

Manipulation of Photoprotection to Improve Plant Photosynthesis¹

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Light is of course essential for photosynthesis and supports most life on earth. However, light intensity and spectral quality are highly variable in space and time according to time of day, season, geography, climate, and the position of leaf within canopy and cell within leaf. This has resulted in the evolution of a remarkable suite of processes within the photosynthetic system to accommodate these fluctuations. In fact, these regulatory mechanisms are tightly integrated with photosynthesis itself, and there is emerging evidence that when these processes are altered, the ability of plants to assimilate carbon over long time periods and to produce biomass may be affected.

Photosynthesis begins with the absorption of light by chlorophyll, much of which is located in the light-harvesting complexes (LHCs) of PSII and PSI within the thylakoid membrane of chloroplasts. Chlorophyll enters its singlet excited state, and excitation energy is transferred to PSII and PSI reaction centers where charge separation occurs and photosynthetic electron transport is initiated. Electrons derived from water splitting ultimately reduce NADP⁺ to NADPH, and the transmembrane ΔpH is used to drive ATP generation by the chloroplastic ATP synthase. NADPH and ATP are then used in the Calvin-Benson cycle and other assimilatory reactions. In addition to this linear electron flow, there is flexibility in the electron transport system with multiple pathways and electron acceptors possible. These include cyclic electron transfer and oxygen as an electron acceptor.

Absorbed solar energy may be defined as excessive when it exceeds the capacity of photosynthesis to use it for assimilation. Although excess light is potentially harmful, plants have a plethora of mechanisms that manage the excess absorbed energy on a molecular level in a way that does not result in photooxidative stress. Photoprotection is a rather broad term that can be used to cover mechanisms that prevent light energy

from inducing damage via the generation of high levels of reactive oxygen species (ROS). Although ROS are important signaling molecules in plants, they can have deleterious effects on photosynthesis and other leaf processes that ultimately will reduce growth and plant fitness. The most extreme example of this is photobleaching and cell death.

Much of our current knowledge about photoprotection comes from studies of mutants and transformants of *Arabidopsis* (*Arabidopsis thaliana*) and other plants in which the level of expression of key genes has been altered with subsequent changes to protein level, resulting in changes to the capacity and the kinetics of some photoprotective processes. This work has resulted in advances in understanding the mechanisms and the physiology of these processes. An exciting possibility is that manipulating photoprotective pathways is a means to enhance both stress resistance and photosynthetic productivity of crop plants. However, there may be a balance between the need for photoprotection to limit damage on the one hand and enhancing productivity on the other (Murchie et al., 2009). There seems to be much yet to learn: Here, we review the current state of photoprotection research focusing on mechanisms that are potential targets for manipulation to improve photosynthesis.

PHYSIOLOGICAL PRINCIPLES OF PHOTOPROTECTION AND PHOTOINHIBITION

The response of leaf photosynthesis to light is best demonstrated with a light response curve (Fig. 1). As light (photon flux density) increases, the rate of photosynthesis rises until it is saturated (A_{max}). The slope of the initial linear portion of this curve is the maximum quantum yield (efficiency) of photosynthetic CO₂ uptake (Φ_{CO_2}) or oxygen evolution (Φ_{O_2}). The maximum quantum yield of PSII can be estimated by the ratio of variable chlorophyll fluorescence to maximal fluorescence (F_v/F_m).

Plants are subject to a huge variety of factors that limit growth and photosynthetic rate. These can be imposed by the environment, such as water and nutrient deficiency and temperature, or they may be intrinsically enforced by low sink strength or a genetically

