

Plant Physiology

Applying Photosynthesis Research to Increase Crop Yields*

Clanton C. Black*, Shi-Jean S. Sung**, Kristina Toderich***,
Pavel Yu. Voronin#

* The University of Georgia, Biochemistry & Molecular Biology Department, 120 Green Street, Athens, GA 30602 USA

** USDA-Forest Service, Southern Research Station,
2500 Shreveport Highway, Pineville, LA 71360 USA

*** Samarkand Division, Uzbekistan Academy of Sciences, Timur Malik st., 703000 Samarkand, Uzbekistan

Plant Physiology Institute, Russian Academy of Sciences, Moscow 127276, Botanicheskaya St., 35, Russia

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ABSTRACT. This account is dedicated to Dr. Guivi Sanadze for his career long devotion to science and in recognition of his discovery of isoprene emission by trees during photosynthesis. Investigations on the emission of isoprene and other monoterpenes now have been extended globally to encompass other terrestrial vegetation, algae, waters, and marine life in the world's oceans. And new understandings are emerging on the important roles of monoterpenes and other volatile chemical emissions in plant biological signaling and in global atmospheric chemistry. Such investigations can be traced historically through Guivi's pioneering isoprene emission research as a young graduate student. Dr. Sanadze took a formative sabbatical leave in my photosynthesis lab at the University of Georgia, USA in 1976. I admire his strong commitment to science and am indebted for his warm friendship over these decades (CCB). © 2010 Bull. Georg. Natl. Acad. Sci.

Key words: photosynthesis, photoprotection, xanthophyll cycle, light interception, crop yield, plant growth.

Plant growth, specifically crop yields, and all heterotrophic life ultimately are completely dependent upon sustained photosynthesis. All life forms are totally dependent on the sustained presence of reduced organic carbon regardless of whether these are needed momentarily, over one's life span, in an ecosystem, globally, or over the 3.7 billion years of life's existence on Earth. Only two primary sources of dependable sustained energy have existed during all of Earth's history - solar and nuclear. It is vital that all biological creatures through electrochemistry and photochemistry have lived on these energy sources for billions of years. Even so, only in the last hundred years have humans begun to understand how our primary energy sources function, and particularly how they are captured in biology or can be more effectively used by humanity. Thus, our efforts to

understand and then hopefully to modify and more effectively use our two primary energy sources are still primitive; especially regarding the subjects of this article, namely increasing net photosynthesis and the resulting yields of crop plants.

As the nature of photosynthesis was studied in the last century, it soon became evident that the basic requirements of sustained photosynthesis are: sunlight; a source of electrons such as water or H_2 ; inorganic mineral nutrients; CO_2 ; liveable temperatures; and a suitable aqueous cellular host. But in nature the available supply of these essential components is remarkably and naturally variable both in the myriad of Earth's ecological environments where organisms live and in the wide variety of cellular environments where the photochemistry, electrochemistry, and biochemistry of photosyn-

thesis occurs. As a result, many photosynthetic organisms have evolved to cope with such extreme and dynamic variations in the availability of essential photosynthesis components! Therefore, in the last half century, photosynthesis research has continually asked how do various photosynthetic creatures cope with so many environmental variations especially when essential components may be limiting or in some environments present in damaging excess? Still photosynthetic organisms have evolved to inhabit these multitudes of environments! Today humanity continually asks, how can we use these biological capabilities? Thus in agriculture, and in all plant production work, much effort was and is expended asking how to overcome environmental components that may limit or be detrimental to yields, e.g., plant nutrients, water, CO_2 , light, temperature, or toxic inorganic and organic chemicals. Here the question addressed is how has the fundamental knowledge we now have about the photochemistry, electrochemistry, biochemistry, and physiology of photosynthesis been used successfully to increase the growth, production, and yields of plants? A partial answer is yes; and that question will be further examined here by considering: i) our current understandings of plant photosynthesis from a temporal view point; ii) how photosynthesis is protected from environmental extremes, detrimental processes, and toxic chemicals; iii) examples of successful efforts to apply our accumulating knowledge about photosynthetic processes to in-

creasing crop yields; and iv) conclude with a compilation of research target opportunities that could increase photosynthesis and crop yields.

