Meetings

Photosynthesis and Photorespiration

The discovery of the C_4 dicarboxylic acid pathway for CO_2 fixation has provoked great interest in many aspects of photosynthetic processes. There have also been advances in the study of photorespiration and in the description and function of plant microbodies. Within these concepts, most plants fix CO_2 by the photosynthetic carbon cycle first into the C_3 compound, 3-phosphoglycerate; hence, in jargon, they are called C_3 plants. They also have high rates of glycolate biosynthesis and metabolism which are reflected by high rates of photorespiration and a resulting high CO_2 compensation point. Most of the glycolate metabolism occurs in microbodies, called leaf peroxisomes. Some plants, mostly of tropical origin, first incorporate CO_2 by mesophyll cells into the C_4 dicarboxylic acids—oxalacetate, malate, and asparate. These plants are therefore dubbed C_4 plants. They have no CO_2 loss or apparent photorespiration, have a zero CO_2 compensation point, and leaf peroxisomes are mainly located in bundle sheath cells. Because of the greater potential photosynthetic capacity of plants which possess the C_4 pathway of CO_2 fixation and related metabolic and structural attributes, a clarification of current research was of fundamental interest and importance, and also of potential practical significance.

Much of the work in the field is being conducted by Australian and U.S. scientists, and the recently signed agreement, relating to scientific and technical cooperation between the two countries, provided a means by which funds were contributed by each government to support a meeting of a small group of scientists from both countries, in Canberra, Australia, from 23 November to 5 December 1970.

Topics discussed included the structural and functional aspects of photosynthesis and photorespiration and the evolutionary basis and adaptive significance of C_4 plants. All species which possess the C_4 pathway of CO_2 fixation have an internal leaf anatomy which, in transverse cross section, essentially consists of three concentric cylinders of tissue: the vascular bundle; the bundle sheath, which is a dense, single layer of dark green cells surrounding the vascular bundle; and the mesophyll, which is a loosely packed layer of cells surrounding the bundle sheath. This arrangement has been referred to as the Kranz anatomy.

The integration of biochemical processes with these structural features was emphasized by several contributors. O. E. Björkman described extensive hybridization experiments with the genus *Atriplex*. The F_1 and F_2 progeny from parents of C_3 and C_4 plants displayed a complete range of structural types, but none performed photosynthetically or metabolically as efficiently as the C_4 parent species. Surveys on wheat and soybean varieties, reported by D. N. Moss, revealed no forms intermediate between normal C_3 and C_4 types of plants, all having compensation points of 40 to 60 ppm of CO_2 or near zero.

The compartmentation of biochemical events between the mesophyll and bundle sheath layers, and their coordination after the photochemistry of photosynthesis, became a recurrent theme of the seminar. The techniques used to separate cells from the two layers were critically examined in the laboratory during workshop sessions. Isolation of intact functional cells from each tissue in *Digitaria* (crabgrass) leaves, demonstrated by C. C. Black, will allow the separate investigation of these related and sequential events during photosynthesis in C_4 plants.

A large amount of data was summarized by M. D. Hatch and C. R. Slack to support their interpretation of CO_2 fixation products and subsequent carbon transport between cell types in C_4 plants. It became clear that the bulk of the CO_2 fixed passes through the C_4 dicarboxylic acid cycle in the mesophyll cells and is decarboxylated and refixed by way of the C_3 photosynthetic carbon cycle mainly in the bundle sheath cells. The spatial separation of the primary carboxylase [phosphoenolpyruvate (PEP) carboxylase] from the decarboxylase (malate enzyme or pyruvate carboxylase) and the secondary carboxylase [ribulose diphosphate (RuDP) carboxylase], provides the basic mechanism for the total system. These conclusions have been demonstrated by enzymatic distribution after tissue fractionation and cell isolation. The movement of metabolites between tissues in C_4 leaves was implied in many discussions and suggested a highly efficient symplastic transport. This nearly unexplored area of investigation will be a concern of further work. Chloroplasts so far isolated from leaves of C_4 plants, which are difficult to grind, have yielded puzzling results, and there was much speculation as to the association of PEP carboxylase with mesophyll chloroplasts or with a peripheral sheath or cytosol.