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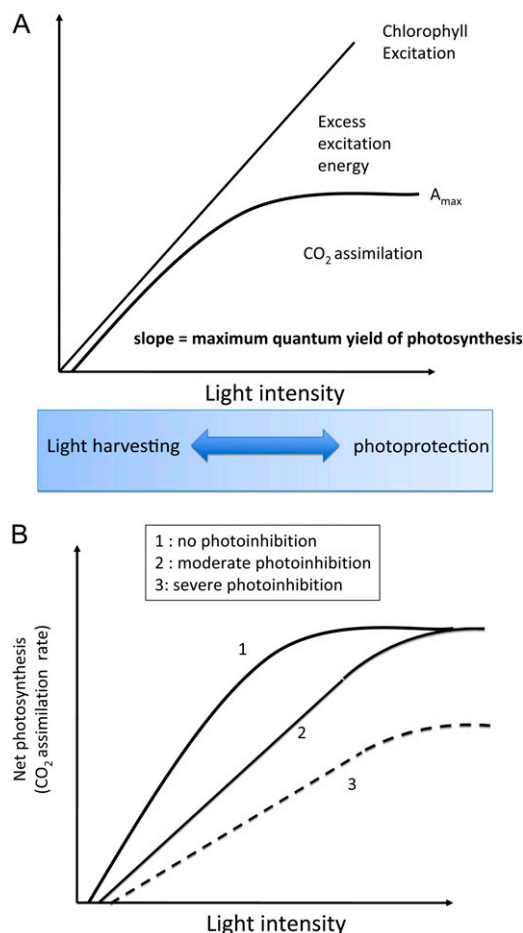


Figure 1. A, A concept diagram describing the principle of photoprotection by distinguishing absorbed light used in photosynthesis from excess light that results in excitation energy that needs to be removed. B, A concept diagram describing the effect of photoinhibition on the quantum yield and light-saturated photosynthetic rate (A_{max}). Note that although a reduction in A_{max} is often cited as a product of PSII photoinhibition, in fact it may be caused by processes associated with photoinhibitory conditions other than PSII function, e.g. stomatal closure or Rubisco inactivation at high temperature. Hence, it is drawn as a dotted line.

determined growth rate. As a direct result, light may be frequently in excess of that required for CO_2 assimilation, thereby necessitating photoprotective responses to avoid severe photoinhibition.

As described in detail below, photoprotection includes mechanisms that regulate absorption and dissipation of light energy. Plants have a limited ability to regulate the amount of sunlight they absorb through changes in leaf area, leaf angle, chloroplast movement, and, on a molecular level, through acclimatory adjustments in LHC antenna size. Once excess light has been absorbed, it can be dissipated via several routes, including thermal dissipation of excess excitation energy. A number of other reactions within the chloroplast can act as photochemical sinks for excess electrons. In addition, plants have efficient antioxidant

systems for the removal of ROS (see Foyer and Shigeoka, 2011; this issue).

Photoinhibition is a term that is often used to refer to a light-induced decrease in ΦCO_2 and/or A_{max} . However, some flexible photoprotective processes will also unavoidably reduce ΦCO_2 and F_v/F_m , resulting in symptoms of moderate photoinhibition (Fig. 1B) that are usually transient. More severe photoinhibition causes a sustained reduction in ΦCO_2 , F_v/F_m , and even A_{max} (Fig. 1B) that requires repair of photooxidative damage, in contrast with flexible photoprotective responses that have a duration of a few minutes. It should be emphasized that changes in A_{max} are usually associated with more severe photoinhibition and multiple stresses, so it can be difficult to link reductions in A_{max} with photoinhibition directly. Because photoprotection and photoinhibition processes can give similar symptoms, it can be difficult to distinguish them. Even some cases of severe environmental stress and long-term photoinhibition have been attributed to sustained photoprotective responses, for example, in overwintering evergreen leaves that cannot photosynthesize at extremely low temperatures (Demmig-Adams and Adams, 2006).

AVOIDANCE OF EXCESS LIGHT ABSORPTION

Many plants position their leaves to optimize light absorption: this can occur by movement or positioning during development and growth. In high light, leaves of some species turn or develop so that they reduce the angle of incidence and increase reflection, thereby reducing the amount of light absorbed (Raven, 1994) and reducing leaf temperature (Pastenes et al., 2004). This is known to be an important attribute of crop physiology. In the case of tropical rice (*Oryza sativa*), upright leaves are common, and they do not affect the saturation of photosynthesis but do reduce the amount of light absorbed around the hours of mid-day, substantially reducing photoinhibition (Murchie et al., 1999). Upright cereal leaves theoretically give a higher rate of canopy photosynthesis. Leaf angle in crop plants specifically in relation to photoprotection is an area deserving more attention.

