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GENETIC ANALYSIS OF THE STRUCTURE AND FUNCTION OF THE PHOTOSYNTHETIC APPARATUS AND ITS EFFICIENCY—A REVIEW

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ABSTRACT

Scientific research towards improving the biomass productivity of crops has become inevitable because of the inherent constraints towards improving the biomass partitioning. This factor alone so far has been of great significance for rapid spurt in economic yield. Photosynthetic efficiency is expected to be directly related to biomass production. Hitherto, this trait has not been affected by selection and genetic improvement. A substantial number of photosynthetic mutants have been isolated and characterised but it remains an open question yet as to what component or step(s) in photosynthesis are rate limiting under specified conditions. In the absence of this knowledge, screening of genotypes for maximum photosynthesis rate (P_{max}) has been resorted to, but it may not be directly correlated with yield. Adequate genetic variability has been reported for this trait along with fair degree of genetic advance. Further, where the factors responsible for diluting the association of biomass productivity with photosynthetic efficiency were taken care of, perfect relations have been established. The incorporation of photosynthetic indices in breeding protocols is, therefore, strongly advocated and depending on the nature of gene action appropriate breeding programme formulated. Further stability and adaptability studies are unavoidable as photosynthetic indices are labile to the environmental conditions. Integration of the tools of classical genetics and molecular biology in manipulating the photosynthetic efficiency for improving biomass productivity will become an absolute necessity in the years to come.

Key words: Photosynthesis, photosynthetic efficiency, photosynthetic apparatus, biomass, crop productivity.

The yield of a field crop is governed by its net photosynthetic capacity (gross photosynthesis minus photo- and dark respiration) and by the proportion of photosynthates

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converted into the desired end product [1, 2]. The former component refers to the total biomass production or biological yield and the latter to the final economic yield formation. The sharp increases in the yields of field crops, e.g. wheat 140, barley 110, rice 100 and maize 240 q/ha [3] during the last 80 years of experimental breeding have been achieved primarily through the latter [4, 5]. It is fast becoming evident that some of the major crops are beginning to reach yield plateaus and it is doubtful whether the harvest index of many cereals can be raised further [6, 7]. If the harvest index is beginning to reach optimum values, the future increases in crop yield must accrue through improving the photosynthetic efficiency by which the intercepted radiation is converted to biomass [8]. This warrants directing our research priorities towards understanding the key process of photosynthesis since genetic improvement of photosynthetic efficiency will be a new step towards another green revolution and improving the productivity potential of field crops. Before attempting any genetic improvement in photosynthetic efficiency it is imperative that the genetic components of the photosynthetic apparatus and their individual functions in photosynthesis are properly understood. This involves understanding of the mode of inheritance, the nature of gene action in respect of its fine structure and function, allelic relationships and associations among different gene blocks of the photosynthetic apparatus. The knowledge obtained thereby will be useful in formulating appropriate breeding protocols. This review on photosynthesis is organised in two sections.

A. Basic genetic studies on the components of photosynthetic apparatus.

B. Applied genetic studies in improving the photosynthetic efficiency.

BASIC GENETIC STUDIES ON THE COMPONENTS OF PHOTOSYNTHETIC APPARATUS

For any genetic investigation of a metabolic pathway the primary material must be the genetic mutants where intermediate steps have been blocked at a number of points. Such an approach envisages the elucidation of the pathway in relation to the number and order of reactions through the genetic blocks.

In organisms where genetic analysis is possible, it has been shown that the mutations affecting photosynthesis are both in nuclear and extranuclear genes. However, the major problem of physiological genetics is the discrete analysis of the contribution of a gene to the formation of a character, following the one-gene–one-character pathway since the development of a character is not determined by genetic activity in isolation but by the entire genotype by a process of graduated, sequentially interrelated biochemical reactions.

During the last two decades, there has been massive accumulation of literature on chloroplast development, regulatory interactions between the nuclear and plastid genomes, structure and organisation of the chloroplast genome, and the finer mechanisms of photosynthesis. It is not intended here, to review the developments in photosynthesis in entirety. The reader is referred to some excellent reviews on the developmental aspects of photosynthesis [9–12]. The present review is attempted with a bias towards those studies

which directly attempt to improve the efficiency of the photosynthetic apparatus and crop productivity.

Photosynthetic mutants. The photosynthetic mutants have been broadly classified into two categories:

In the first category, the development of chloroplast from proplastid is arrested at some stage, leading to gross structural abnormalities, e.g. the absence of thylakoid system. Such grossly distorted supramolecular assemblies are often difficult to analyse genetically, since a large portion of the photosynthetic apparatus has either not been assembled or has been secondarily destroyed. Such mutations most likely result from the direct effect of the genetic factors.

