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Photosynthetic Productivity: Can Plants do Better?

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1. Introduction

By the time you finish this paragraph you will be a changed person. Change, of course, takes a variety of forms, from eroding mountains and melting snowflakes to the major changes we experience in our own lives - birth, growth, reproduction, and death. Less tangible, but changes nonetheless, are the small shifts in perspective that occur as we go through our days - new ideas, new feelings, and new understandings. But, as the Second Law of Thermodynamics reminds us, these varied and seemingly unrelated expressions of change do, in fact have a common source. All change arises from the decay of order - an increase in entropy. Sometimes the increased disarray that defines change is obvious, as when a crystalline cube of ice turns into a higgledy-piggledy puddle of water. Other times, the increased disorder is less obvious. Indeed, in living systems, change often seems to be associated with an *increase* in order. The gradual recovery of a lush and materially diverse living forest in the years following a catastrophic fire would seem to represent a net increase in order. The sequential nature of biological development, from zygote to adult, or from acorn to ancient oak, would seem to represent a net increase in order. The regulated changes in neuronal connectivity and brain architecture that occurs as the mind grasps new insights would seem to represent a net increase in order. Subtler still are the numerous changes in living systems where the initial and final states appear unaltered. The life of every cell depends upon the numbers, locations, and shapes of a multitude of complex molecules. These molecules themselves have a finite existence, a 'lifespan' that, in most cases, is considerably shorter than the life of the cell itself. The median half-life of various protein molecules sampled from various eukaryotes is only 1.8 hours (Hatfield & Vierstra, 1997). Consequently, even static living materials, such as the long-lived neurons in a human brain or the living cells in the trunk of an ancient oak tree, are constantly in the process of rebuilding themselves from within. Even with no obvious change, we are all in a state of constant material flux for the duration of our lives. We are different now from who we were at the start of this paragraph.

At first glance life seems to violate the Second Law of thermodynamics. The fact that all changes in the Universe lead to decreases in order and the fact that living matter acts to increase its own internal order is sometimes referred to as Schrödinger's paradox. But Schrödinger (1992) resolved this famous paradox. He acknowledged that the order inherent in living systems represented a thermodynamically off-balance condition. But Schrödinger

also realized that a continuous input of 'high-quality' energy was required to maintain this off-balance or non-equilibrium state. Live organisms require a reliable source of energy in the form of food or chemically-reduced minerals or sunlight in order to postpone the descent into the disorder of thermodynamic equilibrium. At the same time, the production and maintenance of this non-equilibrium living state is coupled to energetic processes that do increase entropy in the Universe. For example, energy released in thermonuclear reactions on the sun simultaneously powers photosynthesis on Earth while adding to the overall entropy of the Universe. Likewise, energy released in the digestion of food powers the ordered changes in our bodies while also increasing the overall kinetic chaos of the matter around us thereby adding to the entropy of the Universe. Life exploits rather than violates the Second Law of thermodynamics.

Positioned at the interface of biology and physics, of life and non-life is photosynthesis. This biophysical process is the key to life's exploitation of the Second Law. Plants, algae, and many bacteria use solar energy to convert simple energy-poor substrates of water and carbon dioxide into complex, energy-rich, organic materials. More simply, plants and their photoautotrophic kin use sunlight to reverse the local flow of entropy. The carbohydrate products of photosynthesis are, in turn, used to energize and materialize the production, operation, and maintenance of the rest of the organism. These green organisms themselves serve as the energetic foundation of most biological communities. Indeed, photosynthesis is typically the central biological determinant of the overall productivity and species composition for any local community of organisms (Whittaker, 1975). Globally, photosynthesis also helps dictate the habitability of the planet. The soils that support our natural and agricultural ecosystems, the oxygen-rich atmosphere that permits our own existence, and the stratospheric ozone that shields us from hazardous ultraviolet sunlight are all byproducts of photosynthesis (Schlesinger, 1997). Our modern civilizations and economic systems are also beholden to this fundamental bioenergetic process. Food, fibers, pharmaceuticals, and fossil fuels are a few examples of economically important goods that are derived directly or indirectly from photoautotrophs (Roston, 2008). Today we have begun to ask even more of photosynthesis as we confront the tripartite challenge of overpopulation, dwindling fossil-fuels, and anthropogenic climate change. Provisioning food for a population of 10 billion in the face of finite water, deteriorating soils, and changing climates will be a daunting task. There is hope that improvements in the photosynthetic productivity of crop species can make a substantial contribution to this effort (Evans, 1993; Long et al., 2006). Meeting rising demands for global energy will also depend in part on replacing non-renewable fossil fuels with renewable plant-based resources. Presently there are many uncertainties associated with biofuels (Tilman et al., 2009). But, if properly executed, the use of renewable plant-based fuels, while leaving the remaining geological deposits of organic carbon in the ground, would have great economic, ecological, and climate-stabilizing benefits (Calvin, 1980; Robertson et al., 2011). Climate-stabilizing strategies also include long-term storage of photosynthetically-fixed CO_2 in wild and managed forests. Forest growth in the United States presently offsets approximately 15% of the annual U.S. emissions of CO_2 from fossil fuels (Ryan et al., 2010). A global increase in photosynthetic re-cycling of atmospheric CO_2 and the sequestration of that carbon into long-lived trees and soils should compensate for much of the CO2 emissions arising from humanities' profligate use of carbon-based fuels (Griffin & Seemann, 1996). The energetic, environmental and economic importance of photosynthesis cannot be overestimated.

One can imagine several strategies for squeezing more human benefit out of plant production including increased plant resistance to diseases and pests, increased plant tolerance to environmental stressors such as drought or heat, increased allocation of plant growth to the desired product such as grain in cereal crops or woody stems in forestry trees. Fig. 1 emphasizes how the overall rate of light-driven carbon fixation by the plant underpins all of these production-enhancement strategies. Thus, the most generally applicable approach to improving plant productivity, regardless of the species or the desired plant product, may be to find ways of increasing plant photosynthesis itself. Moreover, it has been argued that improving photosynthesis is the only viable production-enhancing strategy that remains for row crop species (Long et al., 2006; Zhu et al., 2010). Success at improving photosynthetic plant productivity requires an appreciation of how cellular photosynthesis translates to increased whole-plant production and an appreciation of where constraints are to be found that limit the flow of energy and carbon from the individual green cell up to the whole plant.

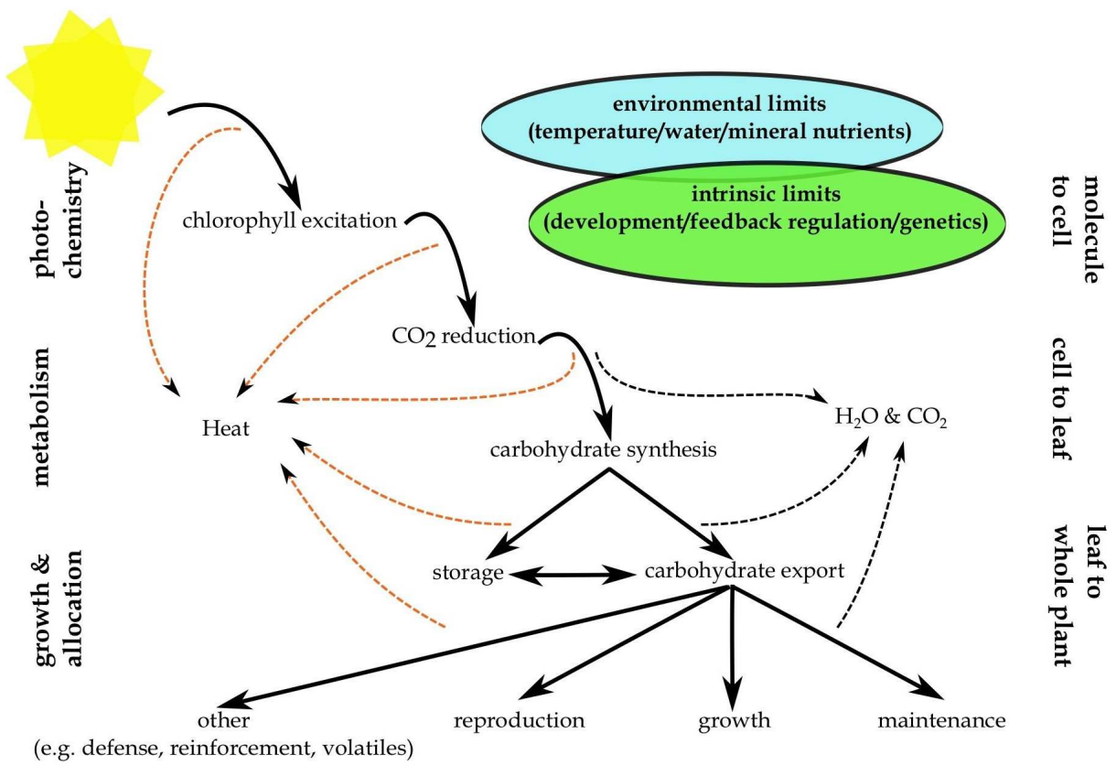

Fig. 1. A simplified energy flow diagram for pondering plant productivity possibilities. Moving down through the figure we go from quantum mechanical phenomena at sub-cellular scales (photochemistry) to biochemical and physiological phenomena at the cell to leaf scale (metabolism) to developmental phenomena at the leaf to whole-plant scale (growth and allocation). Solid black arrows represent energy transformation steps as light-energy is transduced into plant biomass and associated biological functions. Orange dashed arrows indicate the loss of useful energy to entropy ('heat') at each energy transformation step. Black dashed arrows indicate the loss of organic carbon to CO_2 at energy transformation steps powered by respiratory carbon oxidation. After Horton (2000).

Several key steps in photosynthetic production, defined as the net rate of light-driven plant growth, are depicted in Fig. 1. Briefly, light absorbed by photosynthetic pigments in the green cells of plants is used to power the conversion of CO_2 into a simple sugar product. This product is then used in the synthesis of more complex organic molecules. These photosynthates (i.e., the organic carbon products of photosynthesis) may be stored within the leaf or transported for use elsewhere in the plant. Photosynthates are considered as both energy and material resources for cellular metabolism and plant growth. Energetically, these photosynthates may be re-oxidized to CO_2 in mitochondrial respiration in order to produce cellular ATP, which, in turn, powers all other metabolic and transport processes in the plant. Materially, these photosynthates may serve as the carbon 'backbone' for the assembly of the rest of the cell, the leaf, and the whole plant. All essential whole-plant functions (e.g., growth, defense, maintenance, reproduction) depend upon this common and finite supply of photosynthate.

We define 'constraint' as a mechanism or process that limits the evolutionary or engineered response of a biological trait (or set of traits) to natural selection or genetic manipulations. For simplicity and clarity, this review, like the energy flow diagram in Fig. 1, tends to locate constraints on photosynthetic productivity at the level of the cell, the leaf, or the whole-plant. This simplifying perspective omits a great deal of important biology. In particular, we note that all of these processes are conditioned by the developmental and/or acclimatory state of the plant ('intrinsic limits' in Fig. 1), and are subject to the complex vagaries of environmental resources and stressors ('environmental limits' in Fig. 1). These dynamic processes also interact in complex regulatory web-like networks that are necessarily omitted from Fig. 1. This chapter presents some examples of these regulated interactions in order to illustrate how the system-like nature of plants can constrain their photosynthetic productivity.