Chloroplasts in low light typically position themselves where they can maximize light interception, toward the periclinal walls perpendicular to the incident light. In high light, they move toward the anticlinal walls where absorption is reduced (Kasahara et al., 2002) to decrease the amount of excess excitation energy and presumably to minimize the saturation of photosynthesis. This process can occur on a timescale of minutes to hours, and the velocity of movement depends on light fluence rate. The exact mechanism is still unknown, although it involves the blue light photoreceptor phototropin and movement along actin filaments (Suetsugu and Wada, 2007). Recent progress has been made in identifying the genes that confer movement away and toward light sources. The phys-

iological advantage of such subcellular movements is clear; after all, photosynthesis takes place on the level of the single chloroplast, and such microscale movements could match microvariation in light intensity. There may be mileage in optimizing chloroplast movement in leaves for both light harvesting and photoprotection; however, more quantification is required regarding the energetic cost/benefit of movement. The impact on gas exchange in the leaf also needs to be taken into account because there is evidence that the anticlinal movement impairs CO₂ diffusion (Tholen et al., 2008).

PHOTOACCLIMATION

The amount and proportion of photosynthetic components are typically altered on a timescale of days to match the prevailing light intensity in a process that is termed photoacclimation. This involves changes in amounts of soluble enzymes of photosynthesis, electron transport components, and pigment-protein complexes and has a number of effects, one of which is to match the amount of available light with the plant's capacity to absorb it and use it for carbohydrate synthesis. For example, if a shift to high light intensity occurs, the capacity for CO₂ assimilation and electron transport rises, but there is a net degradation of LHCs. This represents an economy of resources, but it also results in an increase in the capacity for photosynthesis that maintains the *in situ* rate at a point that is below A_{\max} , thus reducing the level of photoprotection required and the risk of photooxidative stress. There is evidence that some crop plants may be impaired in some aspects of photoacclimation, and this area is in need of further work to identify factors that might be altered to improve photosynthesis (Murchie et al., 2009). Adjustment of antenna size is reviewed elsewhere in this special issue (Ort et al., 2011; this issue).

Photoacclimation may have an impact on growth and development. Plants that were compromised in their ability to acclimate dynamically to growth light intensity by altering the protein and pigment composition of their photosynthetic apparatus were grown in controlled environment and natural conditions. The wild-type plants (able to acclimate) had a higher fitness than the mutants, indicating that the dynamic responses of photosynthesis are indeed important in determining yield (Athanasiosou et al., 2010)

NONPHOTOCHEMICAL QUENCHING

After light has been absorbed, the first site of photoprotection is within the LHCs themselves. If light is excessive and excited chlorophyll is unable to drive photochemistry, then the lifetime of the singlet state is extended, resulting in a higher yield of triplet state formation. This is undesirable because energy transfer from triplet chlorophyll to oxygen generates singlet oxygen, a highly reactive type of ROS. However, there is

more than one route for deexcitation of singlet chlorophyll: in addition to driving photochemistry, a singlet state chlorophyll molecule energy can return to the ground state by the emission of light (chlorophyll fluorescence) or by the harmless emission of heat (thermal dissipation). The latter route is a major component of photoprotection, termed nonphotochemical quenching (NPQ; Müller et al., 2001; Horton et al., 2008).

A number of processes contribute to the induction and relaxation of NPQ over time. One component, termed qE, is turned on and off rapidly (seconds to minutes) and depends on the formation of the Δ pH across the thylakoid membrane (Fig. 2). A second component, recently named qZ (Nilkens et al., 2010), is induced and reversed on a slower timescale of tens of minutes, correlated with the synthesis and disappearance of zeaxanthin. Another component, termed qI, is slower to relax (hours or longer) and has similarities (e.g. lowered F_v/F_m) with more severe types of photoinhibition, and it may also be associated with accumulation of zeaxanthin.

