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RESEARCHING PHOTOSYNTHESIS AND AGRICULTURE'S NEW CHALLENGES

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Abstract

Photosynthesis is an intricately controlled and sequential procedure that involves various steps. The process involves the collection of solar energy, the transfer and conversion of this energy, the transportation of electrons from water to NADP+, the creation of ATP, and a series of enzyme-facilitated reactions that incorporate carbon dioxide and generate carbohydrates.

The study of photosynthesis plays a significant role in the field of plant science. Its foundational principles were established in the mid-20th century, and since then, scientists have uncovered the intricate mechanisms involved. A crucial finding emerged from assessing the efficiency of photosynthesis at different light wavelengths, known as quantum yield. This analysis revealed the existence of two distinct forms of chlorophyll (Ch) that participate in oxygenic photosynthesis. Further exploration led to the identification of two photochemical systems, namely PSII and PSI, which were distinguished by changes in light absorption in the red region. Specific chlorophylls, with absorption peaks corresponding to these wavelengths, were proposed as the primary receivers of light energy. It was demonstrated that these chlorophylls initiate the separation of charges, thereby facilitating electron transfer. Researchers inferred a connection between electron transfer and the assimilation of CO2 through investigations on the Hill oxidant. By examining the redox state of cytochromes, they proposed a linear electron transport system characterized by two light-driven reactions, known as the Z scheme. Additionally, it was discovered that photophosphorylation occurs in conjunction with thylakoid fragments. In the 1950s, Calvin's research group utilized radioactive tracers of 14CO2, leading to the identification of the metabolic pathway responsible for carbon assimilation through CO2 fixation. This pioneering work represented a significant advancement in biochemistry through the application of radioactive tracers. The initial catalyst for CO2 fixation, initially referred to as Fraction 1 protein, was identified. Rubisco, the enzyme responsible, is the most abundant protein globally,

despite having the lowest catalytic turnover rate (1-3 s-1), making it highly inefficient. Another pathway for CO2 fixation, known as C4 photosynthesis, was subsequently identified in sugarcane.

Introduction

Between 2007 and 2008, there was an unprecedented surge in global food prices. The Food and Agriculture Organization (FAO) has reported that basic food items have reached historically high prices worldwide, leading to an 18% inflation rate in China, 13% in Indonesia and Pakistan, and 10% in Russia, India, and Latin America. Additionally, the FAO warns that global food reserves are currently at their lowest point in 25 years and predicts that prices will remain elevated for an extended period. These circumstances have multiple underlying factors and clearly indicate that agricultural systems are becoming increasingly vulnerable to changes in land use, the economy, and climate. It is evident that the expanding human population and anticipated conflicts over land use in the near future will require a roughly 50% increase in current production rates per hectare to avert a catastrophe. Tackling this challenge will necessitate substantial investment in plant and crop science research, collaborative efforts spanning various fields, and an innovative approach reminiscent of the transformative revolution in agriculture that occurred over half a century ago.

Photosynthesis from an Agricultural Perspective

From where will the necessary boost in crop production originate? The maximum productivity of a crop and its surrounding environment is constrained by thermodynamic properties. In relation to the theoretical upper limit of yield, the boundaries are defined by how efficiently the crop absorbs and converts light energy into biomass. The crucial inquiry revolves around whether these limitations have already been reached in existing crop systems or if there remains untapped potential for enhancements.

Advancements in harnessing and converting light energy have played a crucial role in enhancing crops throughout the last century. An example of this is the upward positioning of leaves, which has allowed for a greater leaf area per unit of ground space, referred to as the leaf area index (LAI). This adaptation enables crop canopies to efficiently absorb sunlight. Additionally, the use of fertilizers has not only increased leaf area but also improved the rate of photosynthesis per unit of leaf area, further enhancing the conversion process. Moreover, the development of resistance to pests and diseases, along with various adjustments to local conditions such as photoperiod, growing season duration, and temperature, has contributed to improved yields across diverse agroecological zones. Nevertheless, many of these characteristics of crop plants, which have played a significant role in creating ideal plant varieties during the green revolutions (such as harvest index, nitrogen responsiveness, stature, and canopy structure), may already be optimized or approaching optimization.