Current Understandings of Photosynthesis

One way of readily understanding photosynthesis is to consider the speed or time required for various steps or processes in photosynthesis to occur. A very informative temporal summary was devised by M.D. Kamen [1] when he divided the sequential events occurring within photosynthesis on the basis of the "logarithm of the reciprocal of time, expressed in seconds"; which is somewhat analogous to the pH scale for acidity and alkalinity. Thus, time can be presented in orders of magnitude such that sequential events or processes happening over specific times can be thought of in terms of speeds or starting and endurance times. Fig. 1 gives such a time scale for photosynthetic events that spans about 26 orders of magnitude of time in seconds from initial light absorption, near 10^{-15} sec, to growing our oldest plants, near 12,000 years. The temporal eras for many photosynthetic events show marked contrasts, e.g., the extremely rapid speed of photon absorption and stabilization versus the much slower speeds of biochemistry, physiology, growth, or environmental ecology. Nevertheless, all of these sunlight powered processes are integral components of Earth's sustained photosynthesis.

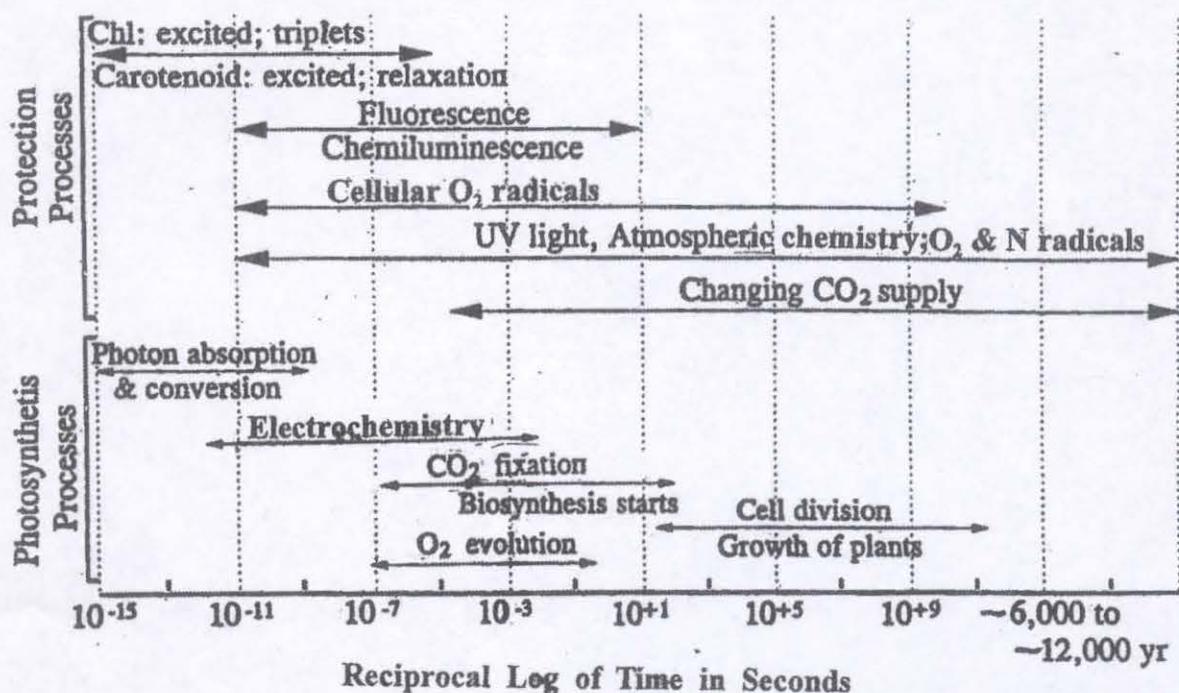


Fig. 1. Time Scales of Photosynthesis Processes. Time is given as the log of the reciprocal of time in seconds. The time scale of photosynthesis begins with light absorption near 10^{-15} sec and extends to the growth of the oldest known plant near 12,000 years. An approximate era for each process is indicated by the arrows.

In the last century photosynthesis has been extensively studied from its intriguing mechanisms that reach from radiation physics to global climates in eons of time (Fig. 1). The general pathways of energy flow from light capture to the synthesis of organic molecules is now reasonably well known. Indeed classroom biochemistry and biology textbooks now routinely include detailed presentations on topics such as light harvesting complexes, resonance energy transfer, reaction centers, photoexcited electrons, the Z-scheme of electron flow and electrochemistry during oxygenic photosynthesis, non-oxygenic bacterial photosynthesis, protomotive force, photophosphorylation, ATP synthases, the Calvin-Benson-Bassham C_3 cycle of CO_2 assimilation, plus the C_4 cycle, and Crassulacean acid metabolism photosynthesis. These central aspects of basic photosynthesis occur sequentially within the times indicated in Fig. 1.