Carbon dioxide fixation in C_4 plants has many parallels with Crassulacean acid metabolism (CAM) which were succinctly distilled by W. M. Laetsch to "CAM mit Kranz." In CAM plants CO_2 is also fixed into the C_4 dicarboxylic acids, even in the dark. Other parallels, particularly in relation to PEP carboxylase isozymes and nonautotrophic dark CO_2 fixation, were emphasized by I. P. Ting.

Structure and function are associated at a finer level as evidenced by the relation between photochemical activity and anomalous grana development in bundle sheath chloroplasts of some C_4 grasses. There was agreement in principle with a deficiency in photosystem II associated with agranal chloroplasts in *Sorghum*, as reported by N. K. Boardman, J. M. Anderson, and colleagues. The extent of the deficiency varies with species and perhaps with growth conditions, particularly light intensity, thus providing ample scope for controversy at this early stage. The question of a mechanism for photophosphorylation in the photosystem II deficient chloroplast remains. It was apparent that the range of photochemical activities found in anomalous chloroplasts from C_4 plants is associated with modification of the biochemistry of CO_2 fixation and may be reflected in the initial products of photosynthesis as proposed by W. J. S. Downton.

The presentations of the biochemistry of photorespiration were one of the highlights of the seminar. M. Gibbs emphasized the close association of carbon metabolism and light reactions during glycolate synthesis, and N. E. Tolbert reported advances with respect to glycolate metabolism in leaf peroxisomes or microbodies. This work was complemented by the structural studies of plant microbodies by E. H. Newcomb and the comparative view of plant microbodies presented by H. Beevers. Photorespiration was considered to be the biosynthesis of glycolate from the photosynthetic carbon cycle and its metabolism in peroxisomes. The magnitude of this respiration increases with O_2 concentration and under conditions of impaired CO_2 fixation. Glycolate biosynthesis in the light in the chloroplasts was viewed as unavoidable, and its subsequent metabolism as gluconeogenic to conserve part of the carbons. W. A. Jackson described the exchange of oxygen associated with photosynthesis and photorespiration, and this technique may permit quantitative estimates of photorespiration in C_4 plants in which the CO_2 produced does not escape from the leaf. In many instances, C_4 plants appear to conserve photorespiratory carbon by refixation of the CO_2 during photosynthesis. In addition, C. B. Osmond provided data suggesting that some C_4 species are deficient in the photorespiratory apparatus. The biochemistry of CO_2 release during photorespiration and in serine formation were evaluated.

Several contributors helped to place the biochemical and anatomical information from the seminar into a physiological and ecological context. It was shown that minimum stomatal diffusion resistances tend to be higher in C_4 than in C_3 plants. Therefore the C_4 plant tended to have a reduced transpiration per unit leaf area. Although CO_2 transport into the leaf also was similarly impeded, this extra gas phase resistance is more than counterbalanced by the much lower intracellular CO_2 resistances in C_4 plants. Hence, total net CO_2 transport resistance tends to be lower, and overall photosynthesis more efficient, than in C_3 plants. As a consequence of higher stomatal and lower intracellular resistance, water use efficiency tends to be higher in C_4 than in C_3 plants.

The intracellular resistance is composed of physical and biochemical components, the latter being identified with the carboxylation reactions. Several attempts were made to partition the intracellular resistance into these two major components by theoretical analysis, but these procedures were queried. Experimental evidence implied that the main component of the intracellular resistance was the carboxylation resistance. This was also supported by other data for a close relationship between intracellular resistance and levels of RuDP carboxylase activity. Such evidence suggests that, even in C_4 plants, levels of RuDP carboxylase activity may be a major limitation to photosynthetic rate. In C_4 plants the lower intracellular CO_2 resistances probably result from the efficiency of the PEP carboxylation system in the CO_2 concentrating ability of the mesophyll cells.

In terms of adaptation and evolution, it is clear that, in arid environments with high solar radiation and high day temperature, C_4 plants have several advantages over C_3 plants. The C_4 plant has no apparent photorespiration, greater photosynthetic efficiency under high light intensity and higher temperature optimums, and makes more efficient use of water. However, R. O. Slatyer emphasized that one cannot extrapolate directly from single leaf studies to the behavior of whole plants or plant communities, since many factors contribute to overall growth and water use. Furthermore, with regard to economic food yield, such as yield of grain, many other factors must be considered and potential rate of leaf photosynthesis is only one determinant.