This review examines the question of whether or not it is reasonable to expect success at squeezing more benefit out of plant photosynthesis. This is a broad question encompassing a multitude of disciplines and perspectives. We will limit ourselves to exploring some representative intrinsic biological constraints on the photosynthetic productivity of terrestrial C3 plants that emerge at the level the cell, the leaf, and the whole-plant. At the cellular level we will briefly describe the primary carbon metabolism of terrestrial C3 plants. This will make it possible to review results from a variety of molecular studies that have shown how targeted manipulations of carbon metabolism can improve on photosynthesis in ways that potentially enhance overall plant production. These kinds of studies imply that improved photosynthetic productivity, at least among plants grown in intensively managed agricultural and forest plantation settings, is possible. However, as Fig. 1 implies, complex leaf-level traits can limit plant productivity. There is broad variation among plant species in various aspects of leaf structure, function, and persistence or 'lifespan' and comparative studies can give insight into these limits. We will present results from a comparative leaf-level study that demonstrate how the photosynthetic potential of a leaf is constrained by traits associated with leaf persistence. Photosynthetic metabolism and foliar lifespan must be considered together in predicting the overall carbon-gain potential of an individual leaf. Next, moving up to the whole-plant level, we will present results from a study using plants that have been genetically modified to have longer-lived leaves in order to see how this affects aspects of whole-plant performance, including growth. We will conclude with some thoughts on the central question of whether or not plants can 'do better' as informed by our review of advances in the cellular-molecular genetics domain and the trade-offs that emerge as cellular processes scale up to the leaf- and

whole-plant levels. We will suggest that analysis of results from studies designed to improve plant productivity will yield the greatest insight if considered from a 'systems' perspective. This perspective enforces a dialectic view of both reductionist and holistic understandings of plants and their energetic activities.

2. What constrains photosynthetic productivity?

The interest here is on the feasibility of increasing the intrinsic potential for photosynthesis and growth. The photosynthetic response of a leaf to light (Fig. 2) illustrates some important aspects of the intrinsic constraints on photosynthesis. Here we see that in complete darkness leaves are net producers of CO_2 as a result of mitochondrial respiration (R_m). Although R_m rates decrease in illuminated leaves, respiration does not stop entirely (Atkin et al., 1998). Thus, in the light, the rate of carbon assimilated by a cell or a leaf or a plant must be understood to be the net balance between ongoing carbon oxidation processes, including R_m, and chloroplast carbon reduction (i.e., gross photosynthesis). Mitochondrial densities and respiratory activity vary among species, among tissues in the same plant, and across growing conditions (Griffin et al., 2001). Wilson & Jones (1982, as cited in Long et al., 2006) were able to improve biomass production in rye grass by selecting for plants with reduced respiration rates. These observations emphasize the importance of R_m as a determinant of net carbon gain and implicate R_m as a target process for improving plant production.

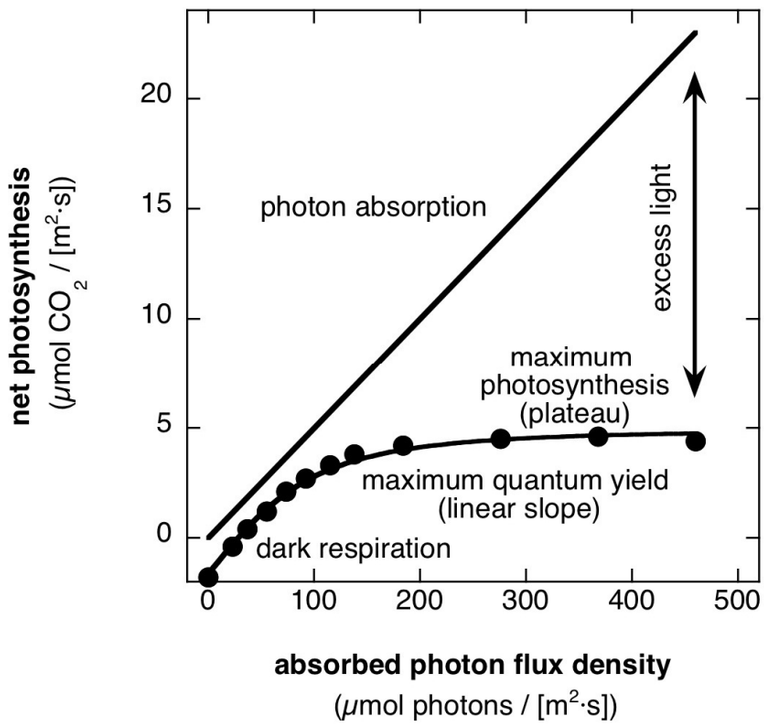

Fig. 2. Photosynthetic response of a healthy C3 leaf to variation in light under ambient CO_2, O_2, and moderate temperatures. The curvilinear scatter plot depicts the net rate of CO_2 uptake of a leaf as a function of light (photon flux density;PFD) absorbed by the leaf. Noteworthy parameters of the curve are discussed in the text.

The slope of the linear portion of the light-response curve (Fig. 2), the quantum yield (QY), is a measure of the maximum *realized* efficiency for the conversion of light energy into carbohydrate by the leaf. When measured under similar conditions, there is little variation in the maximum QY across the breadth of healthy, non-stressed C3 species (Ehleringer & Björkman, 1977). This suggests there is strong selection for plants to produce leaves that are as efficient as possible in capturing solar energy in carbohydrates. Interestingly, the maximum *realized* QY, measured under ambient CO_2 and O_2 concentrations, always falls well below the maximum *potential* QY determined in the lab under optimal, albeit artificial, controlled CO_2 and O_2 concentrations (Skillman, 2008). This 'real world' inefficiency is largely due to energy losses associated with photorespiration (discussed below). The observed difference between the maximum potential QY and the maximum realized QY in healthy C3 plants suggests photorespiration might be a suitable target for improving photosynthetic productivity.

The maximum capacity for net photosynthesis (Pmax) is quantified as the rate of CO_2 uptake (or O_2 production) at light-saturation (Fig. 2). Pmax, measured under identical conditions, varies considerably across species and varies for the same species grown under different conditions (e.g., Skillman et al., 2005). Much of our review focuses on efforts to increase Pmax as a means of improving photosynthetic productivity. But the assumption that changes in Pmax translate to changes in whole-plant growth is open to debate (Evans, 1993; Kruger & Volin, 2006; Poorter & Remkes, 1990).

The solid diagonal line in Fig. 2 takes its slope from the linear portion of the light response curve (QY). This shows that, in principle, if there were no upper saturation limit on Pmax, increasing absorbed light would continue to produce increasing amounts of carbohydrate all the way up to full-sun (~2000 μmol m^{-2} s^{-1} PFD). However, real leaves become light-saturated well below full-sun. The shade grown leaf in Fig. 2 is fully saturated at 200 μmol m-2 s-1 PFD or about 10% of full-sun. As photosynthesis becomes increasingly light-saturated, an increasingly greater portion of the light absorbed by the photosynthetic pigments is not used to drive carbon fixation and must therefore be considered as excess light. If the 'ceiling' on Pmax could be raised, leaves in high-light could theoretically improve plant production by using a greater portion of the available photo-energy for carbon fixation. In the context of trying to improve on photosynthetic production, the fate of excess absorbed light is intriguing and will be discussed below.

2.1 Cellular photosynthesis: molecular manipulations of carbon metabolism

At the cell-molecular level, net photosynthesis depends upon the integrated interactions of a set of interdependent biochemical processes. An abbreviated and simplified illustration of nine of these key interactive processes is given in Fig. 3: (i) ATP & NADPH-producing light- or photochemical-reactions on thylakoid membranes in the chloroplast (green stacked ovals in Fig. 3); (ii) CO_2 diffusion from the atmosphere into the leaf, the cell, and the chloroplast (dashed arrows from Ca to Ci to Cc at the top of Fig. 3); (iii) ATP and NADPH-dependent fixation and chemical reduction of CO_2 in the chloroplastic Calvin cycle (circular reaction sequence in the chloroplast in Fig. 3); (iv) chloroplastic starch biosynthesis from carbohydrate products of the Calvin cycle (linear reaction sequence in the chloroplast in Fig. 3); (v) cytosolic sucrose biosynthesis from Calvin cycle carbohydrates exported from the chloroplast (left-hand linear reaction sequence in the cytosol in Fig. 3); (vi) cytosolic glycolysis where hexoses (glucose or fructose) are oxidized to form pyruvate (right-hand linear reaction sequence in the cytosol in Fig. 3); (vii) mitochondrial citric acid cycle where pyruvate imported from the cytosol is oxidized to CO_2, producing chemical reducing

equivalents $FADH_2$ and NADH (circular reaction sequence in the mitochondria in Fig. 3); (viii) respiratory electron transport on the inner mitochondrial membrane wherein electrons from NADH and $FADH_2$ are passed sequentially onto O_2, establishing a H^+ gradient which, in turn, drives mitochondrial ATP synthesis (membrane-bound reaction sequence near the bottom of the mitochondria in Fig. 3); and (xi) the photorespiration cycle where phosphoglycolate, a side-reaction product off the chloroplastic Calvin cycle, is modified and transported over a series of reactions spanning the chloroplast, the peroxisome, and the mitochondria before the final product, glycerate, feeds back into the Calvin cycle (cyclic sequence of reactions near top of figure occurring across all three organelles in Fig. 3). Below we will see that each of these interdependent cellular processes have been targeted for molecular manipulations of cellular carbon metabolism and we will note some cases where these modifications have improved photosynthesis.

2.1.1 The light-reactions and the fate of excess light

The photochemical- or light-reactions of photosynthesis involve light-driven electron and proton (H^+) movement at the inner set of chloroplast membranes (thylakoids) leading to the oxidation of H_2O to O_2 and the production of ATP and NADPH (Fig. 3; Blankenship, 2002). ATP and NADPH, the key light-reaction products, are needed for the subsequent fixation and chemical reduction of CO_2 in the Calvin cycle. The passage of electrons from H_2O to NADPH is mediated by a chain-like series of thylakoid-bound electron-carrier molecules including a special set of electron-carriers called photosystems. Photosystems (PS) are trans-membrane, multi-subunit, chlorophyll-binding protein complexes in the thylakoids where light-energy is transduced first to electrical- and then chemical-energy (Fig. 4). Two different classes of photosystems exist (PSII and PSI) that work in series in the light-reactions. In this reaction sequence, PSII precedes PSI (Fig. 4). Electron transport from H_2O to NADPH could not occur without the PS-mediated input of light energy. In particular, the light-dependent PSII-mediated oxidation of H_2O, releasing O_2 as a byproduct, is quite exceptional. The disassociation of H_2O into O_2 and H^+ and electrons does not normally happen under conditions present at the Earth's surface. This light-driven flow of electrons from H_2O to NADPH also results in the movement of protons (H^+) from the stroma space of the chloroplast into the inner thylakoid space (the lumen). This light-generated H^+ gradient is, in turn, used to drive ATP synthesis via another thylakoid multi-subunit protein complex called ATP-synthase, (not shown). The chemical energy held in the light-reaction products ATP and NADPH, represents a fraction of photo-energy initially absorbed by the PS pigments (Fig. 3). Indeed, a variable but substantial fraction of the absorbed light-energy is dissipated as thermal-energy from PS associated pigments ('heat' in Fig. 3 & 4) thereby lowering the energetic efficiency of the light-reactions.

Chida et al. (2007) showed the potential for increasing plant production by increasing electron transport rates. Cytochrome c6 is a photosynthetic electron transport carrier that operates between PSII and PSI in algae but which does not normally occur in land plants. *Arabidopsis thaliana* plants transformed to constitutively express the algal CytC6 gene sustained higher electron transport rates and had 30% higher Pmax rates and growth rates than wild-type plants (Table 1). Notably, these plants were grown under modest light levels (50 µmol photons/(m^2• s) PFD). It would be interesting to know how these transformed plants perform in brighter light because, as discussed below, rapid photosynthetic electron transport potential can actually be a liability in bright light.