Protection of Photosynthesis

Photosynthetic organisms live in a multitude of environments that also can be detrimental, e.g., excess sunlight. During active photosynthesis the absorption of light energy is so rapid, about a femtosecond, that photoprotection mechanisms must be in place before chlorophylls and other biochemical components of pho-

tosynthesis are synthesized much slower (Fig. 1 & 2) and correctly positioned in chloroplasts. Thus as each light dependent process occurs, it must be protected from sunlight. A comparison of the photosynthetic processes in Figs. 1 and 2 indicates an involvement of processes both for the beneficial utilization of sunlight and for the dissipation of excess light energy, e.g., carotenoid relaxation; non-photochemical quenching (NPQ); the photochemical production of O_2 radicals; or protection from UV light. Photoprotection involves some very fast events that can act near the times of light absorption, stabilization, and light harvesting as reduced entities (Fig. 2) as well as slower developing daily protection processes, e.g., the xanthophyll cycle, for photoprotection from intense midday sunlight. If photoprotection is not present, then fatal sets of events can occur very rapidly, i.e., most deadly is the destruction of chlorophylls since chlorophylls are the heart of photosynthesis! It's instructive to pause and to reemphasize some reasons why protecting chlorophyll is so crucial for crop plants. After World War II with the availability of ^{14}C , $^{28}Mg^{++}$, and other radioisotopes, Sam Aronoff and others labeled chlorophyll in various plants and demonstrated that the specific activity of carbon and Mg^{++} in chlorophyll did not change in mature leaves after labeling them during

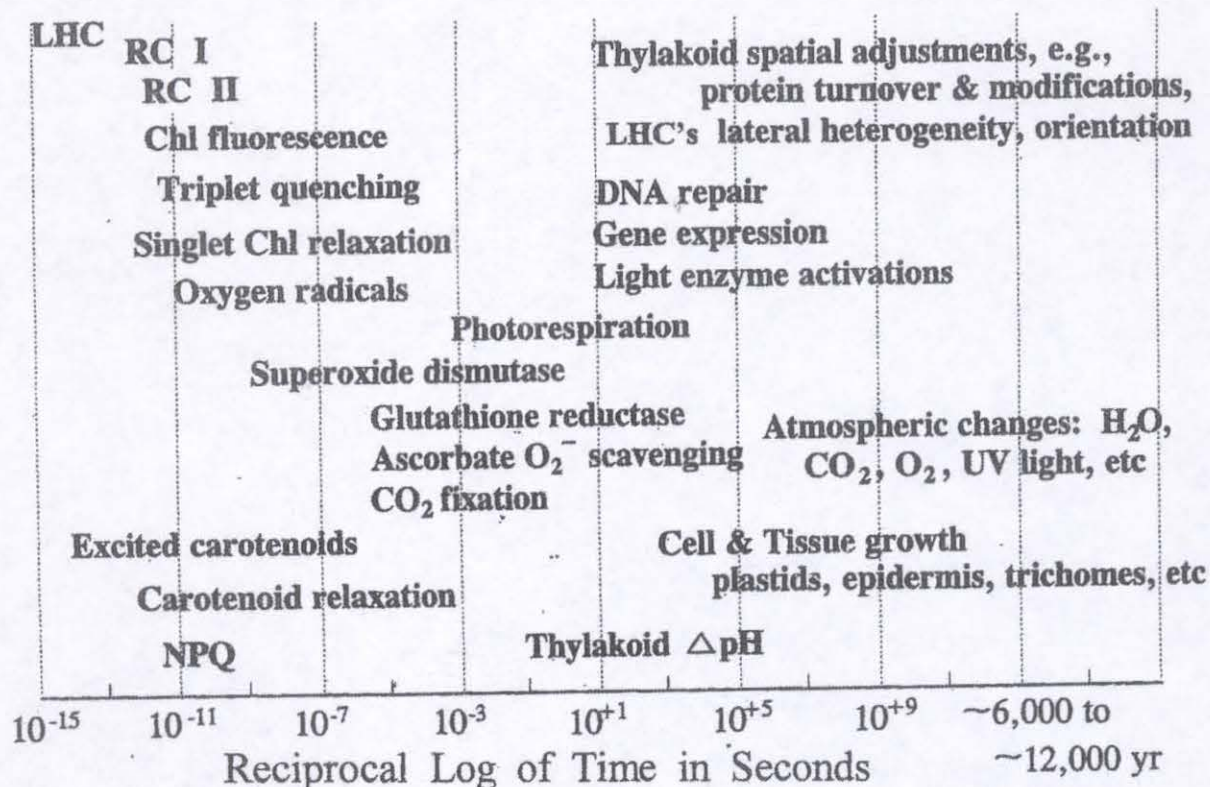


Fig. 2. Starting times for photoprotection and photosynthetic activities. These activities start near the time of first capital letter for each activity. Time is expressed as in Fig. 1.

early leaf development [2,3]. It was evident that mature leaves, particularly of annuals like many crops, do not replace chlorophyll if it is destroyed. In other words, annual crop leaves with their short life times only fully construct a cells chloroplasts once! Therefore, it is axiomatic that, preventing the photodestruction of chlorophyll is essential and that photoprotection allows short-lived leaves to avoid the costs of repairing and replacing chloroplasts! In fact, photosynthesis is constantly being protected within its photochemical, electrochemical, biochemical, and plant growth processes by a variety of mechanisms shown in Fig. 2 that are too extensive to detail here [4-7].