Hence, the inquiry remains regarding whether the rate at which crops produce biomass is similarly optimized. It may be assumed that the advancement in yield is linked to an enhancement in overall biomass production, but certain studies indicate a lack of significant correlation between yield and biomass. Nevertheless, evidence suggests that the ability to generate more biomass is increasingly crucial for crop production. Specifically, when it comes to rice, the correlation between biomass production rate and yield appears to have emerged since the early 1980s. Recent developments in wheat production in the United Kingdom have shown that there has been a notable enhancement in biomass generation. This is supported by concrete empirical evidence, as observed in field experiments where crops grown in conditions with increased levels of carbon dioxide (CO2) exhibit greater biomass and yield.

As per conventional crop physiology, the overall yield of dry matter during harvest is closely and directly connected to the cumulative solar radiation received by the crops. The correlation between these factors is expressed through the radiation use efficiency (E), which quantifies the amount of dry matter produced per unit of intercepted radiation (measured in grams of dry matter). Consequently, the methods to enhance the overall biomass are as follows:

1. Enhancing the length of time during which crop photosynthesis occurs;
2. Enhancing the capture of solar radiation by the crop canopy; and
3. Enhancing the effectiveness of converting light energy into plant biomass.

The length of time during which crop photosynthesis occurs is highly important. There is a belief that the emphasis on achieving higher yields and the application of greater amounts of nitrogen fertilizer have played a role in prolonging the duration of leaf life in contemporary crops. The rate of development, which is determined by temperature, influences the available time for capturing radiation. In tropical regions, it is possible to achieve multiple harvests in a year, leading to efforts in reducing crop duration for faster harvesting. In areas with moderate climates, elevated temperatures can reduce the duration available for grain-filling, leading to a decline in the rate at which biomass is produced. There has been a focus on altering the timing of senescence to improve crop yields. Nevertheless, senescence is a crucial biological process that redistributes nutrients for grain development, and any attempts to manipulate it should take into account its interaction with the regulation of reproductive physiology and suitable adaptations to environmental conditions.

Crop canopies that are fully grown have a generally high efficiency in capturing solar radiation, which refers to the amount of incoming sunlight absorbed after accounting for reflection. This is particularly true for many cereal crops due to their erect leaves and high Leaf Area Index (LAI), which allows for better penetration of light into the canopy. The incorporation of reduced height genes, leading to a semi-dwarf growth habit, has significantly enhanced cereal yields by increasing the harvest index. Although it is often believed that this also enhances the capture of radiation, semi-dwarf varieties demonstrate comparable efficiency in utilizing radiation as taller varieties. The genetic factors responsible for dwarfing in other significant crops have been recognized, indicating the possibility of additional advancements. Additionally, there is scope for enhancing the structure and growth of the plant's uppermost layer, ensuring that the formation of a dense canopy coincides with periods of maximum radiation intensity. This aspect becomes especially crucial in colder temperate regions, where temperature constraints affect developmental stages such as leaf emergence. In such regions, the rapid establishment of a crop canopy holds particular significance.

The main factors contributing to increased crop yields are the duration of crop photosynthesis and the utilization of solar radiation. In this analysis, we will specifically focus on the third factor, which is the efficiency of converting absorbed radiation into dry matter. We propose that this factor is crucial and may be the only way to achieve significant improvements in yield. Since biomass typically consists of 40% carbon by weight, any increase in overall biomass production leads to better carbon fixation through photosynthesis. It is widely agreed that enhanced carbon fixation played a vital role in increasing crop yields in the latter half of the previous century. Surprisingly, the substantial increase in carbon fixation was primarily achieved by improving CO2 assimilation per unit of land area, rather than per unit of leaf area. This improvement was made possible through better agronomic practices, including optimizing plant density, nutrition, water supply, and the use of pesticides and herbicides. These practices created favourable conditions for plant growth and mitigated the negative effects of both biotic and abiotic constraints. As a result, there has been little to no improvement in the inherent efficiency of converting light energy into plant biomass (known as photosynthetic efficiency) at the individual leaf level. Interestingly, studies on various crops have shown that an increase in photosynthetic rate per unit leaf area rarely corresponds to improved crop yield, and in some cases, it may even have a negative correlation. For instance, in wheat, the assimilation rate appears to have decreased after domestication, although there is one instance where yield improvement is associated with an increased leaf assimilation rate. In rice, wild Oryza species generally have lower photosynthesis compared to O. sativa, and within varieties, there is some evidence suggesting a trend towards higher assimilation rates in more recent cultivars. On the other hand, other studies show no discernible trend or even a lower assimilation rate in cultivated varieties. However, it is important to note that yield improvement has focused on traits and practices that do not necessarily rely on increasing or maintaining the rate of leaf photosynthesis. Therefore, the increase in photosynthesis per unit of land area might have occurred without any change (or paradoxically, a decrease) in photosynthesis per unit of leaf area. Attempts to enhance yield through direct selection or breeding of crop plants with high leaf photosynthesis rates have been relatively limited and have produced mixed results.