In higher plants, there are two well-characterized molecules that regulate qE. First, it has long been known that the development of qE is associated with the accumulation of the xanthophyll cycle (XC) carotenoid zeaxanthin (Demmig-Adams, 1990). The XC is a reversible interconversion of zeaxanthin and violaxanthin that is directly linked to the energization of the thylakoid membrane during the induction of photosynthesis in the light. As light saturation is reached, the rise in Δ pH increases the proton concentration within the thylakoid lumen. This has a number of effects, including the activation of the enzyme violaxanthin deepoxidase, which converts violaxanthin to zeaxanthin and increases the deepoxidation state of the XC pool. The reverse reaction, converting zeaxanthin to violaxanthin, is catalyzed by zeaxanthin epoxidase. Although there is no doubt that zeaxanthin plays a key role in qE, there is still discussion over whether zeaxanthin is a direct quencher of singlet excited chlorophyll or an allosteric effector that alters the sensitivity of qE to the Δ pH: evidence exists for both mechanisms.

The second component is the PSII protein PsbS, whose role in qE was discovered by screening mutant populations of *Arabidopsis* for altered chlorophyll fluorescence quenching (Li et al., 2000). Mutants lacking PsbS are specifically defective in qE, are more sensitive to photoinhibition (Li et al., 2002), and show decreased fitness (measured as seed yield) under fluctuating light conditions in the field or in the laboratory (Külheim et al., 2002; Krah and Logan, 2010). Although PsbS is a member of the LHC protein family, it does not appear to bind pigments and instead functions as a sensor of lumen pH that is necessary for the rapid induction and relaxation of qE (Li et al., 2004). NPQ with similar characteristics to qE can be induced on a much slower timescale in the absence of PsbS (Johnson and Ruban, 2010). A different LHC protein, called LHCSR, was recently found to be necessary for qE in

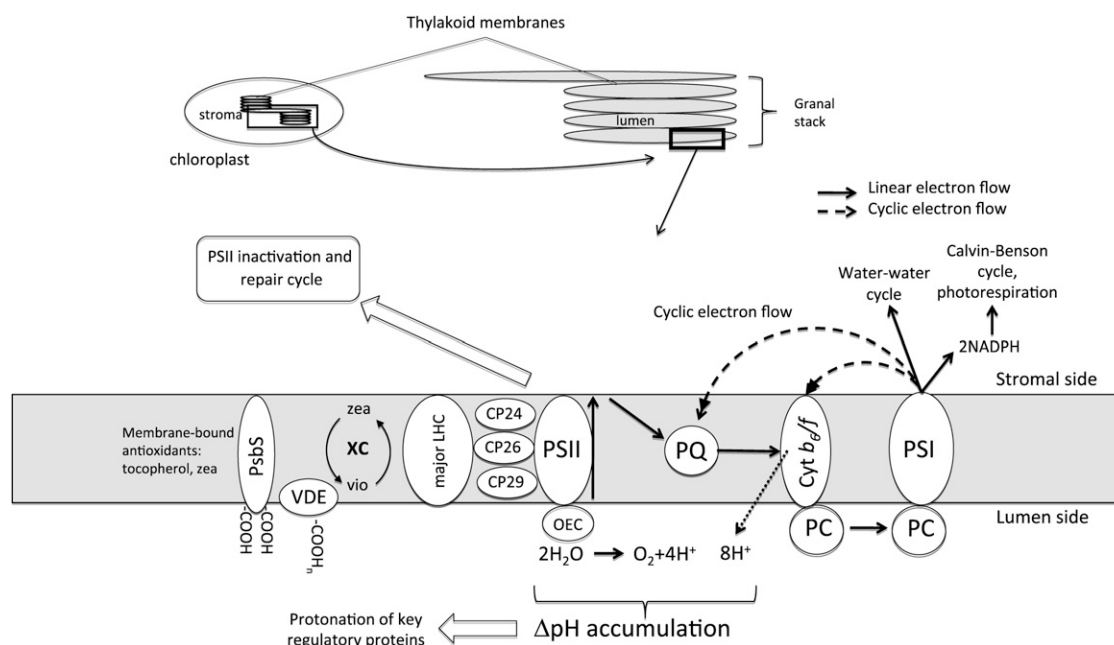


Figure 2. A highly schematic figure summarizing the thylakoid processes involved in photoprotection. CP24, CP26, and CP29 refer to the minor LHC. OEC, Oxygen-evolving complex; PC, plastocyanin; vio, violaxanthin; zea, zeaxanthin. The 4H^+ and 8H^+ refer to linear electron flow only.

the green alga *Chlamydomonas reinhardtii* (Peers et al., 2009). This protein is not present in higher plants, but both the PsbS- and LHCSR-dependent qE systems are present in the moss *Physcomitrella patens*, where the two types of qE appear to operate independently and additively (Alboresi et al., 2010).