A common genetic variant affecting the pigmentation of higher plants is virescent, in which the seedling first appears as pigment-deficient but gradually intensifies in colour and may become normal green [13]. The virescent phenotype is usually temperature dependent. The virescent mutants map to different regions and have individually specific, temperature-sensitive threshold levels of expression. All of them have been found to be deficient in their 70S chloroplast ribosomes [14]. It has been suggested that the reduced number of ribosomes in virescent mutants causes a delay in development by delaying the accumulation of chloroplast coding protein required for normal chloroplast development.

Thylakoid ultrastructure. A predominant ultrastructural characteristic of thylakoid membranes of higher plants is the presence of granal stacks. Stacking is mediated by the light harvesting complex-II (LHC-II) adhesion [15]. Many mutants are reported in which thylakoid ultrastructure is altered e.g. chlorina-f_2 mutant of barley, which lacks several polypeptides associated with LHC-I and LHC-II, but permits normal stacking of thylakoids contrary to expectation. Ryrie [16] used antibodies to show that 23 and 23.6 kD polypeptides were found in greatly reduced amounts but still permitted normal stacking. It might be interesting to survey the polypeptide composition of several mutants that do not form the thylakoid stacks to determine the genes involved in stacking.

In the second category, the entire structural and biochemical apparatus of the chloroplast is intact with the exception of, ideally, a single component which has been affected by a mutation in a single gene or few genes. This component could be an enzyme of carbon reduction cycle of photosynthesis, a carrier molecule in the photosynthetic electron transport chain or a factor required to couple photosynthetic phosphorylation to electron transport.

Mutations affecting chlorophyll and pigment synthesis. The mutants which reduce pigmentation come under this category. Such mutations may be viable, semilethal or lethal. These changes altering the relative proportion of the pigments most likely result from the indirect effect of the mutant genes on the pigment system. There are at least 117 separately

designated loci in maize and 96 loci in barley that directly or indirectly affect the photosynthetic pigmentation. The study of *Chlorella* mutants with defects in chlorophyll biosynthesis was instrumental in elucidating the chlorophyll biosynthetic pathway [17] but few studies have been carried out in higher plants because mutants with defects in chlorophyll biosynthetic pathway do not accumulate significant quantities of precursors. Batalov and Kvitko [18] proposed a scheme for the genetic analysis of lethal chlorophyll mutants of *Arabidopsis thaliana* which were maintained in the heterozygous condition. In case of nonallelic mutations, the segregation of the genes was not expressed (4:0 ratio) while in case of allelic mutation a segregation of 3:1 for green colour: nonpigmentation was obtained. Among these mutants, allelic mutations are of special significance because all of them are induced at a single locus and an accumulation of a series of such mutants for one gene opens the way to study the nature and function of individual genes and their interaction in the genotype of plant organisms. Such alleles differ from each other in response to external conditions (like changes in intensity of illumination, temperature and other factors). Thus, different forms of reaction to the external factors strongly suggest that these mutants changed the activity of the same enzyme but to different extents.

The discovery that the detached dark green shoots provided with exogenous δ-amino levulinate accumulated the chlorophyll precursors [19] opened the way to investigations in higher plants with its direct implications on the regulation of chlorophyll biosynthesis [20, 21]. The simplest of the mutants was the tigrina-d mutant (tig-d), in which there was a constitutive synthesis of δ-aminolevulinate. Therefore, the tig-d^+ gene product was postulated as the specific repressor of the activity or synthesis of δ-aminolevulinate synthase [22]. The regulatory influence of metabolites on chlorophyll biosynthesis is revealed by the xantha mutant (xantha f-10) [22]. The locus codes for a protein that participates in the insertion of Mg in protoporphin IX. Unlike wild type, induction of δ-aminolevulinate synthesis does not take place in xan-f mutants, suggesting that the photoreduction of protochlorophyllide to chlorophyllide is a prerequisite for induction of δ-aminolevulinate synthesis by light. Construction of the double mutants $\frac{\text{tig–d}}{\text{tig–d}}$, $\frac{\text{xan–f}}{\text{xan–f}}$ resulted in constitutive protoporphin accumulation, indicating the regulatory effect of tig-d mutation [22].

Carotenoid deficient mutants. A number of mutants are partially or completely pigmented in low-intensity light but are completely bleached by strong light because of defects in carotenoid biosynthesis. The tig-b, f, m, n and o mutants have revealed partial blocks in carotenoid biosynthesis. The analysis of tig-o and tig-b mutations suggested that the mutants are defective in the synthesis of the heme-containing enzymes required for carotenoid biosynthesis [22]. They bleach in light because δ-aminolevulinate synthesis is no longer inhibited by heme [20], as a result of which they accumulate protochlorophyllide in darkness and bleach during the subsequent light period. Carotenoids are believed to protect chlorophyll by quenching of ^{3}Chl by singlet or triplet carotenoid. In contrast to chlorophylls, triplet carotenoids do not interact directly with O_2 by dissipated energy by radiationless

decay. A large collection of mutants is now available in different crop plants, viz., *Zea* and *Hordeum*, but few studies have been carried out because mutants with defects in chlorophyll biosynthesis do not accumulate significant quantities of the precursors.

