (PSII) and the Q cycle in cytochrome b_6/f translocating protons from the stroma into the lumen. High ΔpH triggers the rapidly induced energy-dependent quenching (qE) component of non-photochemical quenching (NPQ) to dissipate excess light at PSII as heat (Wraight and Crofts, 1970) with the help of the PSII chlorophyll-binding protein PSBS and zeaxanthin (Demmig-Adams, 1990; Li et al., 2000). Insufficient qE capacity induces the slower photoinhibition (qI) component of NPQ, which occurs as the PSII D1 protein, and likely other proteins involved in electron transport and photoprotection, incur photodamage (Aro et al., 1993; Li et al., 2018; Bethmann et al., 2019). Although costly to repair (Melis, 1999; Murata and Nishiyama, 2018), PSII photoinhibition may present a last line of defense in protecting PSI (Tikkanen et al., 2014). Although PSI effectively quenches excess absorbed light energy as heat, excess electron flow from PSII can irreversibly photoinhibit PSI (Sonoike, 2011). State transitions (qT) also function in NPQ to help balance

excitation energy between the two photosystems (Bonaventura and Myers, 1969; Murata, 1969) through phosphorylation of the light-harvesting complexes (Allen et al., 1981; Larsson et al., 1983; Allen, 1992), which especially helps protect PSI during rapid light fluctuations (Grieco et al., 2012).

Cyclic electron transport (Munekage et al., 2002) also helps prevent photoinhibition of PSI, especially in fluctuating light (Suorsa et al., 2012; Kono and Terashima, 2016; Yamamoto and Shikanai, 2019). In cyclic electron transport, electrons from PSI reduce the plastoquinone pool via ferredoxin and the PROTON GRADIENT REGULATIONS5 (PGR5)/PGR5-LIKE PHOTOSYNTHETIC PHENOTYPE1 (PGRL1) and NADH dehydrogenase-like complexes in the thylakoid membrane to further increase the ΔpH (Munekage et al., 2002; Munekage et al., 2004; Dalcorsio et al., 2008). By increasing ΔpH , cyclic electron transport favors ATP production and slows the electron flow from PSII to PSI in two ways: (1) by slowing the rate of plastoquinone oxidation at cytochrome b_6/f (known as “photosynthetic control”; Foyer et al., 1990) and (2) by increasing the qE component of NPQ (Chaux et al., 2015).

Excess electrons at PSI may also be diverted to reduce O_2 . In pseudocyclic electron transport, O_2 reduces to H_2O through the Mehler reaction in the water–water cycle (Mehler, 1951; Asada, 1999). Although the contribution of