Increasing qE capacity might improve photoprotection and crop production in adverse environments (Horton, 2000). The PsbS protein has been shown to act in a dose-dependent manner in leaves; the more PsbS present, the higher the capacity for qE (Li et al., 2002). Hence, overexpression of PsbS would be one obvious approach to enhance photoprotection. When grown in a light regime with a single daily sunfleck of high light, *Arabidopsis* plants that overexpress PsbS exhibited significantly larger rosettes (Logan et al., 2008). Although higher carbon gain at the whole-plant level is the most straightforward explanation, it is possible that an unexpected metabolic shift related to methyl jasmonate signaling could be involved (Frenkel et al., 2009). An alternative way to increase qE capacity in crop plants would be to reintroduce the LHCSR system, which was presumably lost sometime after the divergence of mosses and higher plants.

Because NPQ decreases ΦCO_2 , the complex kinetics of different NPQ components means that there will be situations when the relaxation of NPQ does not match the dynamics of light intensity changes in nature. Under conditions that result in rapid plant growth, rapidly relaxing qE is usually the major component of NPQ, but there are situations when qZ and qI become more prominent. In the field, it is also important to consider that many plant canopies, especially those in

plant communities, are complex three-dimensional systems (unlike *Arabidopsis* rosettes). The absorption of light can often be described using relatively simple means, where leaves behave as randomly distributed elements in space. However, the distribution of direct radiation in canopy space over time (sunflecks) is more difficult to measure. Sunflecks can provide a significant carbon resource for the plant, but they can also induce the more sustained components of NPQ. A recent theoretical study (Zhu et al., 2004) attempted to calculate the cost and benefit of NPQ during and after sunfleck formation by assuming that there is a delay in the recovery of ΦCO_2 that impairs carbon assimilation during the low light period following a sunfleck. By analyzing daily solar movement, the cost to total canopy carbon gain was estimated to be between 13% and 32%, depending on prevailing temperature. Accelerating the recovery of NPQ could therefore enhance canopy photosynthesis considerably.

It seems possible to manipulate the kinetics of NPQ by altering the XC. An increase in the XC pool size was achieved by increasing the expression of β -carotene hydroxylase (Davison et al., 2002). However, these plants had slower rates of formation and relaxation of NPQ, attributable to inertia in the change in deep-oxidation state resulting simply from large quantities of XC constituents (Johnson et al., 2007).

Another possibility is manipulation of the activity of the XC enzymes themselves. A violaxanthin deepoxidase mutant of *Arabidopsis* does not form zeaxanthin in high light and has an impaired ability to induce NPQ (Niyogi et al., 1998). On the other hand, mutants that lack zeaxanthin epoxidase activity accumulate

zeaxanthin constitutively: these plants still require ΔpH to form qE; however, their response during photosynthetic induction is more rapid, as predicted. Altering the kinetics of formation of zeaxanthin and violaxanthin, without altering overall XC pool size, therefore seems possible via fine-tuning of the activities of the enzymes involved. Indeed, overexpression of violaxanthin deepoxidase was shown to increase the initial rate (but not the final extent) of both zeaxanthin synthesis and NPQ induction in tobacco (*Nicotiana tabacum*; Hieber et al., 2002). Increasing the rate of reepoxidation of zeaxanthin to violaxanthin is one possible route to speed up the relaxation of qZ and qI. This might be achieved by overexpressing zeaxanthin epoxidase; however, it would be necessary to minimize competition with violaxanthin deepoxidase activity to avoid a slowing down of NPQ induction.