Mutations affecting Rubisco: Rubisco is the key enzyme in photosynthetic CO_2 fixation and photorespiration, therefore, there is substantial interest in mutations affecting the expression and activity of Rubisco. The gene for the large Rubisco subunit in maize was among the first plant genes cloned and its use as a heterologous probe has led to the isolation of Rubisco genes from a large number of photosynthesizing organisms [23]. With these cloned genes it is now possible to analyse mutations that affect the expression of activity of this enzyme at the molecular levels. In one such study, the mutant rbcL gene (coding for the large polypeptide subunit) was cloned and the DNA sequence compared to that of wild type. A single nucleotide substitution was found to convert Gly 171 residue to Asp and the revertant was shown to have restoration of wild type sequence [24]. This mutation permitted the correlation between the genetic and physical cpDNA maps. Some Rubisco mutants require a higher CO_2 concentration for the activation of Rubisco. It has been suggested that such mutants lack the Rubisco activase protein(s) which facilitates activation of Rubisco [25]. This discovery may also explain why higher CO_2 concentration was required to activate Rubisco in vitro than in vivo. Several recent applications of recombinant DNA technology have created the possibility of studying the structural basis of Rubisco function. The Rubisco genes from a number of organisms have been expressed at high levels in *E. coli*, however, the products are insoluble and catalytically inactive. Nonetheless, there are good possibilities of obtaining a functional enzyme by coexpression of rbcL and rbcS genes in the same cell. Since rbcL gene is chloroplast encoded while rbcS gene is nuclear, there is uncertainty about the mechanisms which must coordinate the synthesis of two genes that are present in different copy numbers. Since no mutation has been isolated that regulates the synthesis of Rubisco, an attempt was made [26] to examine the gene-dosage effect in aneuploid series of wheat Rubisco levels. Although differences in the amount of Rubisco per cell were observed in the aneuploid series, the pleiotropic effect of these gross genetic changes precludes a single genetic interpretation.

MUTATIONS AFFECTING PHOTOSYNTHETIC ELECTRON TRANSPORT

PS-I deficient mutants. Several PS-I deficient mutants have been collected and most of them lack two proteins, viz., 66 kD polypeptide and chlorophyll protein complex (CPI). In a most comprehensive genetic analysis of thylakoid complex of different mutants it was shown that all of these mutants lacked a putative apoprotein of PS-I (CPI) and six low molecular weight proteins [27]. It was proposed that the missing polypeptides were the components of a multisubunit complex in which the absence of one or more of the constituent polypeptides blocks the synthesis or assembly of other polypeptides of the same complex. Since the number of loci involved was larger than the number of polypeptides affected, the majority of the genes identified did not code for the missing polypeptides. In

barley, lethal mutations at five nuclear loci (xantha-q, viridis h, q, n, zb) give rise to PS-I deficiency [28]. Recent advances in the correlation of genetic and molecular maps in *Chlamydomonas* have opened the possibilities of characterizing such mutations at the molecular level. At least three chloroplast loci in *Chlamydomonas* have been shown to cause the loss of CPI complex from thylakoid membranes, indicating that several chloroplast gene products were necessary for CPI.

PS-II deficient mutants. There are, in principle, two kinds of PS-II deficient mutants. In the first group are those mutations in which one or more polypeptides associated with PS-II complex are missing. The second group includes mutants in which the polypeptides are present but inactive. In the first, type BF 25 mutant of *Chlamydomonas* had reduced amounts of five polypeptides and another three completely missing. This mutant was specifically defective in water hydrolysis, suggesting that the missing polypeptides were required for this aspect of PS-II activity [30].

The second type of PS-II deficient mutant was found in *Senadesmum*. The mutant LF-1 was unable to use water as electron donor but retained the activity rates comparable to the wild type using an alternate donor system. The mutant was found deficient in the 34 kD polypeptide but gained the 36 kD polypeptide, i.e. either the protein was not correctly processed in the mutant or the translational reading frame was extended in the mutation [31]. One of the extensively characterised PS-II-deficient mutant in higher plants is the nuclear recessive hcf-3 mutation in maize. It lacks PS-II as well as cytochrome b_{ssq} activities but has normal levels of PS-I, plastoquinone, cytochromes f and b_6, LHC-II and non-PS-II chl activities [32]. However, 6–7 polypeptides of the PS-II complex are conspicuously missing. A lower chl a/b ratio also suggested the loss of specific set of chlorophyll molecules associated with the PS-II reaction centre. It was found that hcf-3 mutant carries a recessive nuclear mutation that leads to the loss of several polypeptides that are synthesised on chloroplast ribosomes.