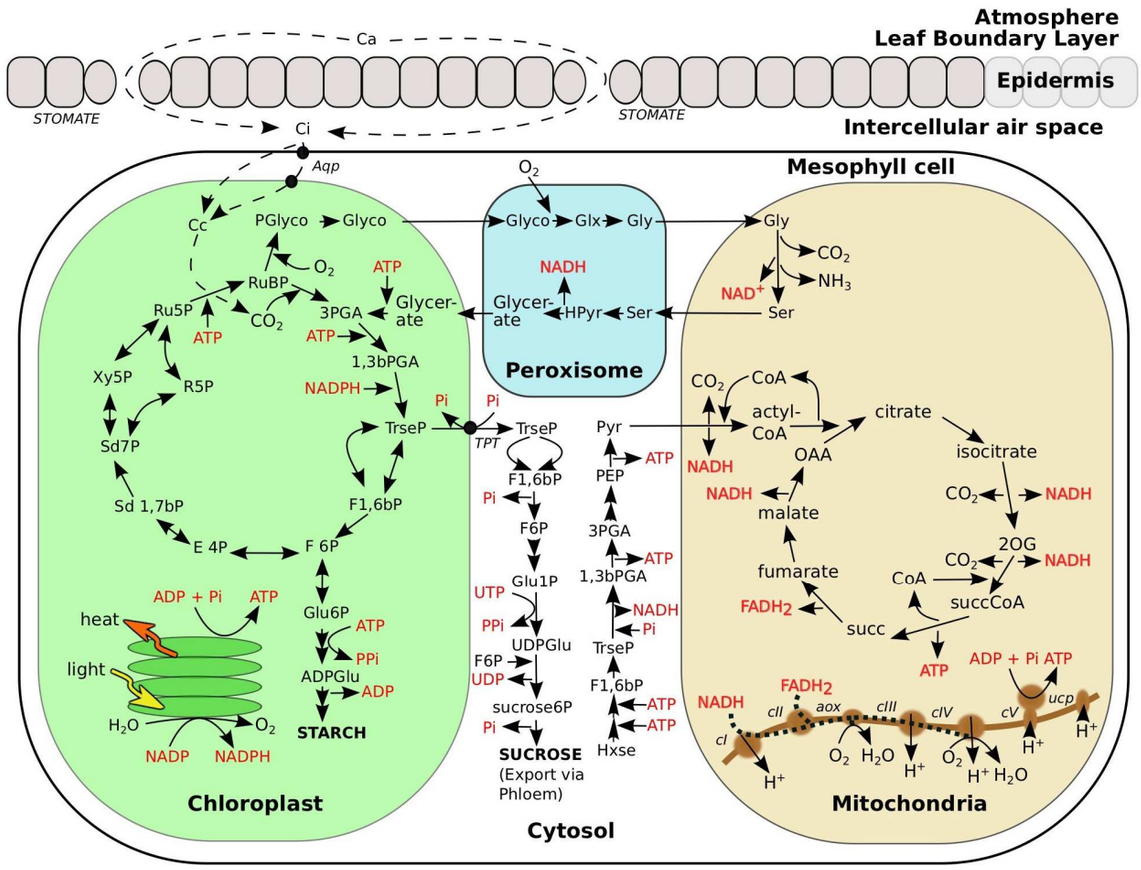

Fig. 3. Primary carbon metabolism in a photosynthetic C3 leaf. An abbreviated depiction of foliar CO2 uptake, chloroplastic light-reactions, chloroplastic carbon fixation (Calvin cycle), chloroplastic starch synthesis, cytosolic sucrose synthesis, cytosolic glycolysis, mitochondrial citric acid cycle, and mitochondrial electron transport. The photorespiration cycle spans reactions localized in the chloroplast, the peroxisome, and the mitochondria. Stacked green ovals (chloroplast) represent thylakoid membranes. Dashed arrows near figure top represent the CO2 diffusion path from the atmosphere (Ca), into the leaf intercellular airspace (Ci), and into the stroma of the chloroplast (Cc).Solid black arrows represent biochemical reactions. Enzyme names and some substrates and biochemical steps have been omitted for simplicity. The dotted line in the mitochondria represents the electron transport pathway. Energy equivalent intermediates (e.g., ADP, UTP, inorganic phosphate; Pi) and reducing equivalents (e.g., NADPH, $FADH_2$, NADH) are labeled in red. Membrane transporters Aqp (CO_2 conducting aquaporins) and TPT (triose phosphate transporter) are labeled in italics. Mitochondrial inner-membrane electron transport and proton transport proteins are labeled in small case italics.

Abbreviations (listed alphabetically); 1,3bPGA, 1,3-bisphosphoglyceric acid; 2OG, 2-oxoglutaric acid; 3PGA, 3-phosphoglyceric acid; acetylCoA, acetyl coenzyme A; ADP/ATP, adenosine diphosphate and triphosphate; ADPGlu, adenosine diphosphate glucose; AOX, alternative oxidase; Aqp, aquaporin; Ca, atmospheric CO_2; Cc, chloroplast CO_2; Ci, intercellular CO_2; cI, mitochondrial Complex I; cII, mitochondrial Complex II; cII, mitochondrial Complex III; cIV, mitochondrial Complex IV (cytochrome oxidase); cV, mitochondrial Complex V (ATP Synthase); citrate, citric acid; CoA, coenzyme A; E4P,

erythrose 4-phosphate; F1,6bP, fructose 1,6-bisphosphate; F6P, fructose 6-phosphate; $FADH_2$, flavin adenine dinucleotide; Fumarate, fumaric acid; Glu1P, glucose 1-phosphate; Glu6P, glucose 6-phosphate; Glx, glyoxylic acid; Gly, glycine; Glycerate, glyceric acid; Glyco/PGlyco, glycolic acid/phosphoglycolic acid; Hpyr, hydroxypyruvic acid; Hxse, hexose (glucose and/or fructose); Isocitrate, isocitric acid; Malate, malic acid; NADH/NAD, oxidized and reduced forms of nicotinamide adenine dinucleotide; NADPH/NADP, oxidized and reduced forms of nicotinamide adenine dinucleotide phosphate; OAA, oxaloacetic acid; PEP, phosphoenol pyruvate; Pi, orthophosphate; PPi, pyrophosphate; Pyr, pyrivic acid; R5P, ribose 5-phosphate; Ru5P, ribulose 5-phosphate; RuBP, ribulose 1,5-bisphosphate; Sd1,7bP, sedoheptulose 1,7-bisphosphate; Sd7P, sedoheptulose 7-phosphate; Ser, serine; Starch, poly-glucan; Succ, succinic acid; succCoA, succinyl coenzyme A; sucrose, sucrose; sucrose6P, sucrose 6-phosphate; TPT, trisose phosphate translocator; TrseP, triose phosphate, collectively dihydroxyacetone phosphate and 3-phosphoglyceraldehyde; ucp, uncoupling factor; UDPGlu, uracil-diphosphate glucose; Xy5P, xylulose 5-phosphate.

Light is highly dynamic in time and space. The cellular photosynthetic apparatus must be able to balance the need to maximize photon absorption and use in the shade against the danger of excessive chlorophyll excitation in bright light (Anderson et al., 1988). Plants in the shade employ multiple cellular traits to maximize the efficient interception, absorption, and utilization of light for photosynthesis. But, under bright light, the challenge is in how to deal with a surplus of photo-energy. If light-driven electron transport exceeds chloroplastic capacity to utilize this chemical reducing power it can lead to the formation of singlet oxygen and other harmful reactive oxygen species (ROS). High-light stress can potentiate cell death when endogenous ROS are permitted to accumulate and damage cellular materials (Takahashi and Badger, 2010). Plants have evolved a suite of processes that lower the risk of broad scale cellular photo-oxidative damage under excess light (Demmig-Adams and Adams, 2006; Raven, 2011). These protective processes include features that (i) limit light absorption by chlorophyll, (ii) dissipate excess absorbed light as heat, (iii) divert light-driven electron transport away from an energy-saturated Calvin cycle towards alternative pathways, (iv) lower the number of functional PSII centers thereby impeding chloroplast electron transport, and (v) maintain high chloroplast complements of antioxidants to scavenge excess ROS. Paradoxically, these protective processes, to one extent or another, have the effect of lowering the energetic efficiency of photosynthesis because a portion of the available photo-energy is not available for carbon fixation. This low efficiency manifests as a light-induced reduction in QY, a phenomenon referred to as photoinhibition (e.g., Skillman et al., 1996).

Thermal dissipation of absorbed photo-energy from the PS pigments (before the initiation of photosynthetic electron transport) is one means for avoiding ROS production in excess light (Fig. 3). This process, termed feedback dissipation (FD), depends upon the conversion of xanthophyll pigments from one form to another in PS-associated proteins. Xanthophyll-dependent FD requires the activity of a number of gene products (Jung & Niyogi, 2009). The best-studied contributor to FD is the PsbS protein, a PSII-associated subunit. Plants lacking PsbS have restricted xanthophyll conversion, are more sensitive to photo-oxidative damage including persistent photoinhibition, and exhibit lower growth rates and reproduction under fluctuating light conditions (Krah & Logan, 2010; Külheim et al., 2002). Thus, xanthophyll-dependent FD, for its role in restricting chloroplast ROS formation, confers a strong fitness advantage for plants growing under natural fluctuating light conditions. High-light induced FD lowers the photosynthetic QY even when the cell is returned to low-light. This is because it takes several minutes for the xanthophyll pigments to return to the non-dissipating state.

Diversion of photosynthetic electron transport to non-productive pathways is another means of minimizing ROS production in excess light (Fig. 4). Alternative electron transport (AET) may be understood as a general strategy for dealing with an over-reduced electron transport chain which, in chloroplasts, manifests as an excessive NADPH/$NADP^+$ concentration ratio. Many metabolic processes fit this definition. The water-water cycle is an AET path that simultaneously acts as a sink for excess reductant and minimizes the accumulation of toxic ROS (Fig. 4). In excess light, when chloroplast NADPH oxidation rates are slower than light-dependent NADPH production rates, $NADP^+$ concentrations begin to restrict the photo-reduction of $NADP^+$ to NADPH. In this over-reduced state, PSI may pass electrons on to O_2 to form superoxide (O_2^-), a highly reactive and toxic ROS (i.e., the Mehler reaction). Superoxide is potentially hazardous to the cell but chloroplasts have a suite of antioxidant metabolites and enzymes that can usually scavenge it before it can do much damage (Foyer & Shigeoka, 2011). Chloroplast antioxidants (e.g. glutathione, ascorbic acid) can rapidly detoxify superoxide by reducing it sequentially back to H_2O (Fig. 4). This sequence of reactions from the PSII oxidation of water (yielding O_2 as a byproduct) through the sequential reduction of O_2 first to superoxide at PSI, and finally back to H_2O (i.e., the water-water cycle) is a energetically futile but it turns out to be an elegant solution to the problem of excess light (Asada, 1999). Photorespiration, another well-known AET example, will be discussed in a later section.

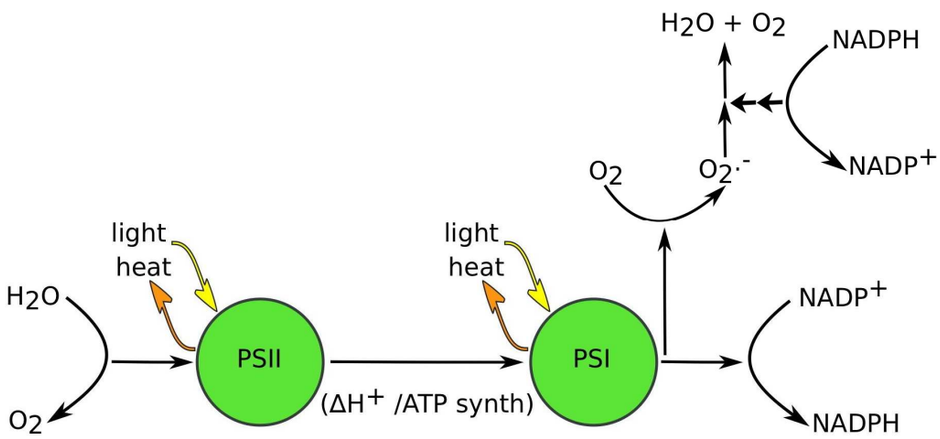

Fig. 4. Photosynthetic transport of electrons from PSII water oxidation is normally used to reduce $NADP^+$ to NADPH for use in Calvin cycle carbon fixation. But, under excess light, when the electron transport chain is over-reduced, electron flow may be diverted at PSI to the Mehler reaction, reducing O_2 to superoxide ($O_2^{\cdot -}$). Chloroplast antioxidant systems can further reduce $O_2^{\cdot}$ back to water, allowing the water-water cycle to function as a protective alternative electron transport path.