The assumption that photosynthesis efficiency in crop systems remains constant and cannot be modified to increase crop yield has been commonly held. This belief is supported by research on the photosynthetic process, which shows that key parameters such as quantum yield are generally consistent across different plant species. However, it has been observed that the radiation use efficiency of crops (E) can vary and may be lower than the maximum theoretical value in practice. To accurately assess the impact of photosynthesis on yield per unit leaf area, it is crucial to minimize the influence of other variables. Therefore, experiments that reduce genetic variation in the background have yielded more successful results. Similarly, by minimizing factors like partitioning, nutrient responsiveness, and leaf area index (LAI), the role of leaf photosynthesis becomes more significant in biomass production and grain yield. Interestingly, the increase in yield observed in rice varieties released after 1980 is more closely associated with an increase in biomass rather than an increase in the harvest index. This observation implies that an improvement in leaf-level photosynthesis in rice is more likely to occur when there is a predominant increase in biomass production. Consequently, selecting varieties that promote enhanced biomass production, either directly or indirectly, has an impact on the physiological process of leaf photosynthesis. Many authors consider the positive correlation between elevated atmospheric CO2 levels and increased crop yield as compelling evidence that a higher rate of leaf photosynthesis can lead to greater yield.

The section discusses the potential for increasing crop biomass production through modifications to leaf photosynthesis. To achieve higher crop yields, it is important to identify specific targets that directly improve leaf photosynthesis. However, there is limited understanding of the mechanisms that connect overall plant processes to leaf-level events. Recognizing that photosynthesis in agriculture is a complex process, it involves not only light absorption and carbon fixation but also carbohydrate synthesis, biomass allocation (including storage compartments), crop yield harvesting, and efficient transportation of water, nutrients, and assimilates. This article suggests two potential approaches: firstly, enhancing the capacity and/or efficiency of photosynthesis itself; and secondly, studying and analyzing the intricate regulation of photosynthesis under real-world conditions to optimize responses to the environment. In both cases, the goal is to increase crop yield without relying on increased nitrogen (N) fertilization or water supply, but rather by improving the efficient use of nitrogen and water resources.

Routes to improving the mechanism of photosynthesis

1. Rubisco-Related Targets

Numerous proposed approaches to improve the absorption of CO2 in crops have primarily centred around a specific enzyme called ribulose bisphosphate carboxylase oxygenase (Rubisco). Rubisco plays a crucial role in the process of converting CO2 into a three-carbon compound known as C3 photosynthesis. However, at typical levels of atmospheric oxygen (O2), oxygen competes effectively with CO2, leading to the production of phosphoglycollate. This compound is subsequently broken down, releasing CO2 in a process referred to as photorespiration, ultimately reducing the efficiency of photosynthesis. Currently, under prevailing atmospheric CO2 and O2 levels, as well as in conditions of abundant light, the quantity and activity of Rubisco in living organisms are regarded as limiting factors for carbon fixation. One potential solution to overcome this limitation involves increasing the quantity of Rubisco in plant leaves. Theoretically, this could further enhance the rate of photosynthesis per unit of leaf area under optimal light conditions by augmenting the overall amount of photosynthetic machinery per unit of leaf area. However, in practical terms, there is an optimal concentration of leaf nitrogen that is influenced in part by limitations imposed by leaf thickness caused by shading within the leaf structure. The accumulation of protein in the chloroplast and the number of chloroplasts in the mesophyll cell also have their limits. To compensate for the inefficiency of Rubisco, plants already store significant amounts of it in their leaves, accounting for 15-30% of the total nitrogen in C3 plants. Nevertheless, relying solely on increased nitrogen fertilization is not a sustainable solution for future crops due to high oil prices and the low nitrogen use efficiency (NUE) of crop systems, which stands at approximately 33% for cereal crops. Therefore, it is crucial to improve the NUE of cereal crops. The distribution of nitrogen among photosynthetic components has been studied, but increasing the amount of Rubisco without additional nitrogen input could lead to the redistribution of internal nitrogen in the plant. This could result in reduced levels of other essential enzymes and create new limitations for CO2 fixation. These factors may explain why plants that have been genetically modified to have higher levels of Rubisco do not show improved photosynthesis.