Coupling factor mutants. Mutants at distinct chloroplast loci have been isolated, which appeared to be blocked in synthesis, assembly or integration of CF_1 into the thylakoid membrane [29]. However, the molecular basis of such mutations remains to be established. Some plant species are resistant to the fungal toxin 'Tentotoxin' while others are not. Tentotoxin binds noncompetitively to CF_1 and inhibits its activity in the sensitive but not in resistant species [33]. Thus the resistant species apparently have an altered gene for CF_1 subunit. Further confirmation was provided by sexual and nonsexual hybrids between resistant and susceptible species of tobacco where this trait was inherited in non-Mendelian fashion [34].

Mutants lacking chlorophyll b. Here chlorina-f_2 mutant of barley has been intensively studied which has the normal PS-I and PS-II activities but lacks chlorophyll b [35]. At higher light intensities, the photosynthetic rates were comparable to wild type but at low light

intensities the mutant had poor rates because it was not light saturated. The biochemical defects in chlorina-f_2 and other related mutants are not known because of uncertainties concerning the pathway of chlorophyll b biosynthesis, and also that chl b-less mutants lack several polypeptides associated with the chlorophyll–protein complex that contains chlorophyll b.

The current understanding of the biochemistry of photosynthesis indicates that except under extreme conditions no single step is dominant in controlling or limiting photosynthesis. Thus, it is not possible, at present, to identify a step or steps that could be genetically altered to increase photosynthesis under normal conditions. In order to accomplish this task, one would require altering the amounts of the components of photosynthetic apparatus by increasing or decreasing the number of copies of the genes involved, or altering the activities of promoters of the genes. The attempts to transfer the genes of C_4 photosynthetic metabolism (characterized by higher biological productivity) into the C_3 plants have proved abortive [36] presumably because this characteristic is controlled by many genes. However, it is doubtful that C_4 characteristics would be beneficial in temperate environments because such areas have generally lower light intensities. Current targets of genetic manipulations include phosphoribulokinase, sedoheptulose-1, 7-biphosphatase and fructose-1, 6-biphosphatase (the Calvin cycle enzymes), and the phosphate translocators cytosolic fructose-1, 6-biphosphatase and sucrose phosphate synthase [37–41].

It is thus important to delineate as to what component step or steps in light harvesting, photosynthetic electron transport, CO_2 access to the sites of carboxylation, and the Calvin cycle or its downstream reactions is limiting maximum photosynthesis (P_{max}) under specific conditions. It will then be possible to set up screening tests to detect variation in the components. In the absence of information on these aspects, screening for P_{max} has been tried (discussed below). If P_{max} were useful, it will be worthwhile to establish linkages between P_{max} and restriction fragment length polymorphisms (RFLPs) and use RFLP as indicators of P_{max}. In principle, this screening technique will prove useful to detect single genes as well as gene combinations [42].

APPLIED GENETIC STUDIES FOR IMPROVING PHOTOSYNTHETIC EFFICIENCY — PLANT BREEDING METHODS BASED ON PHOTOSYNTHETIC TESTS

Bykov [43] has discussed the possibility of improving photosynthetic indices and outlined four main areas of research on photosynthetic apparatus in relation to breeding:

i) structural and functional diversity

ii) pattern of inheritance of structure and function

iii) the relationship of structure and function to yield, and

iv) monitoring the control and improvement of structure and function.

Is it possible to manipulate photosynthetic efficiency ? It is contingent on any breeder to be aware of the problems associated with photosynthetic measurements. One of the outstanding problems in breeding for higher photosynthetic rate is inherent in the methodology used for estimation of photosynthesis. It involves both the technique used under standardized conditions and history of a plant material. There are several techniques both in vivo viz. infrared gas analyser technique (IRGA) [44, 45], $^{14}CO_2$ measurements [46, 47], and in vitro, viz. manometric methods [48], the IRGA [49], $^{14}CO_2$ uptake [50], to measure carbon dioxide exchange rate rapidly, which has been defined by Shibles [51] as an index of photosynthetic rate, although often their results may not be in agreement. Gasmetric methods are in vogue these days, but they are unsuitable for large sample analysis under standardized conditions. In some circumstances, leaf photosynthesis exhibits cyclic fluctuations often with about 30–40 minute periodicity [52] or temporal fluctuations associated with age and maturity [53]. Early maturing cultivars have higher photosynthetic rates than the late maturing ones [54]. There is rapid decline in early cultivars after attaining the peak while the later cultivars maintain their photosynthetic activity longer [55]. Choice of leaf for measurement also causes the problems as CER changes not only with leaf age but also with its position on the plant [56]. Rawson et al. [57] stated that both peak photosynthetic rates and their reduction were hastened with aging and these processes were faster in the successive leaves, and then either stabilized or declined in the upper leaf positions.