Finally, if other protective photoinhibitory processes (e.g., increased xanthophyll-dependent FD or increased AET diversions) are insufficient, photo-generated ROS can cause a net loss of functional PSII reaction centers (Takahashi & Badger, 2010). The ultimate threat of excess-light is that it can lead to unregulated photo-oxidative cellular damage. Paradoxically, the ROS-mediated net loss of functional PSII, is viewed as a last-ditch defense against excess endogenous ROS production and cell damage. Loss of active PSII centers will necessarily inhibit rates of thylakoid electron transport and therefore lower the rate of light-driven ROS

production. But, the protective benefits of photoinhibition, whether arising from the net loss of functional PSII centers or from any other of a suite of ROS avoidance processes, come at a cost. All of these processes lower the efficiency of capturing light energy in plant organic carbon, and so reduce QY.

Several recent studies have made theoretical considerations of the costs of various aspects of photoinhibition (Murchie & Niyogi, 2011; Raven, 2011; Zhu et al. 2004; Zhu et al., 2010). Raven (2011) observes that photoinhibition can slow growth both because of the energetic costs of PSII repair/turnover and because of the foregone photosynthesis resulting from stress-induced QY reductions. Zhu et al. (2004) estimate that a speedier reversion of xanthophyll-dependent FD could improve daily whole-plant carbon gain as much as 25%.

Our discussion so far holds a central lesson; photosynthesis requires a capacity for energetic flexibility. Photosynthesis must be both highly efficient and highly inefficient in its use of light, depending on the light level and the state of the plant. This capacity for regulated adjustments of light-use efficiency by the photosynthetic apparatus appears to be an important and conserved trait among plants. This complicates plant productivity improvement strategies that target gains in cellular photosynthetic efficiency.

2.1.2 Diffusion limitations on carbon acquisition

Products of the light-reactions, ATP and NADPH, are used primarily to energize CO_2 fixation and reduction (Fig. 3). But, along with ATP and NADPH, Calvin cycle carbon fixation also depends upon the stromal CO_2 concentration (Cc). Physical barriers (e.g. cell wall and membranes) and gas- to liquid-phase transitions between the external air and the enzymatic site of carbon fixation lowers the diffusional conductance between the atmosphere and the stroma (Terashima et al., 2011). Conductance limited diffusion from Ca to Ci to Cc varies among species and with environmental conditions and can strongly limit photosynthesis (Warren, 2008).

Stomata, in the leaf epidermis, are key sites of regulated control of carbon acquisition along this diffusion path (Fig. 3). Behaviorally, changes in stomatal aperture regulate the foliar rates of CO_2 uptake and transpirational water loss. Recently Araújo et al. (2011) studied respiratory and photosynthetic physiology in wild-type (WT) and antiSDH2-2 tomato (*Solanum lycopersicum*) plants grown under optimal greenhouse conditions. The SDH2-2 gene encodes a sub-unit of mitochondrial succinate dehydrogenase. This enzyme normally catalyzes the citric acid cycle conversion of succinate (succ) to fumarate (Fig. 3). Engineered SDH2-2 anti-sense plants had as much as 25% greater growth than WT plants (Table 1). Several differences in relevant primary carbon metabolism were observed between the two genotypes including a 30% enhancement in Pmax in antiSDH2-2 plants. Araújo et al. (2011) observed that antiSDH2-2 had lower tissue concentrations of malate, a citric acid cycle intermediate formed down-stream of the succinate dehydrogenase reaction. Malate is known to promote stomatal closure. They concluded that the Pmax and growth enhancements were pre-dominantly a result of greater stomatal conductances in the antiSDH2-2 plants arising from the reduced concentrations of malate.

The relative number of stomata in the leaf epidermis (stomatal density; SD) is subject to developmental control, depending upon the conditions under which the plant is grown (Beerling, 2007; Nadeau, 2009). Schülter et al. (2003) studied photosynthetic physiology in wild-type (WT) and sdd1-1 *Arabidopsis thaliana* plants. The sdd1-1 genotype has a point mutation that results in greater stomatal densities. Over a range of constant light conditions,

sdd1-1 plants consistently had double the leaf SD of the WT plants. Under constant conditions the sdd1-1 plants also had higher rates of leaf transpiration but maximum carbon uptake rates (Pmax) were indistinguishable between genotypes. Thus, under constant light conditions, increased stomatal densities had no detectable effect on carbon gain and lowered the leaf-level water use efficiency (WUE; carbon gain per unit water lost). Interestingly, when low-light grown plants were transferred to high-light, leaf Pmax in the sdd1-1 plants was ~ 25% greater than in the transferred WT plants (Table 1). Apparently, upon transfer to bright light, stomatal density limited photosynthesis in WT but not sdd1-1 plants. The transfer had no effect on relative transpiration rates of the two genotypes and so leaf WUE increased with the change in light more for sdd1-1 than for WT plants. These studies illustrate the potential for bioengineering of stomatal behavior and/or density as means to increasing photosynthetic carbon gain. However, the inevitable trade-offs with water-use suggest the practical applications of these kinds of manipulations would ultimately be limited to plants grown under highly managed cultivation systems where water deficits can be minimized.

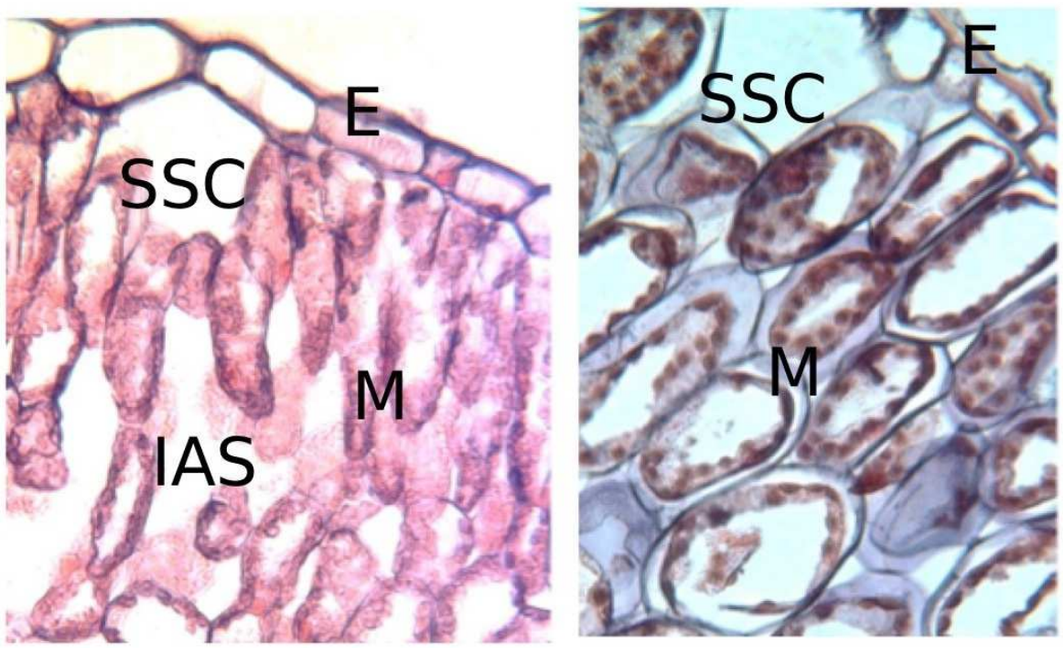

Fig. 5. Leaf anatomy differs among species in ways that affect the mesophyll conductance to CO_2 diffusion. Thin mesophytic *Nicotiana tabacum* leaves (left) have abundant intercellular air space, thin mesophyll cell walls, and, presumably a high mesophyll conductance that could sustain high rates of photosynthesis. Thick sclerophyllous *Agave schidigeri* leaves (right) have large, tightly packed, thick-walled cells, and, presumably a low mesophyll conductance that could restrict photosynthesis. E =epidermis, M=mesophyll cells, SSC=sub-stomatal cavity, IAS=intercellular airspace. (Micrographs by Bruce Campbell.)

After passage through the stomata, CO_2 diffusion from the intercellular space into the stroma where carboxylation occurs depends upon a series of conductances that are referred to collectively as the internal or mesophyll conductance (Terashima et al., 2011). As it turns out, these combined internal conductances substantially limit photosynthesis, and explain nearly half of the drawdown in CO_2 concentration between the atmosphere and the stroma

(Ca - Cc; Warren, 2008). Variation in mesophyll conductance depends upon structural features such as leaf morphology & anatomy, cell wall thickness and composition, cell packing, chloroplast position and density (Fig. 5). Mesophyll conductance is also affected by biochemical factors such as aquaporin membrane transport proteins (Aqp in Fig. 3).

Aquaporins (Aqps) are small trans-membrane proteins that facilitate the osmotic movement of water across membranes (Maurel et al., 2008). Some aquaporins will also transport other small uncharged molecules like CO_2 thereby potentially increasing mesophyll conductance (Fig. 3). Flexas et al. (2006) produced tobacco plants that were either deficient in or over-expressed aquaporin NtAQP1. Under optimal conditions, plants over-expressing NtAQP1 had mesophyll conductances 20% greater than wild-type (WT) plants and Pmax rates 20% greater than WT (Table 1). By contrast, the NtAQP1 deficient plants had mesophyll conductances and Pmax rates that were 30% and 13% lower, respectively, than the WT plants. Aquaporin density as a factor in mesophyll conductance CO_2 is complicated by its role in maintaining tissue water relations and by the fact that other determinants of mesophyll conductance are plastic and highly variable (Tholen et al., 2008; Tsuchihira et al., 2010). Nevertheless, Flexas et al. (2006) provide proof-of-concept evidence that bioengineered enhancements of mesophyll conductance can stimulate photosynthesis.

2.1.3 The carbon-reactions

The fate of stromal CO_2 and light-reaction products is followed here through the Calvin cycle, photorespiration, starch and sucrose synthesis, glycolysis and mitochondrial respiration in the so-called 'carbon-reactions' of a typical photosynthetic cell. In the chloroplast, the key reaction for Calvin cycle carbon fixation is the binding of CO_2 to ribulose 1,5-bisphosphate (RuBP), the five-carbon organic acceptor molecule (Fig. 3). This reaction yields two molecules of 3-phosphoglycerate (3PGA). This newly fixed organic carbon is re-arranged as it is shuttled through the early stages of the Calvin cycle before being diverted primarily to one of three different fates; (i) continuation on through the Calvin cycle for the regeneration of RuBP to sustain ongoing carbon fixation, (ii) departure from the Calvin cycle as six-carbon phosphorylated sugars (fructose 6-phosphate; F6P) for starch synthesis within the chloroplast, or (iii) departure from the Calvin cycle as three-carbon phosphorylated sugars (Triose phosphates; TrseP) for export to the cytosol. Carbohydrates exported to the cytosol are chiefly used for synthesis of sucrose, or re-oxidation in glycolysis and mitochondrial respiration. The Calvin cycle, and starch and sucrose synthesis are anabolic processes requiring the input of energy- and reducing-equivalents derived from either the chloroplastic light-reactions or from carbohydrate catabolism via respiration.