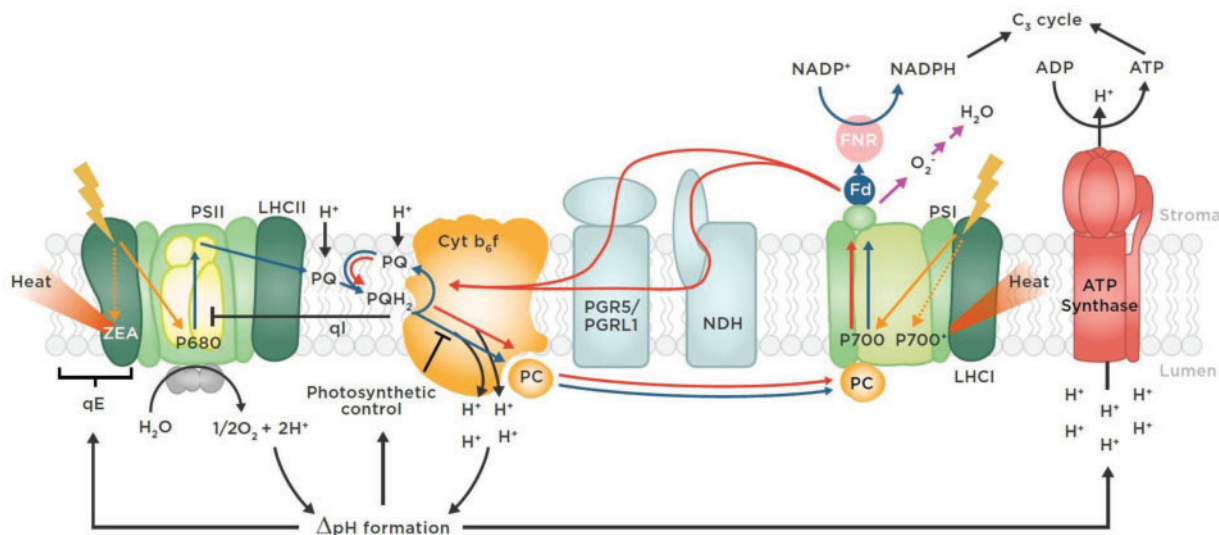


Figure 2 Photoprotection of the photosynthetic membrane. In linear electron transport (blue lines), photosystem II (PSII)-associated light-harvesting complexes (LHCII) transfer excitation energy from an absorbed photon (solid orange line) to PSII, resulting in the splitting of water. Electrons from water flow from PSII to cytochrome b_6/f (Cyt b_6/f) via reduction of plastoquinone (PQ) to plastoquinol (PQH_2), translocating H^+ from the stroma to the lumen via the Q cycle. Plastocyanin (PC) carries the electrons to photosystem I (PSI), where the excitation energy from a second absorbed photon (solid orange line) eventually leads to the reduction of NADP^+ to NADPH via ferredoxin (Fd) and Fd-NADP⁺ oxidoreductase (FNR). Linear electron transport increases the ΔpH across the thylakoid membrane, which drives ATP synthesis through ATP synthase. A large ΔpH triggers dissipation of excitation energy in excess of PSII capacity (dashed orange line) as heat via zeaxanthin (Zea) in the energy-dependent component (termed “qE”) of non-photochemical quenching. P700^+ quenches the excess excitation energy transferred from PSI-associated light-harvesting complexes (LHCI) to PSI (dashed orange line) and releases the energy as heat. Some electrons received by PSI flow through PGR5/PGRL1- or NDH-mediated cyclic electron transport (red lines), which further increases ΔpH and qE and prevents oxidation of PQH_2 to PQ at Cyt b_6/f (termed “photosynthetic control”). This slows electron flow through linear electron transport and induces photoinhibition (qI) of PSII in extreme light stress to prevent irreversible damage to PSI. Excess electrons at PSI may also flow through pseudocyclic electron transport in the water–water cycle (magenta arrows). Figure adapted from Yamamoto and Shikanai (2019).

the water–water cycle is limited in steady-state conditions (Badger et al., 2000; Shirao et al., 2013), it may play a larger role under fluctuating light (Huang et al., 2019). O₂ is also reduced in photorespiration as it competes with CO₂ at the active site of Rubisco, producing p-glycolate rather than p-glycerate (Bowes et al., 1971; Ogren and Bowes, 1971). Photorespiration is energetically expensive and may consume 30% or more of the electrons from PSI in C3 plants (Walker et al., 2016).

The mechanisms outlined above represent a tradeoff between photoprotection and light use efficiency in plants. Photoprotection dissipates absorbed light that could otherwise be used for photochemistry, either in upper canopy leaves with the removal of downstream limitations (see reviews for improving photosynthetic efficiency listed above) or in lower canopy leaves where light is limiting. The processes themselves can also be inefficient. For example, although NPQ is rapidly induced, modeling suggests the slow rate of NPQ relaxation lowers daily canopy photosynthesis by up to 30% in natural light environments (Zhu et al., 2004), and engineering for faster NPQ relaxation increased biomass production in the field by 15% (Kromdijk et al., 2016). Therefore, engineering crops to both reduce the need for these photoprotective processes while improving their efficiency when employed can increase light use efficiency.

Why do monoculture crops overinvest in light capture?

Competition in mixed stands causes plants to overinvest in light harvesting to increase fitness at the detriment of efficiency. This is a “tragedy of the commons” situation in which individuals overexploit a resource at the expense of the population, taking more than is needed by the individual with the added benefit of denying other individuals, who could be considered competitors, of that resource (Hardin, 1968). As exemplified above, an individual plant in a mixed stand that is able to elongate or increase pigment concentration to capture more light will ultimately increase its fitness while decreasing the fitness of the surrounding plants. But why is this competitive nature so prevalent in monoculture crops where high stand production is the goal?

Donald (1968) was the first to examine the impacts of the “tragedy of the commons” notion in crop breeding and showed that inefficient resource use in canopies has been inadvertently selected for in crops. Traditional breeding primarily uses yield of individual plants as the criterion for selection, although marker-assisted or genomic selection of individuals has become more prevalent prior to field plot performance testing (Cabrera-Bosquet et al., 2012; Breseghello, 2013). Selecting choice specimens for higher yields at the level of the individual, rather than at the level of the stand, often leads to selection of individuals with comparatively higher productivity by overinvestment in capturing light (or other resources), thus outcompeting the neighboring plants (Donald, 1968; Zhang et al., 1999). Once grown in a monoculture, the genetic copies of the successful

individual likewise overinvest in resource harvesting for competitiveness at the detriment of stand-level productivity.

In addition to selecting for competitiveness, Donald (1968) also argued selection for yield using individual plants often lacks an understanding of the physiological basis for the yield improvement and is limited to selecting from the genetic material available. Donald (1968) therefore advocated breeding for crop ideotypes whereby modeling determines the characteristics expected to increase yield quantity or quality when incorporated in a crop. Using this approach, Donald (1968) proposed a wheat (*Triticum aestivum*) ideotype with characteristics that seemed contrary to those of a successful plant, including weak competitiveness, but would therefore be more successful in dense monocultures. Although Donald (1968) acknowledged this method likely increases the time to produce commercially viable products, he noted greater potential exists to produce higher yielding varieties than the selection for yield from among the existing genetic material. Thus, breeding began to incorporate traits modeled to improve productivity.