Two schools of opinions seem to be emerging, one arguing that there are hardly any chances of our ability to modify the components of photosynthetic efficiency because they are mutually complementary and thus difficult to manipulate, and increase in one component may not necessarily lead to enhancement of total photosynthetic reduction (PSR) unless it was itself a limiting factor. Secondly, photosynthesis is a hierarchical system operating over scales of organization ranging from 10^{-27} m^3 and 10^{-15} seconds for primary photoacts to 10^5 m^3 and 10^6 seconds for primary productivity of field crops. Such a complex hierarchical system is often difficult to manipulate because the manipulation at one level may not lead to expected response by the entire system after interactions and feedbacks have occurred. Different components of photosynthetic efficiency are mutually complementary and improvement in one part of the photosynthetic system can lead to compensation elsewhere, e.g. selection for higher leaf carbon dioxide exchange rate (CER) may result in reduced leaf area [58] or a good canopy structure may lead to decline in CER [59]; small leaves can compensate for higher RuBP carboxylase [60]. Bhagsari and Brown [61] in a comprehensive survey of the crop plants have reported an omnipresent negative correlation between leaf area and CER which is probably one of the important reasons for lack of consistent correlation between photosynthetic rate and yield. Thus comparisons of CER involving genotypes with different leaf sizes may not indicate inherent difference in photosynthetic potential.

De Wit [62] in a comprehensive review has ruled out differences in potential growth rates among different crop species. On the contrary, evidence has accumulated for an apparent decline [62, 63] or constant photosynthetic rate [64, 65] associated with breeding and selection in many crops like wheat, sorghum, sunflower, cotton, sugarcane and tomato. The presumption that photosynthetically vigorous seedlings give rise to similar adults also has been proved to be far fetched [66, 67]. This precludes the application of seedling results two adult plants. The precise association of photosynthetic rate with final yield formation is lacking in many studies raising serious doubts about the efficacy of higher photosynthetic rates (P_{max}) in improving the base of productivity potential in different crops. This paradox will be critically evaluated later.

The second school of opinion does not share this pessimistic view of manipulating photosynthesis for increased crop productivity [45, 62, 64, 68–75]. Historically, breeding for yield itself with usually limited knowledge of the actual manipulation to be made at the biochemical level has been successful. However, lack of sufficient knowledge of physiological and morphological characters related to yield and their utilization have kept the breeding approaches quite empirical [76]. While changes in physiological traits like photosynthesis and partitioning of assimilates can be associated with increased yields of currently used cultivars, these changes have been achieved indirectly by conventional breeding methods rather than by direct selection for physiological attributes. It is, therefore, important to delineate some important physiological attributes as selection parameters in exploiting the hitherto untouched physiological variation of source components for improving the yield potential by developing a systematic method of hybridization that would incorporate these traits into a single genotype. The following are the basic requirements of suitable selection criteria in respect of physiological indices [77–79].

i. Genetic variability must be present in the breeding materials.

ii. The trait should have high heritability.

iii. The procedures for measurement of traits must be accurate, simple and rapid, since large number of assays are needed in the conventional breeding programmes.

iv. The trait should have high genetic correlation with yield.

v. The trait should be critical to the metabolism, e.g. if an enzyme is the trait it should be rate limiting step in the pathway, preceding a branch point or critical in some manner. Nasyrov [71] has stressed the importance of the methods of plant breeding and genetic modification of carboxylation reactions which enabled him and his coworkers to obtain new varieties of triticales with yield potential of 120 q/ha, increase cotton yields by 10–12%, and improve total sugar content by 0.8%. This substantiates the importance of physiological indices as

selection criteria which can add another dimension to the overall strategy of a breeder.

In consonance with the essentiality criteria of physiological indices, the next section of the review dwells under the following headings:

i) Variability and heritability studies

ii) Correlation studies

iii) Heterosis and gene action studies

iv) Stability and adaptability studies

Variability and heritability studies. Genotypic differences for photosynthetic rates have been documented in maize [80–82], wheat [83], rice [84], potato [85], soybeans [86, 87], peas [88], cotton and sorghum [89], chickpea [90], blackgram [91], and rye [92]. Buttery and Buzzell [93] reported transgressive segregation for net photosynthesis in soybean. The broad sense heritability estimates as high as 90% in *Lolium* [94]; 47–80% in maize [81, 95], 70% in rice [96] and 33–66% in soybean [97] have been reported. Crop lines have been successfully selected for high CER, exceeding the low CER lines in maize [82, 98], dry beans [99], cotton [100], and tomato [74]. Thus there is ample ground for regulating photosynthetic functions of plants by such means as inbreeding, polyploidy, selection and hybridization [101], and also for tolerance to shade or planting density [8], but for the multigene basis of this quantitative character the progress in selection will be slow. A word of caution must be added at this point: it is no use improving photosynthesis if the active sinks are nonresponsive to increased supply. A prerequisite for success in breeding for photosynthesis is a crop system in which the active sinks are highly source limited.