Efforts at enhancing photosynthesis include attempts at improving the Calvin cycle. Ribulose bisphosphate carboxylase/oxygenase (Rubisco), the crucial and enigmatic carbon-fixing enzyme that first introduces new carbon into the cycle has been a particular focus of these efforts (Fig. 3). This is because Rubisco's carboxylation reaction is slow and because it catalyzes two competing reactions: RuBP carboxylation and RuBP oxygenation. RuBP carboxylation products feed entirely into the Calvin cycle and grow the plant. RuBP oxygenation products partially divert carbon away from the Calvin cycle to the non-productive photorespiratory cycle resulting in losses of as much as 25% of the fixed carbon. Plants partially compensate for the inherent inefficiencies of this crucial enzyme by maintaining Rubisco at very high concentrations inside mesophyll chloroplasts. But this

represents a resource cost. More than 25% of leaf nitrogen may be allocated to this one protein (Makino, 2011). The enigma of this enzyme is that it is the means by which virtually all biological organic carbon is produced from inorganic CO_2 and yet, even after >3 billion years of selection, it remains slow, confused, and costly (Tcherkez et al., 2006). To date, molecular engineering efforts have had little success at improving reaction rates or restricting RuBP oxygenase rates through modifying Rubsico kinetic properties (Whitney et al. 2011). Structure/function surveys of Rubsico from different taxonomic groups seem to indicate that the oxygenase reaction is an unavoidable feature of this crucial enzyme (Whitney et al., 2011). Somewhat surprisingly, targeting other Calvin cycle enzymes as a means of improving plant production have had more success (Raines, 2011). For example, tobacco TpS11 plants transformed by Tamoi et al. (2006) expressed Sedoheptulose bisphosphatase (SBPase) 60% greater than wild-type (WT) plants, had Pmax rates ~25% greater than WT, and had 50% greater biomass than WT (Table 1). These authors concluded that SBPase, which converts sedoheptulose 1,7 bisphosphate (Sd1,7bP) to sedoheptulose 7-phosphate (Sd7P), plays a critical and potentially limiting role in the Calvin cycle regeneration of the CO_2 (and O_2) acceptor molecule, RuBP (Fig. 3).

Starch and sucrose may be viewed as alternative and complementary end-products of cellular photosynthesis (Fig. 3). Typically, during the day, both carbohydrates are produced directly from new photosynthate (Stitt et al., 2010). Sucrose, in most species, is the major form by which carbon is transported elsewhere within the plant via the conducting cells of the phloem. Starch serves primarily as a stored carbohydrate reserve that may be used later to support growth, maintenance, reproduction and other carbon demanding functions (Fig. 1). Starch produced and stored in the chloroplast in the day is referred to as 'transitory starch' because it is generally broken down the following night and the sugar products exported to the cytosol. This continual sugar efflux from the chloroplast ensures a relatively constant source of substrate for cytosolic sucrose synthesis throughout the day/night cycle. Starch may also be stored in other tissues (e.g. stems or roots) as a long-term reserve. Both long-term and transitory starch storage represent diversions of carbohydrate away from immediate growth and thus a potential limit on plant production. Indeed, metabolite-profiles of 94 *Arabidopsis* accessions revealed that genotype variation in mesophyll starch content was negatively correlated with genotype differences in growth (Sulpice et al., 2009). Nevertheless, the advantages of carbohydrate reserves for plant resilience are clear, even at a cost of reduced allocation to growth and reproduction (Chapin et al., 1990). For example, studies of *Arbidopsis thaliana* starchless mutants show that the inability to accumulate transitory starch reduced growth and caused carbon starvation symptoms under day/night cycles when night length exceeds about 12 hours (reviewed in Stitt et al., 2010). These and other studies suggest growth is maintained at sub-maximal levels by diverting photosynthate to storage pools to enable plants to cope with periods unfavourable for photosynthesis.

Interestingly, overall plant demand for carbohydrate can feedback to affect the regulation of mesophyll photosynthetic capacity which, in turn, affects subsequent rates of starch and sucrose production (Paul & Pellny, 2003). Feedback regulation, the phenomenon where low carbohydrate demand feeds back to lower Pmax was elegantly demonstrated by Thomas & Strain (1991) who showed that cotton plants raised in small pots grew slower with lower Pmax rates than plants in larger pots. Further, they showed that as simple an act as transplanting plants from small to large pots stimulated root and whole-plant growth, reduced starch reserves, and increased Pmax. This illustrates how limits on

plant growth sometimes control photosynthesis rather than the other way around. Carbohydrate storage and carbohydrate-mediated feedback regulation complicate efforts to increase plant production by enhancing photosynthesis.

Despite these interesting complications, withdrawal of carbon from the Calvin cycle for sucrose and starch synthesis is central to plant productivity (Fig. 1). By contrast, RuBP oxygenation results in the formation of phosphoglycolate (PGlyco) which represents a non-productive drain on the Calvin cycle (Fig. 3). Following the fate of PGlyco in Fig. 3, we see a series of reactions that form a biochemical cycle traversing the chloroplast, the peroxisome, and the mitochondria. This cycle behaves as a salvage pathway because it restores 75% of the carbon lost in the initial RuBP oxygenation reaction back into the Calvin cycle. Photorespiration largely explains why, in C3 plants, the maximum realized QY falls below the maximum potential QY (Fig. 2). The maximum potential QY can only be achieved when measuring photosynthesis under artificial atmospheric mixtures of CO_2 and O_2 that are sufficient for inhibiting the RuBP oxygenation reaction. Photorespiratory effects on QY become worse in C3 plants as Cc declines as happens, for instance, when stomata close to conserve water.

Photorespiration costs also include the resources allocated to the production and maintenance of the elaborate photorespiratory metabolic machinery (Foyer et al., 2009). Interestingly, genetic elimination of components of the photorespiratory cycle turns out to reduce plant production, sometimes to the point of lethality (Somerville, 2001). Thus, in spite of its obvious inefficiency, photorespiration plays various essential roles for C3 plants including service as an AET pathway (Osmond & Grace, 1995). For example, when stomata close and CO_2 becomes limiting for RuBP carboxylation, the coupled operation of the Calvin cycle and the photorespiratory cycle helps poise ADP/ATP and NADP/NADPH concentration ratios and minimize the over-production of ROS from the light-reactions. Kozaki and Takeba (1996) engineered tobacco plants that under-expressed chloroplastic glutamine synthetase (GS2), a necessary enzyme of the photorespiratory cycle (not shown in Fig. 3). As expected, the GS2 under-expressing plants exhibited less photorespiration. But these plants were also more susceptible to ROS-mediated loss of PSII function, presumably because the photorespiratory cycle was not available as a protective 'escape valve' for the flow of excess reducing power.

The carbon-concentrating mechanism found in C4 plants like corn and sugarcane represents an elaborately evolved solution to photorespiration. C4 plants engage additional upstream biochemistry to capture inorganic carbon and concentrate it in chloroplasts near Calvin cycle machinery (Sage, 2004). This high Cc sufficiently inhibits RuBP oxygenation reactions and virtually eliminates photorespiration in C4 plants. This would seem, at first glance, to be the perfect solution to the problem of photorespiration, and there is great interest in trying to engineer C4 physiology into C3 crop plants (Sheehy et al., 2008; Sage & Zhu, 2011). But C4 comes with its own set of trade-offs. For example, the maximum potential QY for C4 plants falls short of the maximum potential QY of C3 plants. This is because additional ATP is required to run the carbon-concentrating metabolism of C4 photosynthesis (Ehleringer & Björkman, 1977). The vast majority (~90%) of described plant species rely upon C3 photosynthesis, suggesting that across most growing conditions, the energetic penalty of C3 photorespiration does not outweigh the energetic cost of the C4 carbon-concentrating mechanism (Foyer et al., 2009).

Kebeish et al. (2007) took a different approach to minimizing the energetic penalty of photorespiration. *Arabidopsis thaliana* plants were transformed by inserting the glycolate degradation pathway genes from the bacterium *Escherichia coli*. The glycolate degradation enzymes were expressed in the chloroplast. This allowed chloroplastic glycolate to be converted directly to glycerate in the chloroplast, effectively bypassing the photorespiratory cycle (see chloroplastic Glyco and Glycerate in Fig. 3). Photorespiration was greatly diminished in transformed plants. Pmax was ~50% greater and shoot growth was ~66% greater in the transformed plants than in WT plants (Table 1). Although untested, this approach presumably permitted the continued operation of the photorespiratory cycle as a protective AET path thereby circumventing the problems reviewed above that arise with the elimination of the photorespiratory cycle.

Leaf respiration (R_m) - comprising glycolysis, the citric acid cycle, and mitochondrial electron transport (Fig. 3) - is coupled to, and coordinately regulated with, photosynthesis (and photorespiration) through multiple metabolic linkages (Nunes-Nesi et al., 2008). The study described above by Araújo et al. (2011) with reduced succinate dehydrogenase expression in antiSDH2-2 tomato plants demonstrates one of these linkages. These authors emphasized how down-regulation of this citric acid cycle enzyme promoted growth through indirect effects on stomatal conductance and photosynthesis. But the antiSDH2-2 plants also had leaf respiration rates that were 10-17% lower than WT plants. A diminished R_m can have major effects on whole-plant daily carbon gain (Amthor, 2010). We suggest that the growth enhancement observed by Araújo et al. (2011) in the antiSDH2-2 tomato plants was a consequence of both reduced respiratory carbon losses as well as the increased foliar carbon uptake associated with greater stomatal conductance emphasized by the authors (Table 1).

Plant mitochondria express a number of gene products that act to lower the energetic efficiency of R_m including the alternative oxidase (AOX) and uncoupling proteins (UCP). AOX reduces O_2 at an early step in the normal electron transport chain thereby reducing the ATP respiratory yield (Fig. 3). AOX activity varies with growth conditions (Searle et al., 2011), is required for heat-production in selected tissues (Miller et al., 2011), and is believed to function as a mitochondrial AET path thereby minimizing mitochondrial ROS production (Maxwell et al., 1999). Mitochondrial UCP also lowers the ATP respiratory yield because it permits H^+ passage across the inner mitochondrial membrane without driving ATP synthesis at Complex IV (Fig. 3). Sweetlove et al. (2006) observed that plants with reduced UCP levels had lower photorespiration rates, lower Pmax rates, and reduced growth. They interpret their findings to mean that, paradoxically, reduced R_m energetic-efficiency, as mediated by UCP, is essential for permitting high rates of coupled photosynthesis and photorespiration. It would be interesting to see what effect mitochondrial UCP over-expression has on plant productivity.

Our review of cellular primary carbon metabolism (Fig. 3) reveals three important points: First, these multiple processes are highly interactive, exhibiting elaborate, adaptive, system-level coordination and regulation (e.g., UCP-mediated support of high Pmax rates or the essential coupling of photorespiration to the Calvin cycle). Second, this coordinated system-level activity is highly variable/flexible and frequently effects low energetic efficiency. Controlled water-conserving stomatal closure, protective photoinhibition, and carbohydrate-mediated feedback are representative processes that down-regulate photosynthetic efficiency and remind us that natural selection acts on whole-organism lifetime fitness, not maximized momentary energetic efficiencies. Third, in spite of complex,

Changed trait (reference)	species	Molecular genetics	Pmax effect	Growth effect	comments
Added thylakoid electron carrier & increased electron transport rate. (Chiba et al., 2007)	*Arabidopsis thaliana*	Inserted CytC6 gene from red algae *Porphyra yezoensis*	~30% increase	~30% increase	Higher leaf levels of ATP and NADPH were also observed in transformed plants
Lower succinate dehydrogenase activity & higher stomatal conductance. (Araújo et al., 2011)	*Solanum lyco-persicum (tomato)*	Anti-sense lowered expression of succinate dehydro-genase gene SDH2-2	~30% increase	~20% increase	antiSDH2-2 plants also had lower respiration rates
Increased stomatal density & stomatal conductance. (Schlüter et al., 2003)	*Arabidopsis thaliana*	Point mutation in sdd1-1	~30% increase	not reported	Pmax enhancement realized for plants after transferring from low- to high-light
Increased aquaporin expression & mesophyll conductance. (Flexas et al., 2006)	*Nicotiana tabacum (tobacco)*	Over-expression of NtAQP	~20% increase	not reported	NtAQP was expressed in both plasma membrane and chloroplast envelope
Increased sedoheptulose bisphosphatase & greater Calvin cycle activity. (Tamoi et al., 2006)	*Arabidopsis thaliana*	Inserted SBPase gene from Chlamydo-monas reinhardtii	~30%	~50%	Leaf RuBP also increased ~25%
Addition of a glycolate catabolic pathway & minimized photorespiration. (Kebish et al., 2007)	*Arabidopsis thaliana*	Inserted five *E. coli* genes encoding glycolate catabolic enzymes	~50%	~66%	This bypass also increases Cc since a de-carboxylation step occurs in the chloroplast

Table 1. Selected genetic modifications at various sites in primary carbon metabolism that have yielded increased maximum photosynthesis.

fine-tuned, system-level co-regulation, targeted molecular manipulations have been able to enhance photosynthetic production for selected species when grown under optimally controlled environmental conditions (Table 1). Squeezing more out of photosynthesis, at least under suitable conditions, is clearly possible.