The necessity of having a high concentration of Rubisco in leaves has been a subject of inquiry. Studies on plants with reduced Rubisco content indicate that there is an excess accumulation of the enzyme. In certain rice varieties, Rubisco accumulation has been found to exceed the amount needed to sustain measured photosynthetic rates. Many crops experience light limitations, especially when the maximum Leaf Area Index (LAI) is reached. The reduction of Rubisco in certain plants has the potential to improve Nitrogen Use Efficiency (NUE). Moreover, it has been proposed that decreasing Rubisco levels could be advantageous in the context of rising atmospheric CO2 concentrations, as plants exposed to elevated CO2 demonstrate enhanced photosynthetic NUE even in current CO2 conditions. Nevertheless, it is important to note that Rubisco also plays a significant role as a Nitrogen storage source, contributing to the nitrogen content in grains and the growth of new tissues. Both the quantity of Rubisco and the timing of its degradation are crucial factors, although how the balance between Rubisco's function as an Nitrogen store and its role in photosynthesis is regulated remains unknown. It may be possible to enhance NUE by achieving the same rate of assimilation with less protein by maximizing Rubisco activity. The activity of Rubisco can be influenced by various inhibitors, and Rubisco activase plays a key role in determining the portion of active Rubisco sites that are free from inhibitors and capable of catalysing reactions. Recently, there have been suggestions that the regulation of Rubisco activity might not be optimized for maximum crop productivity, and manipulating Rubisco activase could be a promising strategy to explore.

One potential approach to enhancing Rubisco involves directly modifying the enzyme to improve its specificity for CO2 compared to O2. Variations in specificity have been observed in different biological systems. To exemplify, Rubisco variants found in stress-resistant plants like Limonium have a higher level of specificity compared to those present in many common crops. However, it has been observed that Rubisco variants with a greater specificity for CO2 often exhibit lower rates of carboxylation per active site. These two factors are known to have an inverse relationship. Thus, if the specificity factor is enhanced at the expense of the carboxylation rate, it would not result in a net increase in carbon fixation. Nonetheless, recent investigations into Rubisco's active site have uncovered a wide range of adaptations in response to substrate availability. This finding has sparked the notion that different Rubisco variants, each possessing distinct kinetic properties, could be artificially engineered. This approach could potentially tailor Rubisco to specific environmental conditions such as light, temperature, and sub-stomatal CO2 levels, opening up new possibilities in Rubisco improvement.

According to available evidence, it appears that the quantities of enzymes in plants, including Rubisco, might not be set at their optimal levels for achieving the highest possible biomass production. As a result, when the level of sedoheptulose-1,7-bisphosphatase is increased in tobacco plants (Nicotiana tabacum), notable enhancements in both photosynthetic rate and early-stage growth are observed. This indicates that the existing levels of this particular enzyme may only meet the minimum requirement or potentially fall short of supporting the maximum rates of photosynthesis. This suggestion is further supported by a theoretical analysis utilizing mathematical modelling of photosynthesis.