The lines/cultivars possessing higher photosynthetic potential can be intermated to form a central gene pool and improve the productivity potential of crop plants by introgression of the genes of this central gene pool. Alternatively, direct selection can be made for yield components among high CER lines which, in turn, will overcome the sink barriers. A preliminary screening of the germplasm can serve as a benchmark for making further genetic studies.

Correlation studies. Direct association of photosynthetic rate with final yield formation is a natural poser in any breeding protocol but this temptation is marred by conflicting reports. As early as in 1938, Heath and Gregory [102] concluded that the mean net assimilation rate (NAR) was essentially constant and the differences in growth rates could be attributed almost entirely to the differences in the rate of leaf expansions [103, 104]. Thus photosynthetic rate per unit leaf area was not correlated with growth or yield and also there is not a single instance where selection for photosynthetic rate increased yield [105]. For instance, attempts made in wheat [106–108], maize [50, 72, 109], barley [59], sugarcane [110],

soybean [111], chickpea [112], alfalfa [113], and orchard grass and timothy grass [114] failed to register any direct association of photosynthetic rate with final yield. This paradox is substantial enough to utilize the direct selection of CER as an indirect tool in place of yield testing because it is much more difficult and expensive to test for photosynthetic rate than to record yield by weight etc. Austin [75] listed seven possible reasons why selection for P_{max} has not resulted in concomitant increase in productivity.

1. The necessary variation in P_{max} does not exist in gene pool so far exploited in breeding.

2. There are close linkages between the genes for higher P_{max} and other genes with undesirable effect.

3. The climate in which a crop grows is not sunny enough to harvest the benefit of high P_{max}. In such climates, high P_{max} may even be detrimental if it is associated with low investment in the light catching antenna, the chlorophyll.

4. There are pleiotropic consequences of high P_{max} which adversely affect crop photosynthesis by reducing leaf area index and leaf area duration. These might include smaller and fewer leaves, resulting in lower leaf area index and hence reduced light interception; thicker leaves but similar leaf mass, also giving a lower leaf area index and reduced light interception, and short-lived leaves.

5. The inability of a plant to utilize carbohydrates for growth under certain circumstances (sink limitation) would ultimately reduce P_{max} by feedback mechanism.

6. The existence of alternative, nongenetic means of increasing biomass, e.g. nitrogen fertilizers promote expansion, increase leaf longevity, and thereby increase canopy photosynthetic rate, biomass, and usually also yield.

7. If the genes for high P_{max} are introduced from wild relatives they may not be expressed if important linkage groups for high yields in the cultivated forms are broken.

These seven reasons are not mutually exclusive and several of them may apply simultaneously for a given crop. The first reason has been established to be of prime importance. An objective analysis of such studies which had failed to register any positive association of photosynthetic rate with plant productivity, in fact, had been due to the fact that photosynthetic rate was measured instantaneously at a single point of time and usually on a specific leaf position at a single stage of development in bright light at constant temperature and frequently under ideal laboratory conditions. Such studies represent the

biomass production under light flux density of field conditions whereas CER estimates were made under almost light-saturation conditions. Certainly, under field conditions, all leaves on each plant are not under the saturating light conditions, nor should one expect all leaves to have identical CER. Such assays might reflect maximum photosynthesis or potential photosynthesis but need not show any relation to the total seasonal assimilation of CO_2 by the entire plant and its translocation to the harvested organs [70]. It is certain that individual leaves in a plant community in the field vary in their net CO_2 assimilation rates, e.g. leaves in the lower canopy have lower CER than leaves in the upper parts of the canopy. Temperature and other climatic factors, besides the stage of development, are the other possible causes which preclude such a correlation. The correlation between CER and biomass production will tend to be more accurate and reliable if whole plant CER was measured [115]. This necessitates studying the canopy behaviour of photosynthesis as well as sampling of the entire range of seasonal variation in photosynthesis.