2.2 Leaf photosynthesis: Co-variation in leaf longevity and leaf photosynthetic capacity

The thesis of this review is that system-level regulation restricts overall plant productivity. New sets of limits to photosynthesis emerge as we move from the cell up to the leaf-level of organization (Fig. 1). In particular, leaf-level carbon gain will depend upon both the carbon costs and benefits of leaf photosynthetic performance integrated over the time the leaf is on the plant. Interestingly, the maximum possible duration of leaves on a plant (leaf lifespan; LL) and Pmax are known to vary inversely with each other across different species (Reich et al., 1997). This may seem counterintuitive because the cumulative contribution an individual leaf can make to the productivity of the plant would be predicted to depend upon both its maximum rate of carbon gain (Pmax) and the time period over which that rate is potentially realized (LL). As such, we might expect selection for various species to produce long-lived leaves capable of high Pmax rates. It seems that no such species exists!

2.2.1 Materials and methods

A comparative study was carried out across a broad range of tropical species to explore relationships between leaf longevity, photosynthetic capacity, leaf structure and nitrogen status, and the potential lifetime carbon gain for the individual leaf. Forty study species were selected from plants growing in separate distinct habitats or 'mesocosms' in Biosphere 2, a novel controlled-environment research facility in southern Arizona (Leigh et al., 1999). Selected species represented a broad range of growth forms and taxonomic groups. Leaf number per branch and leaf 'birth-rates' per branch were followed for ~1 year on three or more separate branches from one or more individual plants of each study species in order to get demography-based maximum LL estimates (Bazzaz & Harper, 1977). Pmax was measured on intact, healthy, fully-enlarged leaves of each species using a flow-through infrared gas analysis system (Li-Cor 6400, Li-Cor Instruments, Lincoln, Nebraska). Specific leaf area (SLA), the ratio of leaf laminar projected area per unit dry mass, was assessed on tissue samples from healthy, fully-enlarged leaves off the same plants. Leaf nitrogen concentration (N_L) was determined from Kjeldahl digests of tissue samples from healthy, fully-enlarged leaves off the same plants. N_L and leaf heat-of-combustion contents were used to calculate leaf energetic Construction Costs (CC) for leaf samples taken from a subset (18 out of 40) of the study species (Williams et al., 1987). Reported CC estimates assume all plants relied solely on nitrate as their nitrogen source. Reported Pmax, SLA, N_L, and CC values are the means of 3-5 measurements from independent leaves from each of the study species growing in Biosphere 2.

These data allowed the application of an empirical model to estimate the maximum potential lifetime net carbon gain that an individual leaf could make to the overall productivity of the plant. Zotz and Winter (1996) found a strong linear association between instantaneous *in situ* measures of Pmax and the total net 24 hour carbon gain (P_{24h}) for individual leaves from a broad range of different species and growth forms growing in a tropical forest in central Panama. For each Biosphere 2 study species, the average measure of

Pmax was input into the empirical formula from Zotz and Winter (1996) to get a best estimate of P_{24h}. This species-specific P_{24h} value was then multiplied over the estimated species-specific LL to get an estimated maximum potential leaf-lifetime carbon gain (P_{life}). One advantage to this empirical approach is that it incorporates the otherwise uncertain effects of day and night respiration into P_{24h} and P_{life} estimates. Likewise, it incorporates maintenance respiration into P_{24h} and P_{life} estimates. We note that the model holds the Pmax value constant over the projected life of the leaf. Leaves often show a linear decline in Pmax with age (Kitajima et al., 1997). An assumption of a linear decline in Pmax is sometimes incorporated into leaf lifetime carbon gain models (Hiremath, 2000; Kikuzawa 1991). As it turns out, making an assumption of a linear decline in Pmax has the simple effect of reducing estimates of P_{life} for all species by half. Because we have no actual measures of how Pmax varies with leaf age and because it has no qualitative effect on interspecific comparisons, a linear decline assumption was not factored into the Pmax-P_{life} model.

2.2.2 Results and discussion

Our study revealed a strong negative association between leaf lifespan and Pmax (Fig. 6A) and, to a lesser extent, negative associations between leaf lifespan and SLA (Fig. 6B) and N_L (Fig. 6C). Study species included various plants sampled from each of four simulated biome mesocosms (tropical rainforest, savannah-orchard, dry thorn-scrub, and sandy beach). There were, in some cases, significant differences in leaf-level characteristics between plants from different mesocosms which explains much of the plot scatter in Fig. 6 (not shown). However, the overall trends were quite robust even without accounting for these mesocosm differences.

This underscores the global nature of these leaf-level patterns. The results agree with observations made frequently on various C3 plant species from various terrestrial ecosystems (Reich et al., 1997). These relationships appear to be so robust that they are now referred to collectively as the worldwide leaf economics spectrum (WLES; Wright et al., 2004). One end of this spectrum represents species having short-lived, thin, high surface area/volume leaves (i.e. high SLA), with high protein or N_L contents and high photosynthetic rates. The other end of this spectrum represents species having long-lived, thick durable leaves (i.e., low SLA) with low protein or N_L contents and low photosynthetic rates. Among plants producing leaves that live ~1 year or less, there appears to be considerable scope for adjustments in Pmax as a means of increasing plant productivity. But, among plants producing leaves that potentially persist more than a year, there appears to be almost no scope for adjustments in Pmax.

The global nature of the patterns exhibited in Fig. 6A, B & C are interpreted as fundamental leaf structure/function trade-offs maintained by natural selection (Donovan et al., 2011; Reich et al., 1997). Thin leaves with low-density tissue can sustain high photosynthetic rates (high Pmax) in part because there is relatively little intra-leaf chloroplast shading and mesophyll conductances are large. But these same leaves will have low durability (short LL). Thick, high-density leaves are more durable (long LL) but tend to be photosynthetically limited (low Pmax) by intra-leaf chloroplast shading and low mesophyll conductances. This leaf-level pattern where Pmax varies inversely with leaf lifespan is not immediately obvious or explainable based on our previous analyses of cellular and metabolic limits on photosynthesis. These patterns illustrate how functional traits above the level of primary cellular carbon metabolism can place strong constraints on Pmax.

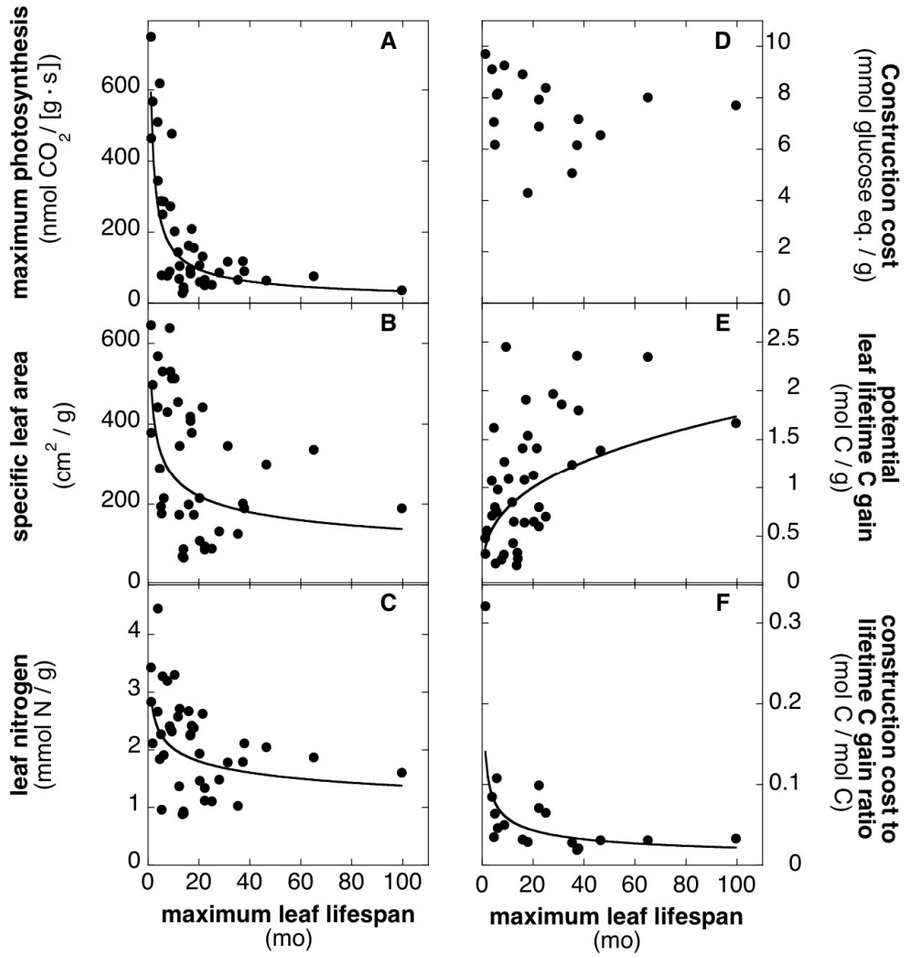

Fig. 6. Interspecific variation in leaf lifespan versus (A) Pmax, (correlation coefficient, r=0.82), (B) SLA, (r=0.51), (C) N_L, (r=0.47), (D) leaf CC, (Non-significant correlation), (E), estimated P_{life}; r=0.54), and (F) a carbon-based leaf cost/benefit ratio (CC/P_{life}; r=0.80). Each datapoint is the mean from 3-4 observations made on each of 40 (A, B, C and E) species or a subset of 18 species (D and F) in controlled environment mesocosms in Biosphere2 in Arizona, U.S.A. Lines of best-fit for power functions are plotted when the association between variables was significant ($P<0.05$) with correlation coefficients (r) as reported above.

Efforts to bioengineer improvements in photosynthetic productivity would generally focus on economically important plants that are grown in managed settings (e.g., commercial greenhouses, agricultural fields, orchards, forest plantations). Many, but not all, plants that might be subject to productivity enhancement efforts will be on the short LL end of the WLES. Genetically modified plants discussed above (e.g., *Arabidopsis* and tobacco) produce leaves that persist no more than a few weeks. Like these species, other economically important species with short-lived leaves may be relatively amenable to bioengineered improvements in Pmax. However, constraints implicit in the WLES suggest that species on the long LL end of the distribution may not be amenable to enhanced productivity through bioengineered improvements in Pmax. Many plant species that are sources of economically

important commodities (e.g., coffee, rubber, olive oil, bananas, citrus), and thus possible targets for improved productivity efforts, are on the long LL end of this spectrum. Likewise, evergreen coniferous trees that produce much of the world's fuel, lumber, and wood pulp produce long-lived foliage with low Pmax rates (Reich et al., 1995). As we begin to extend our efforts at engineered improvements in plant productivity beyond typical lab species (e.g., *Arabidopsis thaliana*), consideration of these leaf-level constraints will become increasingly important.

Bioenergetic costs of producing leaves may be expected to differ among species as a function of foliar structure and chemical composition (Griffin, 1994). However, in the present study, variation in CC across the sampled species was modest and was not significantly correlated (Pearson Correlation Coefficient Test) with leaf lifespan (Fig. 6D). Leaf CC among the 18 species ranged from 4.30 mmol glucose to 9.71 mmol glucose equivalents/g dry leaf mass (0.77 to 1.75 g glucose equivalents/g dry mass), falling well within the range of other published CC values (Nagel et al., 2004; Poorter et al., 2006; Williams et al., 1989).