Photoprotection by the Xanthophyll Cycle Prior to Photosynthesis

Because plants use less than 3% of sunlight's incident irradiance the need for photoprotection from excess light energy is evident. Here we will consider an example of the crucial importance of protection for photosynthesis during leaf greening. We know photosynthetic organisms require chlorophylls and other light harvesting pigments to catalyze photosynthesis; while simultaneously other pigments are required to protect them from excess sunlight. In all photosynthetic organisms, carotenoids [4,8,9] are the other major pigment system that protects photosynthesis [10-13]. In plants the daily xanthophyll cycle provides photoprotection via the rapid, near pico-second, ability of specific xanthophylls such as zeaxanthin and anthraxanthin to dissipate light energy as heat [11,13,14]; likely because the energy of their excited singlet state is lower than that of chlorophyll [15].

The xanthophyll cycle is a light-dependent conversion of violaxanthin (V) to zeaxanthin (Z) via the interme-

diate antheroxanthin (A). The cycle is reversible in the dark; but it may remain in A + Z state in cold weather when enzymes are impeded, e.g. with evergreen leaves [13]. A typical conversion to A + Z over a high irradiance day for leaves is shown in Fig. 3. The maximum A + Z occurs at the maximum PPFD and reverses in darkness. Also shown is a similar xanthophyll conversion in green bracts and sepals of flowers which we also will soon consider related to plant carbon sinks and crop yields. The clearly recognized need of plants in nature to rapidly dissipate excess light [5-7] much quicker than other biochemical processes, e.g., gene expression (Fig. 2), raised question to us, e.g., "When does the xanthophyll cycle become functional to protect photosynthesis in a developing leaf?" We measured both the xanthophyll cycle and net photosynthetic CO₂ uptake via leaf gas-exchange techniques [16,17]. A set of measurements at noon time are shown in Fig. 4. The daily xanthophyll cycle was functional in all leaves from the youngest to the oldest (complete cycles not shown). Net photosynthesis, in contrast, was not detectable in the very young leaves but progressively developed, as expected, with increasing leaf growth, Fig. 4, shown as leaf position. Clearly a functioning xanthophyll cycle was present prior to net photosynthetic CO₂ uptake in these developing leaves and photosynthesis reached maximum values in mature leaves as expected. These leaves were irradiated with PPFD values near those in Fig. 3. Several features of the xanthophyll cycle in developing leaves are noteworthy: first young leaves convert a high fraction of V to A + Z each day and second the fraction converted was lower as leaves matured when other mechanisms, such as the CO₂ fixation cycle, also will help dissipate light energy. In other studies with unopened leaf buds, the daily xanthophyll cycle functioned

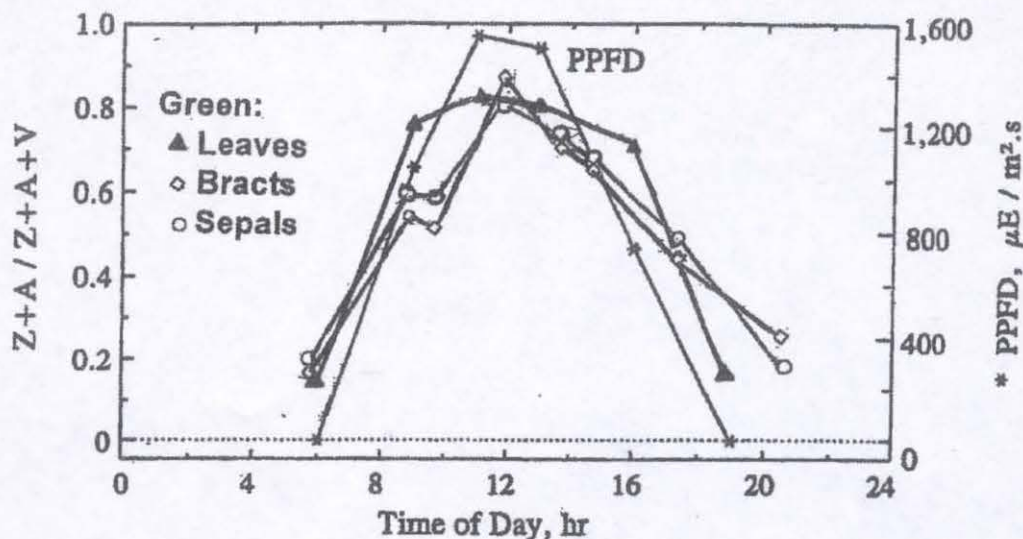


Fig. 3. Typical daily xanthophyll cycles in leaves, flower bracts, and sepals measured as Z + A/Z + A + V.

poised to operate as soon as leaves unfold to the sun and green for photosynthesis (data not shown). Knowledge of the photoprotection provided by xanthophyll cycle has been used to increase photosynthesis and grain yields in hybrid rice [18-20], partially by overcoming the mid-day photo-depression of photosynthesis.