Canopy photosynthesis and yield. Christy et al. [116] measured the net canopy photosynthesis of field grown corn at intervals throughout the growing season. Seasonal photosynthetic activity was calculated in arbitrary units that represented the total carbon fixed. The results showed that two corn hybrids with similar seasonal photosynthetic activities differed in grain yield by 30%. They concluded that grain yield did not appear to be limited by photosynthesis. When artificial shading was done at different stages of plant development, it was found that photosynthetic activity was associated with grain yield. Accordingly, the authors modified their conclusion by indicating that under certain conditions of shading or high yield (by increasing plant densities), photosynthesis could limit grain yield. Various attempts to relate the canopy photosynthesis with final yield have been successful in wheat [117], maize [118], sorghum [119], barley [120], soybean [45, 121] and cotton [122]. The importance of sampling the whole range of seasonal variation of photosynthetic activity was emphasized by Wells et al. [121, 122], who reported that association between yield and integrated canopy photosynthesis from full-pod stage to maturity was quite significant. Christy and Porter [123] reported a nearly perfect correlation between canopy photosynthesis and yield even though no corrections were found for carbon lost during dark respiration and through roots.

Measurements of net canopy photosynthesis of field grown single cross hybrids of maize selected as representatives of those released in the United States of America have revealed some interesting facts:

i. The earlier released, lower yielding hybrids exhibited a faster rate of loss of photosynthetic activity between anthesis and grain maturity than the higher yielding later released hybrids. There was little difference in the photosynthetic activity among the hybrids during vegetative development.

ii. During the grain filling period the hybrids also responded differently to environmental conditions. The hybrids with higher photosynthetic activity

showed greater activity under higher light intensities and favourable conditions while the hybrids with lower activity were depressed more by adverse environments. These results could be due to the fact that the later released hybrids had the greater leaf disease resistance or slower senescing leaves. Thus, there are good reasons to believe that the photosynthetic production during reproductive phase could be increased by selection for greater photosynthetic productions [124] or by the duration of photoactivity during the grain fill [125–127]. Differences in the canopy apparent photosynthesis (CAP) thus plays a significant role in determining the yield potential. The success of using this parameter in the breeding protocols, however, will greatly depend on the technology minimising the cost and time of measuring canopy photosynthetic efficiency.

Gene action studies. The components of photosynthetic efficiency are governed by additive as well as nonadditive genetic variances [72, 74, 94, 115, 128–130]. There are diverse records as to the relative importance of additive and nonadditive genetic variances for different photosynthetic indices. Wilson and Cooper [48] found that additive genetic variance was the most important component for light saturated photosynthesis in ryegrass but the nonadditive and additive components were similar for light-limited photosynthesis. The additive inheritance for photosynthetic rate has been established in soybean [131], *Brassica oleracea* [132]; maize [72, 128] and tomato [74]. The predominance of nonadditive genetic variance too has been reported in maize [115] and tobacco [133].

As regards the nature of gene action, dominance for higher photosynthetic rate was reported in sugarbeet [134], while lower photosynthetic rate was dominant in soybean [135] and cotton [136]. Comparing the extreme sides, overdominance for higher photosynthetic rate was the general conclusion with the occasional implication of epistasis [128, 134]. Overdominance in such cases could be attributed to multiplicative effects of the components that apparently showed simple Mendelian inheritance, thus overdominance was apparent in this sense [137–139]. The total photosynthate production could be considered to be a result of the multiplicative effects of photosynthetic rate per unit leaf area and total assimilatory surface [104, 140]. The photosynthetic rate itself could be considered to be influenced by the interaction of several cellular traits, viz. cell volume [129], mesophyll cell size [141], cellular CO_2 resistance [142], and a host of biochemical characteristics. These cellular, physiological and biochemical traits will participate in a complex interaction pathway where any of them could be rate limiting, giving the final manifestation of CER. Thus complementary gene action coupled with multiplicative effect of the subcomponents seems not only plausible but an unavoidable explanation for the overdominance of higher photosynthetic rates.

Another dimension to the total photosynthate production is the total assimilatory surface, for which additive inheritance has been proposed [143, 144]. In some instances, overdominance was actually encountered [100, 136]. Likewise, the total assimilatory surface could be subdivided into the total number of leaves and size of individual leaf which showed

simple Mendelian inheritance. Complete dominance of increasing leaf number was established [115, 145, 146]. Similarly photosynthetic pigments are governed by additive inheritance [129, 130, 147], however, Mehta [115] observed overdominance gene action which could also be explained in respect of the multiplicative effects of the subcomponents, but chl a/b ratio showed simple dominance.

Although the photosynthetic phenomenon is regulated by the chloroplast genome, cytoplasmic inheritance for photosynthetic rate has been ruled out comprehensively in different crops like maize [128], tomato [74] and soybean [135]. In case of total chlorophyll content Fleming and Palmer [147] detected the differences in reciprocal crosses but some investigators failed to register any difference [74, 129].

In general, such physiological investigations offer the advantage of being able to assess the components of interest and their importance in a range of meaningful character combinations. This may be quite relevant in choosing the parents with complementary physiological attributes and designing the selection criteria to ensure that particular character combinations are recognised and recovered among the progenies.