Modeling canopy characteristics for greater light use efficiency and yield

Early canopy modeling examined the relationship between plant architecture and efficient light capture and light use in carbon assimilation. Boysen Jensen (1932) initially established the connection between leaf arrangement and light distribution within a canopy and showed that while leaf photosynthesis saturates at low light levels, canopy photosynthesis does not. Building on the ideas of Boysen Jensen (1932), Monsi and Saeki (1953) developed quantitative relationships between canopy light distribution and photosynthesis. They showed light attenuation in plant canopies declines exponentially with canopy depth and therefore follows the Beer–Lambert equation ($I = I_0 e^{-k \times LAI}$), where I is the light incident on a leaf layer, I_0 is the light incident at the top of the canopy, k is the light extinction coefficient (assuming k does not change with canopy depth), and LAI is the cumulative LAI from the top of the canopy (Monsi and Saeki, 1953). This light distribution relationship was applied to several early canopy photosynthesis models (Monsi and Saeki, 1953; Saeki, 1960; de Wit, 1965; Duncan et al., 1967). Although the biochemical properties of sun and shade leaves differ due to light availability (Boardman, 1977; Bjorkman, 1981), Monsi and Saeki (1953) assumed equal photosynthetic capacity for each leaf in the canopy and developed their model using diffuse light, not direct. With enhanced computing technology, subsequent models by de Wit (1965) and Duncan (1967) incorporated the difference in diffuse versus direct sunlight, leaf and sun angles, leaf distribution in the canopy, and photosynthetic capacity to increase the accuracy of canopy photosynthesis models. Fast-forward to the last decade of crop modeling, which has incorporated even greater complexity and accuracy in modeling crop canopy light transmission, such as reconstructing three-dimensional canopy architecture (Song et al., 2013; Burgess et al., 2015;

Burgess et al., 2017; Wang et al., 2017; Chang et al., 2019) and accounting for fluctuating incident light (Wang et al., 2020) and canopy movement due to wind (Burgess et al., 2016).

By characterizing the light environment within plant canopies and the effects on canopy photosynthesis using models, potential ways to alter canopy architecture for improved canopy light distribution emerged. With a constant value for k , canopies with limited incident light and lower LAI were predicted to have increased photosynthesis with high k (horizontal leaves), whereas canopies with high light and high LAI would benefit from low k (vertically oriented leaves) to ensure light levels in the lowest leaves were equal to the light compensation point of those leaves (Monsi and Saeki, 1953; Saeki, 1960; de Wit, 1965; Duncan et al., 1967). To optimize canopy photosynthesis, Verhagen et al. (1963) proposed k should change within a canopy to ensure similar light levels for each leaf, and Kuroiwa (1971) proposed an optimal canopy with more vertically oriented leaves at the top and more horizontally oriented leaves at the bottom, which would increase k with canopy depth. More recent modeling predicted upright leaves at the top of the canopy would improve light penetration to the lower canopy and more than double light use efficiency when the sun was directly overhead at high LAI (≥ 3 ; Long et al., 2006b). However, the increase in efficiency declined when accounting for changing sun angles over the course of the day, and canopy photosynthetic efficiency remained the same or decreased at low LAI (< 1.5 ; Long et al., 2006b).

Improving light distribution using altered canopy architecture has been associated with greater yields in some crops. For example, rice (*Oryza sativa*) cultivars bred to match the ideotype with more upright leaves in the upper canopy have played a role in the development of “super” hybrid rice breeding in China (Yoshida, 1972; Beadle and Long, 1985; Peng et al., 2008). Maize (*Zea mays*) yields have also increased with leaf angle but may be confounded by the accompanying increase in planting density (Duvick, 1997, 2005).

Altering leaf absorbance through reduced leaf chlorophyll content offers another potentially more robust strategy for increasing crop productivity through redistribution of light among leaves in the canopy. Light intercepted but not absorbed by leaves, which occurs to a greater extent with lower pigment concentration, scatters due to leaf transmission and reflection. The model by de Wit (1965) accounts for light scattering within canopies and shows more scattering benefits photosynthesis at high LAI under high light intensity, but the opposite occurs under low LAI and low light due to more light lost to the soil or to the atmosphere outside of the canopy. Monteith (1965) showed a similar relationship, noting that ϵ_c increases as transmission of light through leaves increases at high LAI. Gutschick (1988) modeled the impacts of reduced leaf chlorophyll on canopy photosynthesis and found modest increases in canopy photosynthesis are possible in high light conditions. Moreover, these gains occur independently of solar elevation, as

opposed to the gains in canopy photosynthesis predicted with erect leaves (Duncan et al., 1967; Gutschick, 1988; Long et al., 2006b). In WIMOVAC, a sun-shade model (Humphries and Long, 1995), reducing k by approximately half results in optimal rates of canopy photosynthesis, but further reductions in k lower canopy photosynthesis (Ort et al., 2011). Because changes in k can be achieved through changes in chlorophyll content, these results suggest reducing chlorophyll content by half could increase canopy carbon gains, but further reductions in chlorophyll would be disadvantageous (Ort et al., 2011).