2. Decreasing Photorespiration

While photorespiration has been associated with specific metabolic and protective functions, its negative impact on crop yield has been demonstrated by a significant improvement in crop performance when the concentration of CO2 is doubled. Theoretical models suggest that it is possible to enhance yield by eliminating photorespiration under favourable conditions. However, completely preventing the downstream metabolism of photorespiration after Rubisco has proven ineffective, and the consequences of this for plants grown under stress are not well understood. Blocking the flow of photorespiratory intermediates without affecting oxygenation can result in the unfavourable accumulation of compounds. A recent alternative approach involves redirecting a portion of chloroplast glycollate directly to glycerate, which partially reduces the flow of photorespiratory metabolites and increases biomass production. This approach maintains the potential protective role of photorespiration and provides the opportunity to develop plants that are more efficient and perform well under less optimal conditions.

3. Transforming C3 Crops into C4

Certain highly productive crops such as maize (Zea mays) and sugar cane (Saccharum officinarum) possess an impressive ability to concentrate carbon dioxide (CO2), resulting in the removal of oxygenase activity and an enhancement in photosynthetic efficiency. This concentration of CO2 is accomplished through a process referred to as the C4 pathway. In this pathway, CO2 is initially converted into C4 acids using an enzyme called phosphoenolpyruvate carboxylase (PEPC). Subsequently, CO2 is released from the C4 acids and utilized by an enzyme called Rubisco for further fixation. Researchers have been investigating the potential implementation of the C4 pathway in C3 crops like rice. It has been suggested that this could be the key to achieving a significant increase in biomass production, thereby supporting the necessary improvement in crop yield. Although this is an ambitious endeavour, the compelling scientific principles underlying it are gaining more attention.

Initial efforts involved genetic modification of rice, introducing genes encoding C4 enzymes like PEPC, PPDK, and NADP-ME. Transformation experiments have also been carried out in potato and tobacco plants. However, although there have been claims of improved assimilation rates and specific characteristics associated with the C4 pathway, the mechanisms responsible for these effects have not been confirmed. These approaches overlook an important aspect: while certain species are capable of performing both C4 and C3 carboxylation within a single cell, the most efficient species rely on a specialized anatomical structure known as Kranz anatomy for the C4 pathway. This anatomical arrangement ensures that the fixation of atmospheric CO2 occurs in mesophyll cells, while the fixation of CO2 released from C4 acids takes place in bundle sheath cells, thus preventing CO2 leakage and maintaining an optimal CO2: O2 ratio for Rubisco in the bundle sheath. Initially, modifying cellular differentiation, enzyme distribution, chloroplast morphology, and metabolic pathway regulation in each cell type may seem highly complex. However, there are promising observations: certain plants exhibit both C3 and C4 metabolic strategies, some species can switch between C3 and C4 depending on environmental conditions, and C4 evolution has independently occurred in flowering plants at least 45 times. As a result, current efforts primarily focus on achieving Kranz anatomy rather than developing a single-cell system. All these factors indicate that it is feasible to introduce the C4 pathway into crops like rice. It has been suggested that a combination of advanced molecular techniques, targeted gene modifications, and strategic screening of germplasm could lead to positive outcomes within a reasonable timeframe.

The sizes of the sinks in C3 crops have historically been proportional to the size of their photosynthetic source. To improve the carbon fixation efficiency of a potentially modified C4 crop, it is necessary to adjust the sink size accordingly in order to effectively accumulate the harvestable products. This adjustment may involve increasing the harvest index or not. Any future increases in the harvest index of major crops will primarily depend on enlarging the sink size rather than reducing the allocation of dry matter to other plant structures like stems, roots, and leaves, as has been done in the past. Enlarging the sink size seems achievable in major grain crops. However, recent research on tomato (Solanum lycopersicum) and other fruit crops indicates that increasing the sink size is not only associated with higher CO2 assimilation but also with a decrease in dark respiration. This discovery suggests the need to reevaluate the importance of respiratory pathways in photosynthetic metabolism. New evidence suggests that chloroplasts and mitochondria, previously seen as independent entities, can interact and mutually benefit each other, particularly under stressful conditions. Furthermore, the examination of discrepancies between theoretical and in situ measured values of respiratory coefficients, such as waste respiration, indicates that there is room for improvement in these aspects.