Applying Photosynthesis Research to Increase Crop Yields

Axiomatically crop growth is dependent upon photosynthesis; hence a clear goal of photosynthesis research is to increase crop production. However increasing the process of photosynthesis in nature has proved to be a very elusive goal despite the insightful photochemistry, electrochemistry and biochemistry information now available on basic photosynthesis from concerted scientific efforts in the last century. Unfortunately only a small fraction of these basic insights have been successfully transferred to agriculture. Even so crop yields have increased by utilizing some of our photosynthesis knowledge, most clearly with basic environmental type improvements that increased plant canopy photosynthesis. A half century ago it was recognized by crop physiologists such as D.J. Watson, W.G. Duncan, W.A. Williams, R.S. Loomis, J.L. Monteith and others [21-24] that light absorption by crop canopies was not light saturated. Two approaches were devised to obtain maximum light absorption and thereby increase crop photosynthesis. One approach was to increase leaf area index (LAI)

which is defined as the leaf surface area/meter² land. The most direct manner to increase LAI is to increase the number of plants per unit of land area, i.e., to increase plant densities; hence plant breeders selected for tolerance of high plant density.

The second approach was to increase leaf light interception. It has long been known that some plant leaves avoid direct sunlight; leaves of other plants face the sun each morning only, while other plant leaves track the sun. Various workers recognized that by increasing leaf angle relative to plant stems the interception of light increased, especially in dense leaf canopies [21-24]. By breeding for leaves oriented at angles more favorable for light interception crop canopy photosynthesis was increased.

A direct demonstration of increasing canopy photosynthesis by increasing both LAI and leaf angle is given in Fig. 5 [25]. This study capitalized on the upright growth habit of barley seedlings by growing plants at different angles to light and with a range of LAI's. Clear increases in canopy photosynthesis occurred as LAI increased and as leaf angle increased to upright (Fig. 5). Such knowledge has been widely utilized by plant breeders and crop physiologists to increase major crop yields [21-24, 26, 27].

Crop Yield Increases from Basic Photosynthesis Research

While some of the information about basic photosynthetic processes, i.e., photochemistry, has not yet

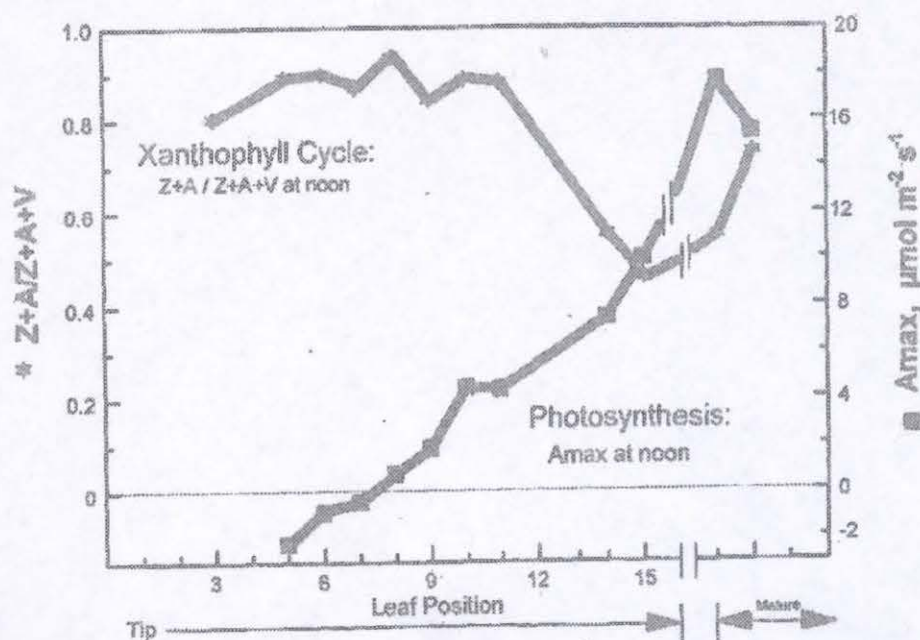


Fig. 4. Noon values for the xanthophyll cycle and for net photosynthesis in developing Northern red oak leaves plus three mature (M) leaves all on the same tree branch.