More sophisticated multi-layer canopy modeling studies estimate additional benefits of reducing chlorophyll content on canopy photosynthesis. A study by Walker et al. (2018) shows chlorophyll content could be reduced by at least half with no penalty to canopy photosynthesis while also resulting in a potential 9% savings in leaf nitrogen. Song et al. (2017) also predicted modest increases in canopy photosynthesis and nitrogen use efficiency with 60% reductions in chlorophyll. Moreover, benefits to canopy photosynthesis with reduced chlorophyll could increase by 10-fold and nitrogen use efficiency by two-fold were nitrogen savings reinvested into photosynthetic machinery (Zhu et al., 2007; Song et al., 2017). Secondary benefits could also manifest with lower chlorophyll content, such as higher albedo lowering leaf temperature at the top of the canopy and increased water use efficiency due to a greater proportion of photosynthesis occurring deeper in the canopy where relative humidity is higher (Drewry et al., 2014).

At the leaf scale, modeling suggests a more even light distribution among chloroplasts within leaves could increase leaf photosynthetic efficiency. As with leaves in a canopy, chloroplasts within a leaf exhibit imbalanced light distribution (Fig. 3), which can lead to inefficient light use at the leaf level. Decreased absorption, or absorption flattening, due to chlorophyll packaged in chloroplasts (termed the “sieve effect”, Duyens, 1956) offsets the increased path-length due to light scattering at cell wall interfaces (termed the detour effect; Kok, 1948), resulting in light attenuation within leaves also following the Beer–Lambert equation (Terashima and Saeki, 1983). Strong absorption of red and blue light by chlorophylls a and b in chloroplasts results in approximately 90% of the available blue and red light absorbed in the upper 20% of the leaf (Cui et al., 1991). Thus, despite the low absorbance of green light by these pigments, green light drives a greater proportion of photosynthesis in the lower leaf, similar to the lower leaves of the canopy (Sun et al., 1998; Nishio, 2000; Terashima et al., 2009).

Light gradients within leaves alter photosynthetic capacity as a function of leaf depth, similar to the change in photosynthetic capacity in sun versus shade leaves. Thus, photosynthetic capacity declines with declining light availability with leaf depth (Terashima and Inoue, 1984; Terashima and Inoue, 1985a, 1985b; Terashima and Hikosaka, 1995; Terashima et al., 2005). Photoprotection and photosynthetic efficiency also vary depending on the light gradients: higher

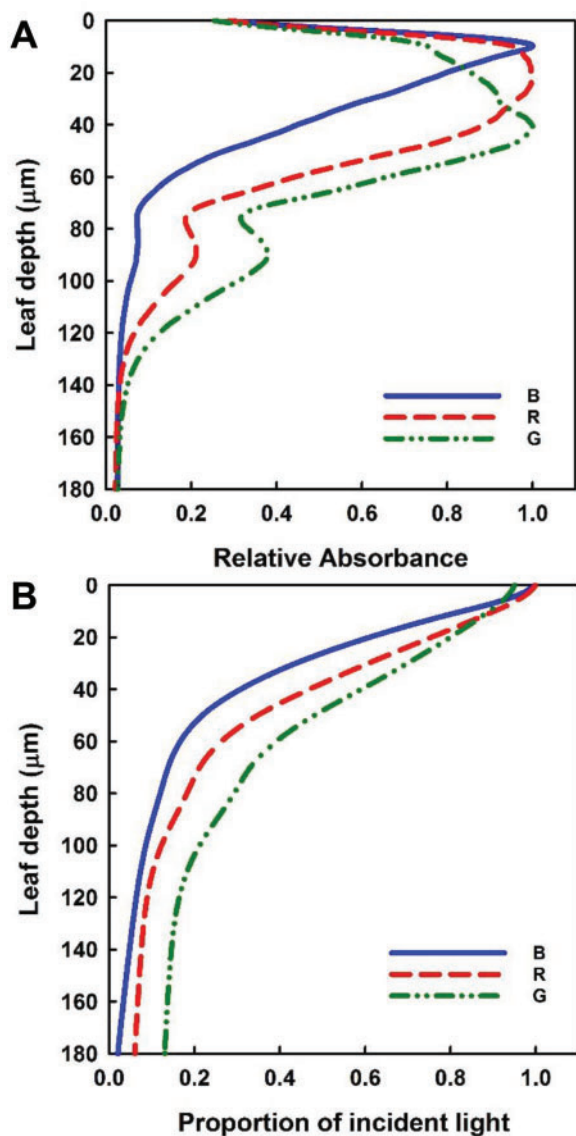


Figure 3 Wavelength-dependent light profiles in leaves. Profiles of relative absorbance (A) and the proportion of available light (B) in blue (B; 488 nm), green (G; 561 nm), and red (R; 638 nm) wavelengths within wild-type soybean leaves illuminated from the adaxial surface (data based on light-sheet microscopy analyses in Slattery et al. (2016)).

levels of photoprotection occur in the upper chloroplasts with red and blue light illumination versus with green light illumination (Schreiber et al., 1996; Oguchi et al., 2011). Thus, achieving more gradual gradients in light within leaves through reduced chlorophyll content, resulting in more light reaching lower leaf chloroplasts, could increase leaf photosynthesis and photosynthetic efficiency.