The potential contribution an individual leaf can make to the overall carbon budget of the plant, P_{life}, depends upon both leaf longevity and Pmax. Interestingly, modeled estimates of P_{life} tended to *increase* with leaf lifespan (Fig. 6E). Hiremath (2000) made a similar observation for a small number of early-successional tropical tree species in the field. Thus, even though Pmax declines as leaf longevity increases, it appears that increased time for photosynthetic operation associated with a prolonged leaf lifespan more than compensates for this. This finding is quite striking in the context of pondering plant productivity enhancements because it implies that targeting the molecular controls on delayed leaf senescence might yield greater carbon gain benefit than targeted enhancements of Pmax. This idea assumes that resource costs to the plant associated with producing more durable and longer-lived leaves is not prohibitive.

The dataset from our study permitted estimation of a carbon cost/benefit ratio for the 18 species for which both Pmax and CC data were available (Fig. 6F). This approach uses CC values as a measure of the carbon cost incurred to the plant for producing a gram of leaf tissue. In turn, P_{life} estimates are a measure of the maximum potential net carbon benefit a gram of leaf may provide back to the plant. A CC/P_{life} value of 1.0, expressed as mol C per mol C, can be considered a 'break even point' in this cost/benefit analysis. All species are expected to fall below this threshold value. Indeed, leaves from all species should fall substantially below 1.0 because many leaves operate much of the time under sub-optimal conditions (e.g., low-light, cold temperatures) and so perform well below Pmax, thereby reducing actual P_{life} below its potential. In addition, many leaves are damaged or abscised long before achieving their maximum leaf lifespan which would also reduce actual P_{life} below its potential. Inspecting the data reveals that the CC/P_{life} values for all species were well below 1.0 mol C/mol C, precisely as expected (Fig. 6F). It is noteworthy that the association between leaf lifespan and CC/P_{life} was quite strong (r=0.80) with short leaf lifespan species exhibiting relatively high carbon cost/benefit values and long leaf lifespan having relatively modest carbon cost/benefit values. This trend emphasizes the importance of having a high Pmax in short-lived leaves as a means of 'paying back' the construction cost before leaf death (see Poorter et al., 2006). This is important because it was suggested above that, in general, the best way to increase overall leaf lifetime carbon gain was through increasing LL. The pattern in Fig. 6F gives nuance to this view because it indicates that for species bearing short-lived leaves (e.g. annuals and deciduous perennials), there is great

advantage to be had from increasing Pmax as a means to improve the overall carbon budget of the leaf and therefore the plant.

Interestingly, Williams et al (1989), using a similar approach, had different results. Where Fig 6F shows a negative association between the cost/benefit ratio and leaf lifespan, Williams et al. (1989) observed a positive association between their estimated carbon cost/benefit and leaf lifespan. In this prior study, the cost/benefit ratio was established as leaf CC divided by estimated A_{24h}. Williams et al., (1989) examined leaf traits in seven different rainforest successional shrub species, some specialized for the shaded understory and some specialized for sunny open sites. It seems that the main factor driving the positive association between CC/A_{24h} and leaf longevity in this earlier study was the segregation of shade and sun specialists. Species from open habitats had leaf lifespans of approximately 100 days and a lower overall CC/A_{24h} as a result of high photosynthetic rates in the bright sun. Species from understory habitats had leaf lifespans of approximately 700 days and a higher overall CC/A_{24h} as a result of limited photosynthetic activity in the deep shade. In contrast, the species selected for our study growing in Biosphere 2 occurred over a range of mostly intermediate light habitats (Cockell et al., 2000; Leigh et al., 2000). Consequently we believe that light effects on Pmax and leaf-lifespan in our study would be modest compared to the work reported by Williams et al., (1989).

Our comparative leaf-level study reveals two important points: First, across different plant species, foliar photosynthetic potential co-varies with leaf composition and longevity. This confirms the generality of the WLES and illustrates the emergence of system-level constraints on photosynthesis not predicted from our knowledge of cell metabolism. Second, an integrated leaf-lifetime cost/benefit analysis of net carbon gain suggests that direct manipulations of cellular photosynthesis may be a useful productivity-enhancing approach only in a limited set of plant species. At the same time, it suggests engineered alterations of other foliar traits such as leaf structure or leaf lifespan may be alternative or complementary strategies for enhancing photosynthetic productivity, depending upon the species.

2.3 Canopy photosynthesis: Does prolonged leaf lifespan enhance whole-plant production?

New sets of restrictions on photosynthesis emerge as we move from individual leaves up to the whole-plant level of organization (Fig. 1). At the whole-plant level, the canopy is the fundamental unit of photosynthesis. Various aspects of whole-plant structure, function, and development can limit canopy photosynthesis and whole-plant productivity. In the previous section we saw how leaf Pmax were constrained by differences in LL and associated structural and compositional traits. Here we examine the influence of leaf-lifespan on plant productivity further in order to illustrate how contrasts in canopy structure might differentially limit whole-plant productivity.

2.3.1 Materials and methods

Gan & Amasino (1995) produced tobacco plants carrying a genetic insert (P_{SAG12}:IPT) that effectively prolongs leaf lifespan over that of wild-type (WT) plants. The auto-regulating physiology underlying this prolonged leaf lifespan phenotype is that the cellular onset of leaf senescence in the transformed plants stimulates endogenous production of the anti-senescent plant hormone, cytokinin. The inhibition of senescence in turn, lowers the rate of

cytokinin production. This elegant auto-regulated approach minimizes pleiotropic effects otherwise associated with constitutive over-production of cytokinins.

We quantified leaf and whole-plant characters in 3.5-mo old P_{SAG12}:IPT and WT tobacco plants to explore how variation in leaf lifespan affects whole-plant performance. Seven plants each of the P_{SAG12}:IPT and wild-type (WT) tobacco genotypes were grown 3.5 mos (to early flowering stage) at low density for maximum canopy light transmittance in controlled environment growth cabinets. Plants were grown under standard soil culture conditions. Plants were initially fertilized weekly with standard commercial nutrient solution (Miracle-Gro All Purpose, Scotts Company, Marysville, Ohio). Starting at the 6-8 leaf stage, plants were fertilized twice weekly. Plants were watered as needed early on and as they matured they were watered daily. Day/night temperatures were set at 20°C/15°C. Relative humidity was not controlled but generally was over 90% at night and dropped no lower than 40% during the day. Light incident at final canopy height was 700±80 μmol photons/($m^2 \cdot s$) PFD. Axial vegetative buds were excised, dried and weighed while the plants grew to prevent branch formation. This maintained monopodal stem architecture and maximized canopy light transmittance. Leaves were mapped to main stem node positions and tagged as the plants grew to follow growth and leaf demography. Dead leaves were collected, dried, and weighed at the time of abscission. Light incident on leaves at different canopy nodal positions was measured *in situ* using a pre-calibrated galium arsenide photodiode to assess self-shading within the canopy (Pearcy, 1991). The light response of photosynthetic oxygen production was measured on tissues from newly enlarged mature leaves near the top of the canopy prior to harvest using a leaf disc oxygen electrode (LD2; Hansatech Instruments, King's Lynn, UK). Light-saturated photosynthesis (Pmax) was also measured on leaves of different ages on representative plants of both genotypes. Standard gravimetric methods were used to assess whole-plant water use (McCulloh et al., 2007). Harvested plants were separated into component organs to quantify live leaf area and the dry weights of different component organs.

2.3.2 Results and discussion

The P_{SAG12}:IPT plants retained their leaves longer than WT plants as expected based upon previous observations (Boonman et al., 2006; Jordi et al, 2000; Gan & Amasino, 1995). The difference between the total number of nodes on the stem, a measure of all the leaves that had ever been produced, and the live leaves present at the time of the harvest is a measure of the number of leaves that had been lost in the canopy due to senescence and abscission (Table 2). The P_{SAG12}:IPT plants still had essentially all the leaves they had ever produced and these leaves were all still intact and green on the plant. The WT plants had lost approximately 12 leaves from the bottom of their canopy as a result of natural senescence and abscission. The lifespan of the seemingly immortal leaves of the P_{SAG12}:IPT plants could not be quantified. Leaf lifespan on the WT plants was approximately 8 weeks. At the time of the final harvest, the P_{SAG12}:IPT plants held about 50% more leaves than the WT plants. Older lower-canopy leaves retained by the P_{SAG12}:IPT plants were considerably larger than the younger mid- and upper-canopy leaves. When compared to WT plants, the P_{SAG12}:IPT plants had double the total photosynthetic leaf area. Total plant production (live + dead tissue) was ~15% greater for the P_{SAG12}:IPT plants than for the WT plants (Table 2). Enhanced leaf lifespan yielded no differences in plant height, live root mass, or allocation to reproduction (Table 2).

Photosynthetic carbon gain becomes light-limited in lower-canopy leaves due to self-shading. This represents an important constraint on photosynthetic productivity that only emerges at the whole-plant level (Valladares et al., 2002). Measures of leaf light-interception as a function of canopy position showed that the youngest vertically-oriented leaves at the shoot apex receive somewhat less overhead light than more-horizontally oriented fully-opened leaves a few nodes down from the apex (Fig. 7A). From here, light availability was attenuated linearly with leaf node position within the plant canopy. Light availability within plant canopies often declines exponentially (Hikosaka, 2005). The linear decline in light observed in the present study presumably results from the wide spacing among plants and the intentional monopodal canopy architecture. The spatial pattern of light availability was indistinguishable for the two tobacco genotypes except near the bottom of the canopy as a result of differences in foliar senescence and abscission.

Photosynthetic capacity (Pmax) tends to decline with canopy position both because of acclimation to the canopy light-gradient and because of age-dependent leaf senescence and associated resource re-mobilization (Hikosaka et al., 1994; Kitajima et al., 1997). To assess how photosynthetic potential varied through the plant canopy, Pmax was measured on selected fully-enlarged leaves at different canopy positions for which leaf age was known (Fig. 7B). Light-saturated photosynthetic O_2 production declined with leaf age in both genotypes but the decline rate was faster for WT than for P_{SAG12}:IPT plants. For example, 50-day old leaves in WT plants had Pmax rates that were approximately half that of similar aged leaves in the P_{SAG12}:IPT plants. Leaves of WT plants did not persist beyond about 60 days but leaves as old as 80 days in the P_{SAG12}:IPT plants were still present and photosynthetically competent, albeit at very low levels. Since intra-canopy light availability was the same for both genotypes, these contrasts represent differences in leaf senescence.

TRAIT	WILD-TYPE	P_{SAG12}:IPT
Live leaves present	19 ± 1 (A)	29 ± 2 (B)
Total live canopy leaf area (cm^2)	2,536 ± 93 (A)	5,222 ± 110 (B)
Stem height (cm)	67.0 ± 3.5 (A)	63.5 ± 5.5 (A)
Nodes present on stem	31 ± 3 (A)	31 ± 2 (A)
Live root mass (g)	30.3 ± 3.4 (A)	31.0 ± 2.2 (A)
Cumulative flower bud mass (g)	4.6 ± 0.4 (A)	6.0 ± 0.9 (A)
Cumulative whole plant mass (g)	95 ± 6 (A)	110 ± 5 (B)

Table 2. Live biomass allocation and cumulative production (living + abscised dead biomass) patterns for PSAG12:IPT & WT tobacco plants at 3.5 months after germination. All masses are dry weight. Values are means of 6-7 plants per genotype ± 1 S.E. Different letters (A or B) within a row indicate significant differences between genotypes (t-test, $p<0.05$).