directly transferred to increase field photosynthesis there has been a strong application of photosynthesis research in agriculture. For instance, shortly after World War II several groups of herbicides such as the substituted ureas and the triazines were developed that inhibit photosynthetic electron transport. With field development these and other herbicides became widely employed in selectively controlling weed competition in specific crops and thereby increasing crop production. Then with continued photosynthesis and biochemical research on herbicides and insecticides their biochemical mechanisms and cellular sites of actions were identified and characterized in plants. Those understandings of mechanisms and action sites then naturally became ready targets with the advent of molecular abilities to modify and transform plants. Now genetically engineered crops are widely available in many countries, e.g., “herbicide ready” and “insect resistant” plants. Resultant reductions in field competition for space, nutrients, and water have resulted in increases in crop yields and photosynthesis. Combining these with very successful breeding strategies, e.g., of corn (*Zea mays*) breeding, have given dramatic increases in commercial grain yields [26,27]. Plant hybrid vigor was the most beneficial crop yield increase discovery of the 20th century; as shown with *Zea mays* in Fig. 6 following the introduction of hybrid Fig. 6 corns in 1939 [26]. These remarkable increases in average farm

corn yields were founded on and catalyzed by hybrid vigor. But the steady yield increase (in Fig. 6) was maintained by i) breeding for upright leaves to increase canopy photosynthesis, ii) breeding to increase plant density tolerances, iii) enhanced weed and insect competition controls, and iv) excellence in agronomic crop cultural practices such as well balanced mineral nutrition and proper water. Indeed greater yield increases are obtainable. For instance using genetically engineered seeds and excellent agronomic cultural management in the fertile James River bottom lands of Virginia, corn grain yields near 23,800 kg ha⁻¹ were harvested in 2008 from 1 acre center of field crop areas (David Hula, personal communication to CCB).

Targets for Increasing Photosynthesis and Crop Yields “All is Leaf” Goethe ~ 1790

Increasing leaf photosynthesis alone is not a “magic silver bullet” that will automatically increase crop production! Axiomatically everything in nature is connected as clearly illustrated by the total dependency of photosynthesis on environmental components, i.e., light CO₂, H₂O, temperature and minerals. An analogous, and equally complex, scenario also must be considered for the cellular environments and cell locations of photosynthetic processes in plants. The famous declaration “All is Leaf” by Goethe long ago recognized that the green of leaves, i.e., photosynthesis, occurred in most all plant tissues and structures. However, plant photosynthesis research has been strongly focused on leaves with little attention given to other green organs or tissues. Plant physiologists have a long history of considering plants from source-sink relationships with the sink often being the harvested crop and leaves being the source [28,29]. Many strong sinks are green and also often are surrounded by green tissues. Commonly seeds when harvested are not green evenso, in fact, most are green during much of their ontogeny. Unfortunately, only a very small portion of basic photosynthesis research is available that is focused on what is happening photosynthetically in sinks such as seeds, pods, glumes, etc. New methods for increasing sink strength and photosynthesis are under investigation [32-34]. A goal of only increasing leaf photosynthesis must recognize that other plant organs also should be targets of both breeding and genetic engineering research [Table 1]. For example, Fig. 3 indicates a daily photoprotection in other plant organs to conduct their roles in net plant photosynthesis. Today plant improvement research has available two strong complementary methods, namely, plant breeding

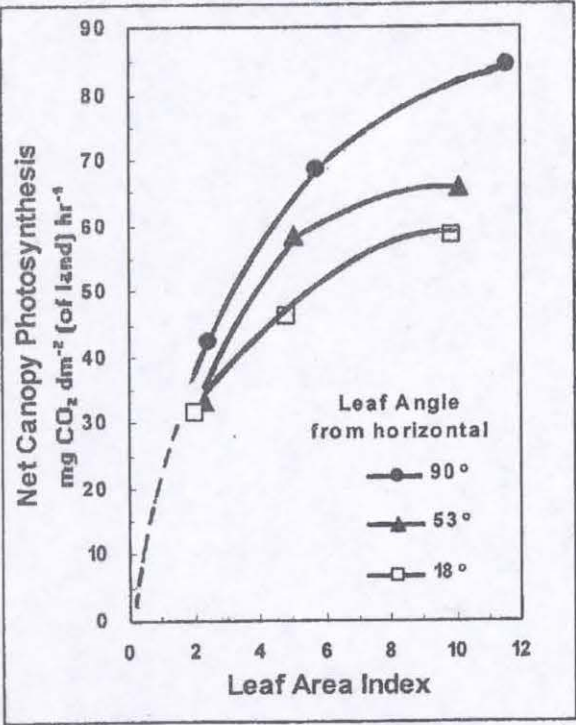


Fig. 5. The influences of leaf area index and leaf angle on net canopy photosynthesis with barley seedlings. Data adopted from reference 25.