Theory versus reality: how experiments compare to expected

Dense cultures of algae used in producing synthetic chemicals and biofuels support reducing chlorophyll content to improve photosynthetic efficiency. As with plant canopies,

imbalanced light distribution occurs in algae cultures, but decreased pigmentation in the *truncated light antennae1* (*tla1*) mutant improves light penetration, photosynthetic efficiency (Melis, 1999; Polle et al., 2002; Mitra and Melis, 2008), and hydrogen production (Kosourov et al., 2011) in the microalgal cultures. Reducing the phycobilisome light-harvesting antenna in cyanobacteria produces similar results (Kirst et al., 2014). Chlorophyllide *a* oxygenase (CAO) catalyzes the two-step conversion of chlorophyllide *a* to chlorophyllide *b* (Oster et al., 2000), and recent work shows translational suppression of CAO expression regulated by high light intensity leads to greater biomass production in green algae (Negi et al., 2020). Although promising, these results from algal cultures may not necessarily extrapolate to plant leaves and canopies due to differences in light environments. For example, refraction at leaf internal airspaces substantially alters light paths within leaves, and plant canopies in the field experience greater variability in light intensity due to self-shading, sunflecks, and intermittent clouds.

Plenty of computational evidence suggests reducing chlorophyll content will increase crop canopy light use efficiency, as discussed above, and experimental evidence at the canopy level has shown promising results. Field studies using a chlorophyll-deficient soybean (*Glycine max*) isolate in the “Clark” background (Y11y11) show the mutant has similar or greater rates of canopy photosynthesis (per unit leaf area) than the wild type despite having less than half the leaf chlorophyll content (Pettigrew et al., 1989; Slattery et al., 2017). A soybean line with the same gene mutation as Y11y11 but in a different genetic background shows similar results despite almost 80% reductions in leaf chlorophyll (Sakowska et al., 2018). Although similar in wide row spacing, ϵ_c increases by 10% in the mutant (albeit non-significantly) in narrow row spacing (Slattery et al., 2017), suggesting the benefits of lower chlorophyll may be more evident under planting strategies where canopy closure occurs earlier. Effects of reduced chlorophyll on end-of-season soybean yields vary from 28% greater in 1 year of study (Pettigrew et al., 1989) to similar or slightly reduced in the Y11y11 mutant compared to the wild type, likely due to pleiotropic effects in the mutant (Slattery et al., 2017). In rice, low-chlorophyll plants with deeper light penetration within the canopy display significantly higher yields than the wild type at high planting density (Gu et al., 2017).

At the leaf level, field-grown chlorophyll mutants in various species match or exceed wild-type rates of photosynthesis per absorbed photon at high light (Highkin et al., 1969; Benedict et al., 1972; Marco et al., 1989; Xu et al., 1993; Habash et al., 1994; Li et al., 2013; Gu et al., 2017; Slattery et al., 2017; Sakowska et al., 2018). Some mutants exhibit equal or greater Rubisco carboxylation rates (Gu et al., 2017; Slattery et al., 2017; Sakowska et al., 2018) and greater photosynthetic nitrogen use efficiency (Gu et al., 2017; Sakowska et al., 2018). Increases in photosynthesis also often coincide with greater photosynthetic efficiency during steady-state conditions. Blue and red light wavelengths attenuate more gradually within low-chlorophyll soybean mutant leaves as

compared to the wild type, corresponding with increased photosynthetic efficiency in the mutant leaves and greater light availability to lower chloroplasts, which in turn corresponds with a more even distribution of modeled rates of photosynthesis (Slattery et al., 2016). Taken together, these results provide evidence of increased photosynthetic efficiency in low-chlorophyll leaves in steady-state conditions.

Although reducing chlorophyll shows promise in improving photosynthetic efficiency, low-chlorophyll mutants often display disadvantages associated with the mutations. Naturally occurring mutants display low chlorophyll at the top of the canopy throughout the season, usually with the lowest chlorophyll content present early in the season before canopy closure, leading to reduced ϵ_i due to increased light transmission to the soil. For example, the soybean mutant $\gamma\gamma 9$ exhibits approximately 40% leaf chlorophyll content compared to the wild type when averaged over the growing season but less than 15% early in the season and significantly lower ϵ_i and yield as compared to the wild type (Slattery et al., 2017). Additionally, increased leaf reflectance results in fewer photons absorbed at the top of the canopy, further lowering ϵ_i . Although modeling suggests the negative impact of lower ϵ_i due to increased reflectance could be offset by the benefits of more even light distribution in the canopy (Drewry et al., 2014; Walker et al., 2018), this may depend on the magnitude of ϵ_i reductions and therefore the timing and extent of chlorophyll reduction in plant canopies.