Complete photosynthetic light-response curves were also measured on fully mature, upper-canopy leaves (2-3 weeks in age) where we expected to find no genotype differences in light-dependent acclimation or age-dependent senescence (Fig. 7C). Dark respiration rates (R_m) and QY values were similar in both genotypes. Likewise, the light level where photosynthesis and respiration are exactly balanced (photosynthetic light compensation point) was ~50 µmol photons m^{-2} s^{-1} PFD for WT and P_{SAG12}:IPT plants alike (Fig. 7C). Photosynthetic tissues below the light compensation point lose more carbon than they fix. We note that only the P_{SAG12}:IPT plants still had lower-canopy leaves growing in light levels

below this critical level (Fig. 7A). Assuming that light compensation point changes little with leaf age and/or canopy position, it would appear that the lower leaves on the P_{SAG12}:IPT stems were a net carbon drain on the plant as a result of self-shading. Boonman et al. (2006) made similar observations for P_{SAG12}:IPT and WT tobacco plants grown at high densities where lower leaves were subject to both intra-canopy and inter-canopy shading. Boonman et al. found that growth rates were indistinguishable between the two genotypes at these high planting densities even though the P_{SAG12}:IPT plants had substantially more photosynthetic tissue than the WT plants. This uncoupling of total leaf area from plant growth was attributed to the older, deeply-shaded leaves in the P_{SAG12}:IPT plants acting as net respiratory tissues even during the day (Boonman et al., 2006). Unexpectedly, in the present study, light response curves for upper-canopy leaves indicated that the Pmax rates of the new, upper-canopy leaves tended to be lower ($p=0.07$; t-test) in the P_{SAG12}:IPT than in the WT plants (Fig. 7C). Given the canopy position and age of these leaves, this tendency for a genotype effect on upper-canopy Pmax rates cannot be explained directly by differences in light availability or leaf senescence.

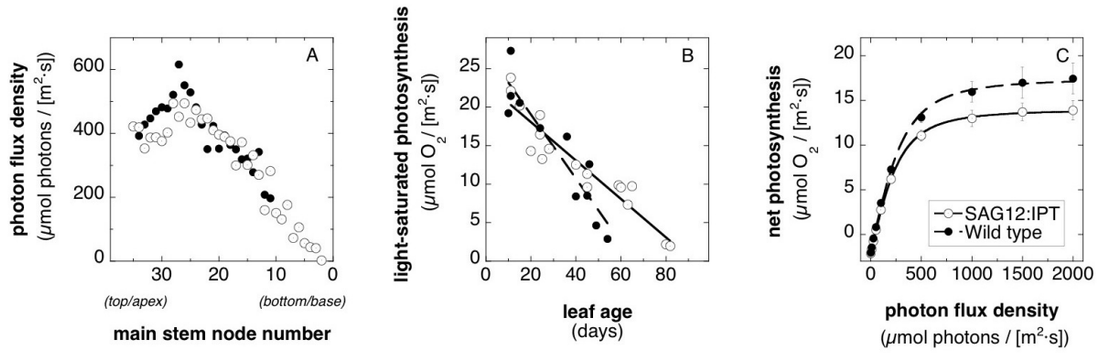

Fig. 7. Light interception by leaves at different positions in the canopy of WT and P_{SAG12}:IPT tobacco plants. Each data point is the mean from 3 different plants of each genotype (A). Pmax for leaves of different ages within the canopy of three WT and three P_{SAG12}:IPT tobacco plants (B). Photosynthetic light response of newly mature upper canopy leaves (2-3 weeks old) from three WT and three P_{SAG12}:IPT tobacco plants (C).

In general, plant canopies exhibit characteristic distribution and re-mobilization patterns of N_L that tend to maximize whole-canopy photosynthesis (Hikosaka, 2005). Upper-canopy leaves typically have higher N_L concentrations, higher complements of Rubisco, and sustain higher Pmax rates than shaded lower-canopy leaves. As older leaves senesce, degrading tissues release nutrient resources, including nitrogen, that may be transported for use in new growing tissues elsewhere in the plant, especially newly emerging, fully-illuminated, upper-canopy leaves. Canopy recycling of N_L is particularly important for plants grown in nitrogen poor soils. Jordi et al. (2000) demonstrated the detrimental effects of prolonged leaf lifespan on N_L and photosynthesis in upper canopy leaves of WT and P_{SAG12}:IPT plants grown under N-starvation conditions. As in the present study, Jordi et al. (2000) found that older leaves in WT plants dried, yellowed, and abscised whereas older leaves on the P_{SAG12}:IPT plants remained intact, green, and photosynthetically competent. However, newer upper-canopy leaves in the nitrogen-limited WT plants had more N_L, and supported

higher Pmax rates than comparable leaves in nitrogen-limited P_{SAG12}:IPT plants. The forced retention of older P_{SAG12}:IPT leaves prevented canopy recycling of N_L to the upper canopy leaves. Under N-starvation conditions this prevented the production of new high N, high Pmax leaves at the top of the canopy. In the present study, N_L was not evaluated. However, the plants were well fertilized with complete nutrient solutions. All living leaves on both sets of plants were a rich green color implying no nitrogen limitations. Limited nitrogen availability seems an unlikely explanation for the marginal genotype differences in Pmax observed in Fig 7C.

All else being equal, a plant with greater canopy leaf area will lose more water through transpiration than a plant with less leaf area. We carried out gravimetric measures of 24 hour water-use for plants of both genotypes to see if whole-plant water use scaled linearly with the total surface area of the leaf canopy (Table 3). It did not. Despite having two-fold greater canopy leaf area, daily whole-plant water-use was ~13% lower in the P_{SAG12}:IPT plants than in the WT plants. When corrections for contrasts in total live leaf area were made, the difference in foliar transpiration was even more striking. The leaf-area based rate of water use was about 36% lower in the P_{SAG12}:IPT plants compared to the WT plants (Table 3). The marginally lower photosynthetic capacities observed for upper-canopy leaves of the P_{SAG12}:IPT plants (Fig. 7C) may be a consequence of stomatally-limited leaf gas-exchange rates presumably to compensate for the greater transpiring surface area in these plants. We speculate that the modest 15% difference in total plant production of the P_{SAG12}:IPT plants, despite having twice as much photosynthetic leaf area with minimal intra- and inter-canopy shading, may partially arise from reduced leaf gas-exchange rates for water-conservation.

	WILD-TYPE	**P_{SAG12}:IPT**
24-hour water use per plant (ml H_2O per plant)	349 ± 15 (A)	303 ± 17 (B)
24-hour water use per unit canopy leaf area (ml H_2O per m^2)	614 ± 53 (A)	391 ± 43 (B)

Table 3. Patterns of whole-plant water use for P_{SAG12}:IPT and wild-type tobacco plants at 3.5 months after germination. Values are means for 4 plants per genotype ± 1 S.E. Soil evaporative water losses have been factored out. Different letters (A or B) within a row indicate significant differences between genotypes (t-test, $p<0.05$)

This study, along with those of Gan & Amasino (1995), Jordi et al. (2000), and Boonman et al. (2006) indicate that longer lived leaves can help to increase overall plant production provided the plants are grown under optimal conditions. This result is qualitatively consistent with predictions made from leaf-level considerations (Fig. 6E). However, these various studies with the two tobacco genotypes also indicate some of the ways that whole-plant structure (e.g., canopy architecture and light gradients) and composition (e.g., canopy gradients in N_L concentration) can limit whole-plant productivity. Table 2 shows that a doubling of leaf area only yields a 15% gain in plant production indicating diminishing returns associated with prolonged leaf lifespan, even when grown under presumably optimal conditions. Prolonged retention of canopy-shaded leaves may slow growth if lower

leaves act as a net carbon drain on the plant. Low canopy transpiration rates and low Pmax rates in fully illuminated upper-canopy leaves of P_{SAG12}:IPT plants suggest that whole-plant water conservation, even under well-watered conditions, may slow plant growth too. We note that unrecognized pleiotropic effects of the genetic transformation and/or unforeseen differential effects of axial bud removal in our study may also have contributed to the observed differences in photosynthesis, transpiration, and plant growth. The assessment of these possibilities awaits further study.

Comparative studies with P_{SAG12}:IPT plants also give insight into the basis of the WLES patterns shown in Fig 6. Leaf lifespan differences can allow for associated differences in leaf lifetime carbon gain if there are adequate resources, such as water, light, and nitrogen, for the leaf to sustain positive net carbon assimilation. But these comparative P_{SAG12}:IPT studies demonstrate how extended leaf lifespan is also associated with increased canopy-self shading, increased transpiring surface area, and reduced N_L re-mobilization rates due to increased nitrogen residence time within individual leaves. Consequently, a *low* Pmax should be favored in species producing longer-lived leaves because of the associated lower water and nitrogen costs and because the carbon gains otherwise associated with a high Pmax leaf would seldom be realized in long-lived leaves due to intra-canopy light-limitations. The global nature of the WLES patterns are re-interpreted as fundamental structure/function trade-offs arising at both the leaf *and* the whole-plant level.

3. Conclusions

The productive capture and use of sunlight by plants and their photoautotrophic kin makes the ordered changes of life on Earth thermodynamically possible. There is great interest in finding ways to increase plant production through different means including new approaches to enhanced photosynthesis. This is inspired, in part, by the need for practical solutions to various global problems of increasing urgency, and, in part, by advances in genetic engineering. Selected examples here illustrated how efforts at improving photosynthetic productivity must be considered from a systems perspective. A 'system' is a set of interacting and interdependent entities that function as a coherent whole (Lucas et al., 2011). Biological systems exhibit three properties; hierarchy, emergence, and resilience. The hierarchical nature of plant photosynthesis was emphasized here by focusing on carbon metabolism at the cellular level, CO_2 uptake at the leaf level, and plant growth at the whole-plant level (Fig. 1). At the cellular level there has been tremendous progress in our understanding of photosynthesis and related metabolic processes and in our ability to improve photosynthesis in selected species under carefully controlled cultivation conditions (Fig. 3; Table 1). These molecular studies demonstrate that plants can 'do better', giving a preliminary positive answer to the question posed by the title of this review. But emergent properties arising from the interactive nature of cellular carbon metabolism also demonstrated many ways in which photosynthetic efficiency is sacrificed for metabolic flexibility, a necessary condition for accommodating the variable environmental conditions plants normally experience. Selected studies at higher hierarchical levels were used to illustrate some ways that constraints on plant production can emerge that are otherwise unforeseen at more reductionist scales. The observed association between leaf lifespan and maximum photosynthesis (Fig. 6) is a leaf-level pattern that is not predictable from cellular biochemistry. A leaf-level view would attribute this trade-off to leaf structural differences associated with leaf 'toughness' that influence light transmission and gas diffusion. But our

consideration of whole-plant performance in tobacco plants with contrasting leaf lifespans (Table 2 & 3; Fig. 7) also indicate that whole-plant water use, canopy light transmission, and canopy nitrogen distribution act to constrain leaf-level traits of photosynthesis and leaf lifespan. Thus, new properties that can limit plant growth continue to emerge as one proceeds up through additional hierarchical levels. Another theme that repeatedly arises as we consider limits on plant productivity is photosynthetic variation within and among species. This is related to the resilience property of complex living systems, where resilience is the ability to perform under a wide range of conditions by having the capacity to accommodate or recover from imposed changes in the state of the system. Stomatal closure for water-conservation, xanthophyll-mediated dissipation of absorbed light energy, divergence of chloroplastic (or mitochondrial) electron flow to non-productive processes, re-mobilization of leaf resources from old canopy-shaded leaves, storage of carbohydrates for future use, production of durable, long-lived leaves with low metabolic activity; these are all examples whereby diminished photosynthetic productivity may permit increased resilience and survivorship. It seems that natural selection favors resilient systems even if there is an associated marginal cost to energetic efficiency. This is an insight we must take into consideration as we strive to develop more productive plants. A more definitive answer to the question posed by the title of this review will emerge as we begin to take various species of photosynthetically-improved plants out of the lab and into the field. Systems-based analyses of results from such studies will give great insight into the extent to which bioengineering of photosynthesis can enhance >3 billion years of evolutionary innovation in photosynthetic productivity.

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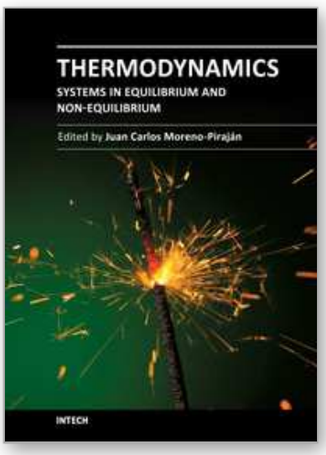

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