REPAIR OF PSII

It has long been known that the D1 protein, which is part of the D1/D2 heterodimer within the reaction center of PSII, is readily inactivated by light (Yokthongwattana and Melis, 2006). This inactivation of PSII is thought to be caused by unavoidable photooxidation and is followed by a repair cycle that includes partial disassembly of the PSII complex, degradation of damaged D1 protein, and repair of D1 by de novo biosynthesis and reassembly. This type of damage results in an easily measured and sustained lowering of the quantum yield of PSII (i.e. photoinhibition) and therefore has similar properties to the qI type of NPQ. It seems likely that the rate of repair can limit the recovery from this type of photoinhibition and that the maximum rate depends on environmental conditions and on the species under study. Impairments arise in suboptimal or stressful conditions, such as low or high temperatures. D1 repair is thought to contribute to chilling sensitivity in some species but not in others, such as winter wheat (*Triticum aestivum*) and Arabidopsis.

Improvements could arise from improving the rate of repair. However, an understanding and fine-tuning of the rate-limiting steps involved are necessary (Yokthongwattana and Melis, 2006). FtsH proteases are involved in both the primary cleavage and degradation of damaged D1 (Bailey et al., 2002; Kato et al., 2009). Recent evidence suggests that a family of Deg proteases is also involved in degradation of damaged D1 (Sun et al., 2010). The protein translation machinery in chloroplasts that is involved in repair synthesis of D1 is susceptible to photooxidation (Takahashi and Murata, 2008) and is thus a possible target for improvement.

PATHWAYS FOR ELECTRON TRANSPORT AND CARBON METABOLISM

In principle, any efficient sink for electrons produced by water splitting in PSII (i.e. a photochemical

sink) has the potential to decrease the reduction state of PSII and lower the risk of photooxidative stress. It is relevant to include the mechanism of CO_2 assimilation itself. In comparison with fast-growing, short-lived species, slow-growing perennial evergreen species with low photosynthetic capacities tend to have a higher capacity for NPQ when grown in high light (Demmig-Adams and Adams, 2006). Many processes involving photosynthetic electron transport have been suggested to act in such a photoprotective manner, including photorespiration, cyclic electron transport, and the Mehler reaction (water-water cycle).

PSI Cyclic Electron Flow

Cyclic electron flow refers to electron flow around PSI that results in ATP synthesis only and does not involve a terminal electron acceptor (see also Kramer and Evans [2011]; this issue). Electrons are passed from either NAD(P)H or ferredoxin to plastoquinone, increasing the ΔpH (Fig. 2). The role of cyclic electron transport is complex. First, it is capable of adjusting the ATP/NADPH production ratio in the chloroplast to meet the demands of the Calvin-Benson cycle. Second, it has a photoprotective role, increasing qE via ΔpH alterations. Cyclic electron flow may increase when linear electron flow is inhibited or during transition periods, such as a dark/low light to high light. Two pathways are known to exist: the NAD(P)H dehydrogenase complex-dependent pathway and the PGR5-dependent route (Shikanai, 2007). Flowering plants operate both cycles, but the predominant pathway is thought to be the latter.

Recent evidence points toward cyclic electron flow having a more significant role in the regulation of plant photosynthesis than previously thought. The precise details of the two pathways and the complexes involved are still being elucidated, but current knowledge has increased markedly in the last few years. *pgr5* was identified as a low-NPQ mutant in Arabidopsis and was shown to be more susceptible to photoinhibition, although it showed normal growth at low light intensities (Munekage et al., 2002). PGR5 is a small thylakoid protein and when overexpressed showed a dose-dependent effect on the rate of cyclic electron transport in leaves, but only during shifts from low to high light and not at steady state (Okegawa et al., 2007). Its biochemical function is still unknown. Mutants affecting the PGRL1 protein have a phenotype similar to that of *pgr5* (DalCorso et al., 2008), and models have been proposed where the two proteins act as facilitators for cyclic electron flow by physical interaction with PSI, ferredoxin, and the cytochrome *b₆/f* complex. Due to the existence of electron transport regulators such as these, it would seem feasible to manipulate the photoprotective behavior of plants via the amount of linear versus cyclic electron flow. However, without more information on the role of cyclic in a wider range of physiological environments and its

impact on growth and development, it is unclear which components would need to be altered.