The mutations resulting in reduced chlorophyll content may also inhibit projected impacts on canopy processes. Low chlorophyll in the soybean mutants $Y11y11$ and “MinnGold” (used by Sakowska et al. (2018)) results from mutations in subunit I of magnesium chelatase (Campbell et al., 2015), which also plays a role in abscisic acid signaling and stomatal movement (Du et al., 2012; Tomiyama et al., 2014). Therefore, these specific mutations could negatively affect yield through soil water depletion, especially when drought conditions occur during key development stages (Slattery et al., 2017). Mutations resulting in severely reduced chlorophyll *b* also inhibit photosynthesis and photoprotection (Leverenz et al., 1992; Havaux and Tardy, 1997; Kim et al., 2009), therefore suggesting more uniform reductions in chlorophyll *a* and *b* are required to avoid detrimental effects. Lastly, specific reductions in chlorophyll may affect NPQ kinetics, which could further limit carbon gain in field settings during high-to-low light transitions (Sakowska et al., 2018). Thus, engineering canopies with lower chlorophyll requires more sophisticated methods than using naturally occurring mutants, as we discuss below.

Opportunities to engineer improvements

Increasing the efficiency of low-chlorophyll plants

The modeling and experimental evidence discussed above shows promise in increasing crop productivity through lowering leaf chlorophyll content, but several strategies are required for low-chlorophyll canopies to reach their full

predicted potential. Reducing chlorophyll content through regulating the enzymes within the chlorophyll biosynthetic pathway requires careful consideration. Enzymes early in the pathway participate in synthesis of all tetrapyrroles, including hemes, which are involved in respiration and photosynthesis, and sirohemes, which are essential for nitrogen and sulfur assimilation (Murphy et al., 1974). Thus, downregulation of shared enzymes may impact levels of tetrapyrroles other than chlorophyll (Kumar and Sö, 2000). In addition, downregulating enzymes in the middle of the pathway could lead to accumulation of phototoxic intermediates (Kruse et al., 1995; Mock and Cri, 1997; Hu et al., 1998; Molina et al., 1999; Ishikawa et al., 2001). Thus, the remaining candidates for modification comprise enzymes specific to the chlorophyll branch of tetrapyrrole biosynthesis (Tanaka and Tanaka, 2007).

Modifying chlorophyll branch-specific enzymes requires further refinement, such as avoiding proteins known to also function in other pathways that could produce pleiotropic effects (e.g. specific subunits of magnesium chelatase, as discussed above). The level of downregulation also requires careful consideration to avoid severe chlorophyll *b* deficiency. For example, partial suppression of the gene for CAO in *Camelina sativa* increases the chlorophyll *a:b* ratio by less than two-fold and enhances photosynthetic performance and growth through reduced antenna size. However, further suppression leads to much higher chlorophyll *a:b* ratios and greater reductions in antenna size that decrease photosynthetic performance (Friedland et al., 2019). Chlorophyll synthase also fits these criteria: downregulated expression in tobacco (*Nicotiana tabacum*) feeds back to regulate the entire pathway without producing phototoxic intermediates, altering levels of other tetrapyrroles, or substantially increasing chlorophyll *a:b* ratios (Shalygo et al., 2009), making it another prime target for reducing crop leaf chlorophyll content.

Reducing pigmentation could also be achieved through mutation of antenna proteins but may require selective modification. Reductions in minor light-harvesting complexes that connect the major light-harvesting complexes to the PSII core, such as CP24 and CP29, are detrimental to excitation energy transfer, photoprotection, and PSII stability (Van Oort et al., 2010; Miloslavina et al., 2011; Dall'Osto et al., 2014). However, mutation of some major antenna proteins reduces chlorophyll content while maintaining both photosynthetic and photoprotective capacity (Bielczynski et al., 2020), especially when occurring in antennae involved in state transitions and therefore absorption energy transfer to both photosystems (Wientjes et al., 2013a, 2013b).

The timing of chlorophyll reduction also requires optimization to minimize transmission of incident light to the soil early in the season. Ideally, the leaves at the top of the canopy would remain fully green until canopy closure, after which chlorophyll production could be lowered in newly developing leaves at the top of the canopy using inducible promoters as a “switch.” At that time, resources that would

otherwise be directed toward chlorophyll biosynthesis, such as nitrogen, could instead be targeted elsewhere. One promising target includes enzymes identified as limiting to the Calvin–Benson cycle, the enhanced expression of which could increase photosynthetic efficiency (Simkin et al., 2017), especially under future climate conditions (Rosenthal et al., 2011; Köhler et al., 2017).

Altered canopy chlorophyll profiles could pair with gradients in antenna size and reaction center number. Reaction centers are costly for plants to make and maintain, so canopies could be fine-tuned to have more reaction centers with smaller antennae at the top of the canopy where light is saturating. Conversely, fewer reaction centers with larger antennae toward the bottom of the canopy would also benefit canopy photosynthesis, especially if designed to capture light in the more readily available wavelengths (i.e. green and far-red; Ort et al., 2015), but the genes controlling these processes remained to be discovered.