Optimization of Photosynthesis as a Highly Dynamic Responsive Process

Understanding how photosynthesis functions in different environmental conditions is crucial to grasp the process itself. Various models have been developed based on the steady-state model by Von Caemmerer & Farquhar (1981), with a primary focus on identifying the limitations imposed by Rubisco or the regeneration of ribulose 1,5-bisphosphate (RuBP). These models have significantly improved our understanding of the factors that limit photosynthetic productivity. Over time, more complex dynamic models of photosynthesis have been created to investigate the regulation of electron transport and carbon assimilation. However, to gain a deeper understanding of photosynthetic responses under changing conditions and expand our knowledge into areas like metabolomics and growth patterns, more comprehensive models are needed. These advanced models should encompass not only the reactions of the Calvin cycle but also photorespiration and downstream carbohydrate metabolism.

A recent model has taken a unique approach to achieve this objective. It uses a series of interconnected differential equations, each representing the concentration of a specific metabolite. In this model, an evolutionary algorithm is employed to allow for variation in the allocation of nitrogen associated with each enzyme. The model selects the highest photosynthetic rate under light saturation for the next generation. After 1500 generations, a significant increase in photosynthesis was observed. The results indicated that there was an excessive allocation of enzymes to photorespiratory metabolism, while there was insufficient allocation to Rubisco, sedoheptulose 1,7-bisphosphatase, and fructose 1,6-bisphosphate aldolase. This experiment has important implications for improving crop productivity, as it provides evidence that current C3 photosynthesis rates are below optimal levels. Two possible explanations for this are: firstly, there has been little selection pressure for photosynthetic capacity during breeding and selection processes, as mentioned earlier; and secondly, crops have not had enough time to adapt to complex factors such as changing atmospheric CO2 concentrations.

Regulation plays a vital role in the allocation of different types of molecules across various biological functions, including storage, signalling, stress responses, and defence mechanisms. To examine productivity in complex systems involving multiple processes, an alternative approach called metabolomics can be employed. This technique allows for a thorough examination of the levels of metabolites associated with specific productivity rates. By utilizing these methods within a suitable genetic framework, distinct patterns of metabolites can be linked to rates of productivity, offering insights into the dominant pathways involved. In a study conducted by Meyer, recombinant inbred lines of Arabidopsis thaliana were utilized, and the results showed a strong correlation between biomass production rates and specific combinations of metabolites. While the flow of molecules through particular pathways holds more significance than the concentrations of metabolites themselves, it is crucial to apply these methods to crop plants at appropriate stages of growth and development. Additionally, integrating these findings with comprehensive models is essential to gain a holistic understanding of these intricate systems.

Concluding Remarks: Crops for Future Climates

In the future, there is a growing need to improve the efficiency of both food and energy crop production. This involves achieving higher productivity while using less land and fewer resources, all while dealing with more frequent extreme weather events. In the past, efforts to enhance crops have mainly focused on altering plant structure, such as improving harvest yield and leaf coverage, as well as refining crop management techniques. However, research indicates that further advancements through plant structure may have reached their limits for many crops. As a result, crop management methods are already evolving to adapt to the changing agricultural landscape, as seen in the increasing adoption of precision agriculture techniques.

While these approaches are important, they still heavily rely on human intervention to manipulate the plant's surroundings, resembling practices from the 20th century. This analysis argues that future progress should instead concentrate on improving the crops' ability to efficiently utilize and convert resources. It underscores the significance of comprehending the biology of crop plant species, including identifying aspects of plant performance that are suboptimal for the new agricultural environment, understanding the reasons behind these limitations, and finding ways to manipulate them. By customizing each crop variety to specific locations and seasons, these manipulations can be implemented effectively.

The analysis highlights that enhancing the efficiency of converting solar energy into biomass is crucial for achieving the necessary advancements in agriculture. It suggests that targeting areas of suboptimal photosynthetic efficiency, which hinder the conversion of solar energy, presents significant opportunities for crop improvement. The review also identifies specific areas that require further research to bridge knowledge gaps and facilitate substantial progress. These improvements would have wide applicability to any crop where energy conversion efficiency is essential, including energy crops and dual-purpose food crops that utilize waste products for fuel.

Therefore, it is essential to give more attention to enhancing photosynthesis, not only in discussions regarding food production but also in the context of energy crops and bioenergy.

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