Heterosis studies. Significant heterosis for high photosynthetic rate associated with grain yield has been reported [72, 74, 104, 128, 148, 149]. In general, crosses involving lines with low photosynthetic rate display more heterosis with respect to mid-parent value than the crosses among lines with higher photosynthetic rates. Nevertheless, reports of high heterosis for both high x high and low x low crosses are available [128]. Generally, when heterosis for such multi-component character as CER is observed, it is more an exception rather than the rule [138]. Gaudry et al. [139] have voiced a similar concern in relation to heterosis for photosynthetic rate, PEP carboxylase, RuBP carboxylase, NADP malate dehydrogenase, and aspartate aminotransferase, where the hybrid either followed one of the parents or was intermediate to the parents. The advantage of the hybrids in producing more dry matter resulted from the multiplicative effects of leaf area and rates of photosynthesis/unit leaf area [104, 140]; photosynthetic rate and chlorophyll content [151], and photosynthetic rate at different stages [72]. Therefore, Ozbun [150] has recommended the selection for more simply inherited subcomponents of CER. Besides, the actual amount of heterosis for grain yield is largely dependent on the genetic diversity of parents and the eventual transmission of this character to the hybrid generation.

Stability and adaptability studies. The nature of G x E interaction could be quite perplexing in the attempts aimed at exploiting the photosynthetic potential. In a field screening programme, Heichel and Musgrave [152] found a maize inbred (P_aP_3) to have CER 236 ng CO_2 cm^{-2} sec^{-1} and another inbred (WF 9) to have the CER value of only 78 ng CO_2 cm^{-2} sec^{-1}. When the self-pollinated progenies from these two inbreds were grown, there was no significant difference in the photosynthetic performance of these two lines, each having CER about 150 ng CO_2 cm^{-2} sec^{-1} [153]. Besides, both the environments of a

plant during growth and its recent environment like temperature could have profound influence on the photosynthetic rate [154]. There are also reports of differential adaptation of photosynthetic rate being influenced by light environment during growth [67]. Volles [155] reported interactions of the type variety x stage of leaf development and variety x growing conditions (day length, temperature and total light energy etc.). Thus, if selection for photosynthetic attributes is ever to be effective for increasing plant productivity, the breeding efforts will have to be highly environment specific.

Breeding and management trials over locations will be important in determining which cultivars are best adapted to the climate and conditions of the area. The lines with superior photosynthetic performance can be released worldwide in a manner analogous to the disease resistant material. A feed back of any high yielding cultivar to the project evaluating photosynthetic rate can serve as a base in future studies and selection.

CONCLUSION

Despite tremendous improvements in the yield potential of different crops in the last three decades, biomass productivity has remained constant because no conscious attempts were made to improve this trait. Such rapid strides in the yield levels have been achieved by manipulating the partitioning of assimilates and tailoring new plant types. A consensus opinion is fast becoming evident that an upper ceiling is being imposed on further improvements in harvest index and the only way out is to improve the photosynthetic efficiency directly responsible for biomass productivity. Understanding of the basic genetic mechanisms of photosynthetic efficiency necessitates the collection of photosynthetic mutants and their characterization. A library of such photosynthetic mutants can be used to make an elaborate genetic dissection of the complex metabolic pathway. An ideal photosynthetic mutant is the one in which the entire structural and biochemical apparatus is intact with the exception of a single component that has been affected by mutation in a single gene or few genes. After characterizing the photosynthetic mutants the next step will be to identify the rate limiting step or reaction and then try to overcome the block for enhancing bioproductivity.

Conventional genetic methods are greatly handicapped in solving these problems but modern techniques of gene manipulation like increasing the efficiency of promoters, introducing multiple copies of cloned genes into plants, in vitro site directed mutagenesis of the gene or delaying the degradation of mRNA can be of great help in overcoming many such hurdles. Besides high photosynthetic efficiency, modification of photosynthetic apparatus to make it less adversely affected by stress (drought, high and low temperature, low or high light intensity, etc) may be more appropriate and rewarding. Answers to such questions may not be forthcoming even in the decades to come.

Despite contradictory data on the utility of photosynthetic indices towards improving

biological productivity, many workers have been successful in standardizing some indices to this end. Therefore, such contradictions can be attributed more to the methodology and sampling fluctuations. Adequate genetic variability and heritability for these indices have been reported, and their strong genetic association with biomass productivity necessitates the incorporation of these indices in breeding protocols. Depending on the genetic architecture of photosynthetic indices in respect of nature and magnitude of gene action, appropriate breeding schemes can be formulated in each crop. Besides, the stability and adaptability studies will have to be carried out because the photosynthetic parameters are highly environment-specific.

The scope of increasing the biological productivity (and through it the economic yield) are tremendous and this calls for integration of the tools of classical and molecular genetics.

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