Expanding the photosynthetic light spectrum

Although reducing leaf chlorophyll *a* and *b* concentration could increase Y_p through increasing ε_o , efficient use of wavelengths outside the PAR region of S_t could also increase Y_p (Blankenship and Chen, 2013). Because photosynthesis is a photonic process driven by the energy of a red photon, the inverse relationship between wavelength and energy means absorption of photons with wavelength < 400 nm results in less efficient energy use. In addition, solar photon flux peaks near 600 nm but declines sharply at wavelengths < 400 nm; thus, expanding beyond the red end of the PAR spectrum has more potential benefit and higher efficiency than toward the blue (Fig. 4A). In theory, absorbing photons in the far-red range (from 701 to 750 nm) in addition to photons within the range of PAR could increase the photosynthetic photon flux by 19% at the Earth's surface (Chen and Blankenship, 2011).

Early work that led to the identification of the two photosystems in oxygenic photosynthesis shows far-red light by itself (> 685 nm) is insufficient to drive photosynthesis (Emerson and Lewis, 1943; Emerson et al., 1957; Emerson and Rabinowitch, 1960). However, more studies are finding benefits of supplemental far-red light to photosynthesis. For example, far-red light helps drive photosynthesis in steady-state conditions when PAR is sufficiently available (Zhen and van Iersel, 2017; Zhen et al., 2019), and supplementing artificial white light with far-red (up to 40% of baseline white light levels) increases canopy and leaf photosynthesis in several C3 and C4 species by balancing the excitation of the two photosystems (Zhen and Bugbee, 2020). In fluctuating light conditions, far-red light helps prevent photoinhibition of PSI (Kono et al., 2017) and maintains photosynthesis rates immediately following transitions from high to low light (Kono et al., 2020). Thus, evidence suggests far-red light should be included in the definition of PAR.

Although far-red light stimulates photosynthesis, greater efficiency of far-red light absorption and use could further enhance carbon assimilation (Ort et al., 2015). Absorption of

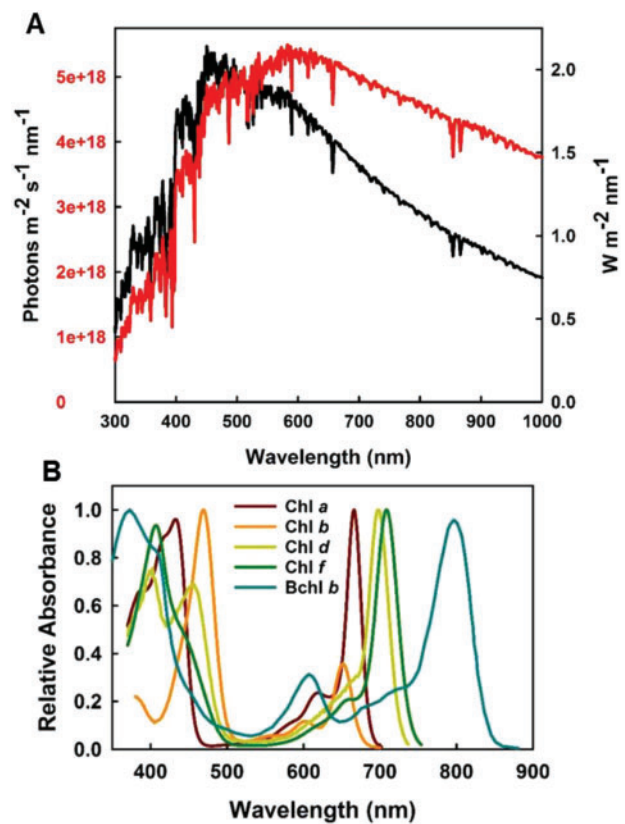


Figure 4 Solar energy spectrum and pigment absorption profiles. (A) Solar output versus wavelength in terms of number of photons (red) and amount of energy (black) from ASTM E-490 (<https://www.nrel.gov/grid/solar-resource/spectra.html>). (B) Relative absorbance spectra of chlorophylls (Chls) and bacteriochlorophyll (BChl) *b* in solvents. Chlorophyll absorbance data were obtained from <http://vplapps.astro.washington.edu/pigments>. BChl absorbance data were obtained from Frigaard et al. (1996).

far-red light would be most beneficial for balancing the excitation of the two photosystems in the upper leaves of crop canopies where shorter wavelengths are sufficient (Zhen and Bugbee, 2020). However, poor absorbance of far-red light leads to greater availability in the lower canopy where the benefits may not be observed due to insufficient white light (Fig. 1). In addition, the benefits of far-red light to photosynthesis decline at higher wavelengths (approximately > 725 nm) due to decreasing absorption of far-red light by chlorophylls *a* and *b* and lower photon energy as wavelength increases (Zhen et al., 2019; Zhen and Bugbee, 2020). Thus, engineering for greater absorbance at optimal locations within the canopy and more efficient use of absorbed far-red light could improve canopy photosynthesis.