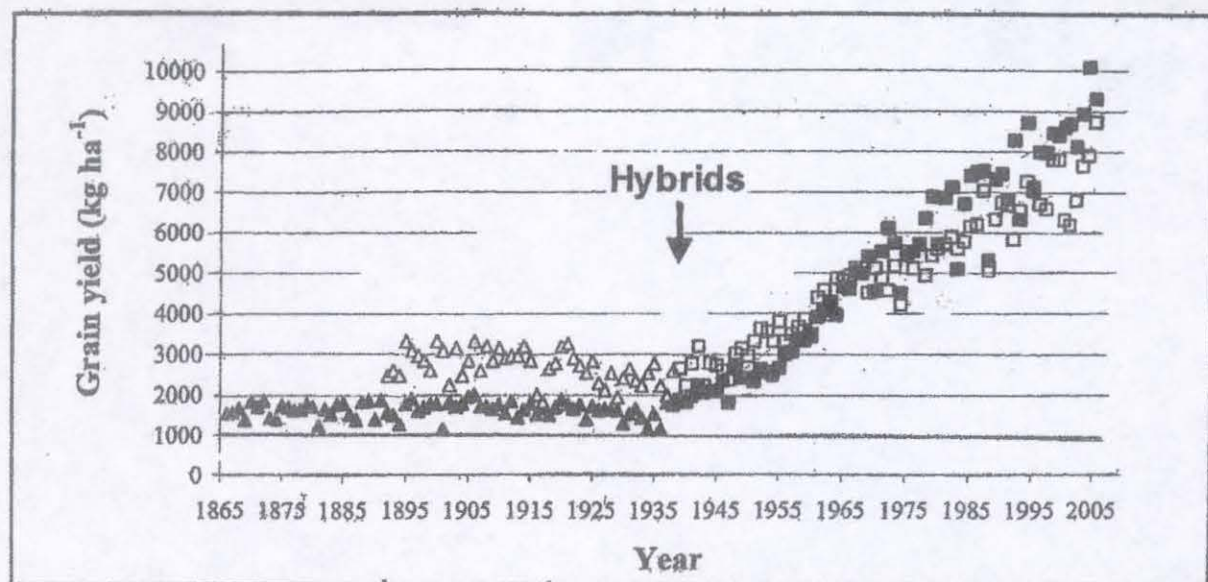


Fig. 6. Average USA and Canadian corn (*Zea mays*) grain yields in Kilograms per hectare. Graph adopted from data and presentation in reference 26.

with definite selection criteria and genomic engineering. The combined uses of both will continue and should expand more from major crops to other useful plants and natural products. With major crops, breeders now know numerous useful quantitative trait loci for selection criteria [26,27]. Simultaneously biochemistry and physiology research continues to supply new targets for genetic engineering [30-34].

In considering opportunities to increase photosynthesis, Long et al. [30] recently summarized some identified targets for hopefully changing the efficiency of photosynthetic light conversion (Table 1). These changes focus on known targets based mostly on earlier research in photosynthetic microbes, algae and much leaf and chloroplast experimentation.

Improving the catalytic activity and decreasing its susceptibility to O_2 with Rubisco (Target 1, Table 1) have been major targets aimed at improving photosynthesis for decades. Recent mechanistic summaries of Rubisco activities remain reluctant about improving whole plant photosynthesis with Rubisco [35,36] despite its vital role for all of biology. But enhancing the activity of other carbon cycle fixation enzymes seems to improve plant growth, photosynthesis, and give plants greater environmental tolerances, e.g., of higher temperatures (37-41). For example, recent genomic transformations with a more heat stable Rubisco activase [38] gave a substantial increase in seed yields in preliminary studies (Fig. 7). The latter targets in non-leaf organs (Table 1) have not been widely investigated but such results are quite promising for increasing,

Table 1.