In evolutionary terms it appears that both C_4 plants and plants with CAM have arisen polyphyletically among several of the more advanced orders of both dicotyledenous and monocotyledenous plants. The Caryophyllales and the Euphorbiales include both CAM and C_4 plants, but several other orders include only one or the other. All plants apparently rely on the photosynthetic carbon cycle for the ultimate steps in CO_2 fixation. In CAM and C_4 plants, the C_4 dicarboxylic acid products serve essentially as mechanisms for prefixing and concentrating CO_2 in the photosynthetic tissue. Furthermore, in primitive aquatic environments with low oxygen levels, low light intensity, and the absence of water stress, plants with the C_3 photosynthetic carbon cycle would be at no disadvantage. Only with the colonization of terrestrial environments of high radiation, increasing oxygen levels, and increasing aridity would CAM and C_4 acid fixation and metabolism be advantageous. Again, though, it was emphasized that competitive evolutionary advantage is not just a matter of leaf photosynthesis.

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Clinical Aspects of Inherited Disorders

Genetically determined growth deficiencies, cancer genetics, genetic carrier detection, prenatal chromosome analysis, and prenatal detection of inborn errors of metabolism were some of the topics discussed at a meeting on the clinical aspects of inherited disorders held at the Medical Center, University of Alabama in Birmingham, on 9 and 10 April 1970. The meeting was opened by J. F. Volker, president, University of Alabama in Birmingham, and John Leslie, regional medical director, Maternal and Child Health Services, Health Services and Mental Health Administration.

D. W. Smith (Seattle) discussed the genetic basis for clinical disorders and presented a new classification of growth deficiency syndromes. He emphasized the importance of genetic disorders in medical problems and classified their source as (i) genetic imbalance in which there is a numerical or structural abnormality of the chromosomes, (ii) a major mutation which is transmitted in an autosomal dominant, autosomal recessive, or X-linked manner, and (iii) polygenic factors which include multiple minor variants interacting with the environment. Smith listed the presumed frequency of newborns who have or will have a disorder due to each of the three types of genetic determinations as 0.5 percent for chromosomal imbalance, 1 percent for one of the approximately 1500 individually rare disorders caused by major mutants, and 10 percent for a disorder due to polygenic factors including common malformations, diabetes mellitus, schizophrenia, and the like.

C. J. Witkop, Jr. (Minneapolis), discussed genetic heterogeneity, particularly in gingival fibromatosis and amelogenesis imperfecta. He indicated that recent developments in biochemical genetics have shown the heterogenetic character of many human traits that previously were thought to be determined by single genes.

After discussing the role of hereditary factors in cancer of the skin, endometrium, breast, and colon, H. T. Lynch (Omaha) emphasized the potential for cancer control through utilization of genetic information for early cancer detection in individuals that are at increased risk.

In discussing the question, "How can the teratogenic action of a factor be established in man?" W. Lenz (Münster, West Germany) indicated that few such factors are definitely known in man though many have been suspected. He contrasted the findings due to thalidomide with the drug Meclizine, which has come under suspicion. Comparison of thalidomide embryopathy was made with phenocopies and other established syndromes having similar clinical features. He further indicated the great need for the collection and analysis of data on intake of drugs, such as LSD, in order to answer the question as to its teratogenic properties in man. J. Warkany (Cincinnati) discussed other aspects of determining the teratogenicity of a drug and observed that we should not neglect the single case that may be caused by an unknown teratogen, and therefore that we should be most careful in drawing conclusions. Use of serum enzymes, muscle biopsies, and electromyography in diagnosis and detection of carriers of the gene for muscular dystrophy were discussed by C. M. Pearson (Los Angeles).

James L. German (New York) discussed disturbances of sexual development and the role in human sexual differentiation of various genetic determinants on the X and Y chromosomes. In the last few years new approaches to the study of growth regulation and to human behavioral disorders have been made through the study of sex chromosomal aberrations.

The autosomal aberration syndromes were discussed by W. Finley (Birmingham).

I. A. Uchida (Hamilton, Ontario)