Other organisms with absorption in the far-red light region of the solar spectrum present models for expanding far-red light absorption in plants. The absorbance of chlorophyll *a* contained in PSI light-harvesting antennae red-shifts to some extent (Rivadossi et al., 1999; Wientjes and Croce, 2011), but some algal species red-shift the absorption of chlorophyll *a* even further and are capable of sufficient up-hill energy transfer to drive PSII under far-red light growth

conditions (Wilhelm and Jakob, 2006; Wolf et al., 2018). Bacteria extend absorbance further into the far-red range through biosynthesis and incorporation of alternative pigments into the light-harvesting antennae (Fig. 4B). The oxygen-evolving cyanobacteria *Acaryochloris marina* primarily uses chlorophyll *d* for photosynthesis in far-red light-enriched environments, which shifts the red absorption maximum to approximately 715 nm (Miyashita et al., 1996). Chlorophyll *f*, which was discovered in 2010 (Chen et al., 2010), allows red absorption at wavelengths >760 nm and plays a role in charge separation in *Chroococcidiopsis thermalis* under far-red light despite its relatively low abundance compared to chlorophyll *a* (Nürnberg et al., 2018). Purple bacteria type 2 reaction centers use bacteriochlorophyll *b*, which absorbs wavelengths beyond 1,000 nm (Blankenship et al., 1995).

Current antenna and reaction centers in crop plants may require modification for the efficient transfer of far-red light excitation energy to reaction centers. Research shows red-shifted absorbance of chlorophyll *a* in algae requires multimerization of the light-harvesting antenna (Bína et al., 2014; Kotabová et al., 2014; Wolf et al., 2018; Litvín et al., 2019), and hydrogen bond strength drives the extent of the redshift (Llansola-Portoles et al., 2020). Although modest uphill energy transfer occurs between the antennae and PSI reaction centers in plants, it slows excitation energy transfer among pigments in the antennae and charges separation within the reaction center (Wientjes et al., 2011). The chlorophyll *a* special pair of plant reaction centers limits how far antenna absorption can shift and still transfer energy to the reaction center in plants, whereas chlorophyll *d* in the reaction centers of *A. marina* allows excitation energy transfer from low-energy, high-wavelength absorbing pigments to drive PSII photochemistry (Itoh et al., 2007; Schlodder et al., 2007). As researchers strive for a better understanding of how cyanobacteria remodel photosynthetic complexes to incorporate chlorophylls *d* and/or *f* in response to far-red light enrichment (Gan et al., 2014; Ho et al., 2020), these changes may be used to alter the photosynthetic machinery in crop plants.

Recent work provides proof-of-concept for incorporating chlorophylls other than *a* and *b* in plant light-harvesting antennae. Chlorophyll *f* synthase, which is encoded by a single gene, converts chlorophyll *a* and chlorophyllide *a* to chlorophyll *f* (Ho et al., 2016), has been expressed in *Synechococcus* spp. PCC 7002 with successful insertion into PSI complexes (Shen et al., 2019), and demonstrates the potential to transform crop plants to produce chlorophyll *f* and expand absorption up to 750 nm into the far-red light spectrum (Kurashov et al., 2019; Tros et al., 2020). However, quantum efficiency declines with wavelength in the far-red region (700–750 nm; Kurashov et al., 2019), and cyanobacteria with native chlorophyll *f* expression and the complete far-red light-induced response absorb wavelengths up to 800 nm (Nürnberg et al., 2018). Therefore, additional engineering of the chlorophyll-binding proteins involved in the far-red light response will be required to optimize far-red light absorption and use in crop plants.

Conclusions

Selection for fitness over cooperation has inadvertently led to resource use inefficiency in crop stands, especially with regards to light. Canopy modeling from the past 60+ years indicates engineering for more efficient light capture and use provides a sustainable strategy for increasing crop production to close the yield gap and help feed and fuel the human population. Although architectural modification of a few key crops has shown some success in improving light use efficiency, early efforts in reducing pigmentation as a more robust alternative also provide encouraging results. Expanding the definition of light wavelengths available for oxygenic photosynthesis through additional red-shifted pigments represents another currently untapped resource with the potential for large gains in overall carbon accumulation. Of course, increasing production is just one facet of feeding the human population, and other aspects of food production will also require attention, such as increasing the proportion of harvestable product directly consumed by humans, to help meet this challenge.

Acknowledgments

We thank Jillian Nickell for her assistance in illustrating Fig. 2. This work is supported by the research project Realizing Increased Photosynthetic Efficiency (RIPE) that is funded by the Bill & Melinda Gates Foundation, Foundation for Food and Agriculture Research, and the UK Foreign, Commonwealth & Development Office under Grant number OPP1172157.

Funding

This work is supported by the research project Realizing Increased Photosynthetic Efficiency (RIPE) that is funded by the Bill & Melinda Gates Foundation, Foundation for Food and Agriculture Research, and the U.K. Foreign, Commonwealth & Development Office under grant number OPP1172157.

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