Potential Targets for Increasing Light Capture During Plant Photosynthesis*

Photosynthesis Targets:

1. Rubisco with decreased oxygenase activity and with efficient or increased catalytic activity
2. C_4 PS engineered into C_3 plants for C, N, and S assimilation
3. Improved plant PS architecture deeper into crop canopies
4. Increased photoprotection both in the amounts of protection and the recovery of PS
5. Increased capacity to regenerate RuBP; e.g., by over expression of SBPase or Rubisco 5-P kinase
6. Engineering focused on the activities and role of light sensitive PS enzymes: Ribulose 5-P kinase, SBPase, FBPase, and Gly 3-P DH, NADPH dependent, in all green tissues
7. Engineering of metabolic and PS activities to increase sink strength especially in green, non-leaf, sources and sinks, e.g., glumes, awns, pods, seeds, fruits

*Table partially adopted from [30]

Rubisco = ribulose 1,5-bisphosphate carboxylase/oxygenase; RuBP = ribulose 1,5-bisphosphate; PS = photosynthesis; SBP = sedoheptulose 1,7-bisphosphate; FBP = fructose 1,6-bisphosphate; Gly 3-P DH = glyceraldehyde 3-phosphate dehydrogenase.

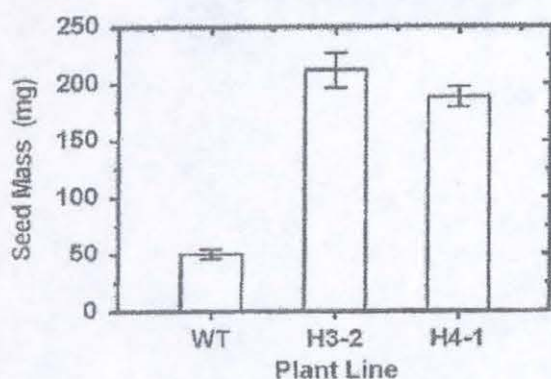


Fig. 7. Increased seed mass with *Arabidopsis thaliana* transformed with a more heat stable Rubisco activase [38]. Wild type (WT); transformed plant lines (H3-2 and H4-1). Graph adopted from [38].

environmental adaptations by photosynthesis and hence crop yields [37].

In conclusion, the application of basic photosynthesis studies to increasing crop yields has been successful when combined with breeding successes. Upright leaves, increased leaf area index tolerances, excellent weed competition control via known biochemical and molecular mechanisms, and well balanced crop mineral nutrition, all combined, are resulting in higher crop yields, Fig. 6. And such continued integrations along with testing and discovering other targets, as in Table 1, plus finding amenable targets in photochemistry and electrochemistry, will help insure future gains in crop production.

მცენარეთა ფიზიოლოგია

გამოყენებითი ფოტოსინთეზური გამოკვლევები მარცვლოვნების მოსავლის გადიდების მიზნით

კლენტონ ბლეკი *, ში-ჯინ სუნგი *, კრისტინა ტოდერიხი ***,
პ. ვორონინი #

* ჯორჯიას უნივერსიტეტი, ბიოქიმიისა და მოლეკულური ბიოლოგიის დეპარტამენტი, ათენი, ჯორჯია, აშშ

** აშშ სოფლის მეურნეობის სამინისტრო, ტყის დაცვის სამსახური, ფაინვილი, ლუიზიანა, აშშ

*** უზბეკეთის მეცნიერებათა აკადემია, სამარყანდის განყოფილება, სამარყანდი, უზბეკეთი

მცენარეთა ფიზიოლოგიის ინსტიტუტი, რუსეთის მეცნიერებათა აკადემია, მოსკოვი, რუსეთი

(წარმოდგენილია აკადემიკოს თ. ბერიძის მიერ)

ეს ნაშრომი ეძღვნება დოქტ. გივი სანაძის მეცნიერებაში ხანგრძლივ მოღვაწეობას და მის აღმოჩენას, რომლის მიხედვით ზე-მცენარეები ფოტოსინთეზის დროს გამოყოფენ იზოპრენს. იზოპრენისა და სხვა მონოტერპენების ემისიის კვლევებმა ამაჟამად მიიღო გლობალური ფორმები და მოიცავენ საზოგადოებრივ მცენარეულობას, წყალმცენარეებს, წყლისა და ზღვის სასიცოცხლო ფორმებს მსოფლიო ოკეანეში. განვითარდა ახალი წარმოდგენები მონოტერპენებისა და სხვა აქროლადი ქიმიური ნაერთების ემისიის როლზე მცენარეთა ბიოლოგიურ სიგნალიზაციასა და გლობალურ ატმოსფერულ ქიმიკატში. ეს გამოკვლევები საწყისი იღებენ გივის როგორც ახალგაზრდა ასპირანტის პიონერულ გამოკვლევებში. დოქტ. სანაძე შემოქმედებითი ვიზიტი იმყოფებოდა 1976 წელს ჩემს ფოტოსინთეზის ლაბორატორიაში ჯორჯიის უნივერსიტეტში (აშშ). მე აღფრთოვანებული ვარ მეცნიერებისადმი მისი დამოკიდებულებით და მადლიერი ვარ მისი თბილი მეგობრობისა ამ ათწლეულების განმავლობაში.

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