The Mehler Reaction (Water-Water Cycle)

The water-water cycle occurs by the photoreduction of one molecule of O₂ to two molecules of water at the reducing side of PSI via electrons generated from two molecules of water in PSII. The reaction sequence involves superoxide dismutase, ascorbate peroxidase, monodehydroascorbate reductase, dihydroascorbate reductase, glutathione reductase, and ferredoxin-NADP⁺ reductase. Details of this reaction are provided elsewhere (Endo and Asada, 2006; Foyer and Shigeoka, 2011).

The main function is the scavenging of superoxide and hydrogen peroxide to prevent damaging reactions in the chloroplast. However, it also dissipates PSII excitation energy and electrons in PSI. Measurements of the water-water cycle have shown that it is particularly active during stresses such as drought and the transition from darkness to light, before CO₂ induction occurs, and when the electron transport chain has the potential to become highly reduced. In these conditions, the maintenance of PSI in a relatively oxidized state would favor cyclic electron transport and help ΔpH-induced qE activation. The increased ratio of ATP/NADPH production would help activation of the Calvin-Benson cycle. It therefore has similarities in function with cyclic electron transport. There may be possibilities for enhancing the activity of this cycle during appropriate conditions.

PROSPECTS FOR MANIPULATING PHOTOPROTECTION TO ENHANCE PLANT PRODUCTIVITY

The photoprotective processes described above clearly serve fundamental roles in maintaining survival, reproduction, and fitness in plants. They do this via two means: first, the regulation of individual photosynthetic reactions, and second, the prevention of photooxidative damage.

Regulation is inherent in processes such as NPQ, one function of which is to prevent overreduction of the electron transport chain over short periods and light transients. However, this is also a good example of a photoprotective process that anticipates light conditions and can prevent reductive processes that have not yet occurred. Given the natural variation that exists for photoprotective processes in nature, it is reasonable to question whether a process that is inherently preventative and that has a discernable cost in terms of carbon gain is actually optimized for carbon gain. The issue of the cost and benefit of photoprotection (or photoinhibition) to plants and plant communities has been addressed, and it is clear that in some individual cases it has been shown to be a major factor (e.g. Raven, 1994). In a striking example using the shade-adapted woodland floor dweller

Oxalis oregana, it was shown that the metabolic costs of high light avoidance movements by leaves during sunflecks were low compared to the repair costs of photodamage if the leaf did not move (Powles and Björkman, 1981; Raven, 1994). Thus, avoiding photoinhibition provided a clear carbon-gain advantage in a severely light-limited habitat.

Many wild species have inherently low growth rates because they are adapted to environments where limitation is imposed by water, nutrients, disturbance, and other abiotic and biotic stresses. Mitigation of stress factors is critical, and so evolution will favor strategies for survival, establishment, and reproductive success that are not necessarily associated with highest potential rates of growth and carbon gain. Why? One answer is because these high rates are simply rarely reached. Instead, appropriate strategies might be long-lived seed, high fecundity, and short life cycles. The list of adaptive traits is long. It can be shown that some crops adapted to stressful environments often do not possess a high yield potential in favorable environments and vice versa (Lizana et al., 2006).

An interesting working hypothesis is that the ability to optimize photosynthesis in resource-poor environments, as plants have evolved to do, therefore may not be suitable for agriculture, which often relies on high inputs of water and nutrients that result in elevated rates of carbon assimilation and rapid growth. It seems reasonable to question whether photosynthesis in our crops plants is too conservative. This is a difficult question to answer because assessment needs to be made using realistically changeable conditions that are constantly monitored and recorded and an appropriate genetic platform with which to test the impact of individual components and processes. Most work has been carried out on plants grown under constant conditions or in field conditions where environmental monitoring is difficult.

It is important to consider the complexity of the light environment, temporally and spatially, as clearly demonstrated by Zhu et al. (2004). Raven (1994) pointed out that most of the evidence is present for the whole-plant level but not the plant-community level, and substantial progress in this area has yet to be made.

To conclude, it is clear that we can genetically manipulate and enhance a plant's capacity for photoprotection. This may have beneficial effects for crops in suboptimal environments, but it must be weighed against the evidence that such processes have a cost that could limit carbon gain in optimal conditions. The solution should come from a combination of rigorous measurement in real conditions and complex models that span from the molecular level to the field.

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