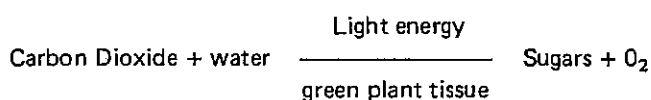


BIOLOGICAL ENERGY PROCESSES IN CROP PRODUCTION

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Photosynthesis is the central biological process in the production of organic matter by vegetation. It can probably be considered as the most fundamental biochemical and physiological process, in that it is essential for all life on this planet. It is the process responsible for supplying the highest proportion of man's energy needs in terms of fuels, both fossil and present, as well as his total food supply. In addition it is essential for the production and maintenance of the oxygen level in the atmosphere, so necessary for life processes. The overall reaction for photosynthesis may be simplified as follows:



The above process is a reaction of the first magnitude over the earth's surface, involving the fixation of some 400 billion tons of carbon dioxide annually. It is therefore timely that the influence of photosynthesis on plant productivity be considered when concern grows for conserving non-renewable energy resources and increasing world food production.

As crop production limitations related to infestation by pests, nutrient deficiencies, and water limitations have been all eradicated so more attention to basic limitations on yield has been required. The four primary determinants in the efficiency of light energy conversion of atmospheric carbon dioxide to dry matter production are:—

- (1) The efficient trapping of the light energy by plants. Green plants only use light with wavelengths from 400 to 700 nanometers. The photosynthetically active radiation makes up 43 per cent of the total solar radiation at the earth's surface.
- (2) The photosynthetic fixation of carbon dioxide into photosynthate.
- (3) The photorespiratory carbon dioxide evolution, this is the light dependent release of carbon dioxide from plant tissue, utilizing the photosynthate as the substrate.
- (4) The conversion of photosynthate into the production of new plant dry matter, this is accompanied by carbon dioxide evolution due to respiration, independent of light.

To increase the efficiency of solar energy conversion of carbon dioxide into plant material, it is necessary to build into crop varieties the capacity for increased carbon dioxide

fixation per solar energy unit available on a ground area basis, and at the same time decrease the rate of carbon dioxide lost due to photorespiration, and dark respiration. The carbon dioxide lost due to dark respiration should be minimised by increasing the efficiency of photosynthate conversion to plant structural material essential for growth and crop yield.

Methods that may be employed in plant breeding programmes, to improve crop production, bearing in mind the above, will be considered briefly.

Leaf Morphology and Leaf Structure

To increase the utilization of available radiant energy it is necessary to manipulate the leaf surface area to obtain maximum radiation interception so that maximum photosynthetic activity may be achieved per unit ground area. Less than full cover permits photosynthetically active solar radiation to escape interception by the photosynthetic apparatus, this is a problem of considerable importance with cultivated crops during the early stages of growth. The shorter the growing season, the more dependent crop yield will be upon the rate at which full cover is reached.

The ratio of leaf area to the basal ground area occupied by that leaf area is referred to as the Leaf Area Index. LAI

$$\left(\text{LAI} = \frac{\text{Leaf Area}}{\text{Area of ground it occupies}} \right) \text{ is frequently}$$

employed as a descriptive parameter in growth analysis, as photosynthetic activity is directly related to LAI at the lower levels (Figure 1). During the development of a crop, there is a change in the leaf area index, there is therefore a need for structural changes to obtain maximum light interception, due to the shading of the lower leaves by the upper leaves. When the LAI is low, horizontal leaves are advantageous, as larger values of LAI are achieved with development more erect upper leaves would give greater productivity. This is an example where leaf structural changes would improve light interception. However it is necessary when considering such features to bear in mind that changes in canopy morphology affect more than just visible light distribution among leaves and photosynthesis. The patterns of leaf distribution influences air circulation, canopy roughness, and hence the efficiency of eddy turbulence which in turn affects carbon dioxide concentration, water vapour and heat transfer, in effect the microclimate at the leaf level, which markedly influences photosynthetic rate.

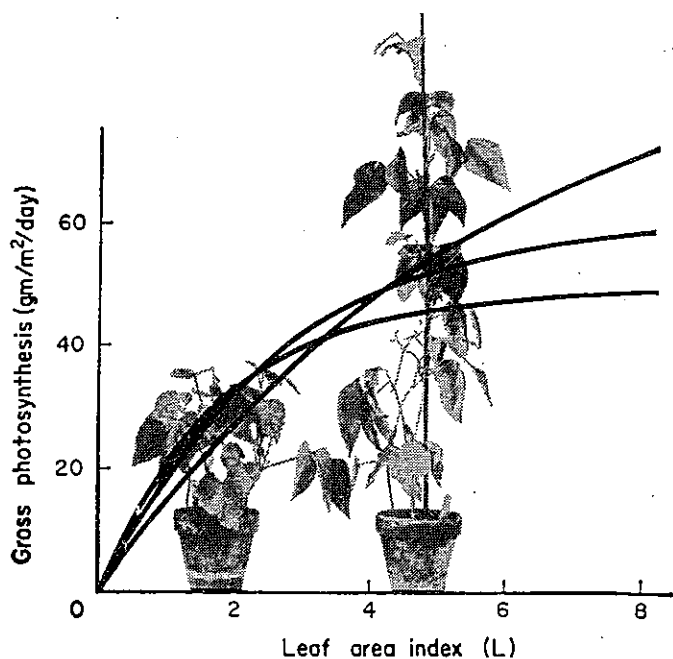


FIG 1 The relationship between photosynthetic activity and Leaf Area Index (LAI)

Interaction between Light Intensity, Carbon Dioxide Concentration and Temperature

The rate of photosynthesis is dependent upon the level of irradiance (Figure 2). At low light intensities the photochemical process is limiting, as the irradiance increases the carbon dioxide supply becomes more important, and eventually limiting. In the agricultural areas of Southern Africa light is very seldom a limiting factor, but carbon dioxide is and therefore by supplying increased levels of carbon dioxide, rates of photosynthesis may be increased and in turn plant productivity. At normal atmospheric concentrations of carbon dioxide (0,03%) there is little or no effect of temperature on photosynthetic rate, due to carbon dioxide being the limiting factor at high light intensities. However, at high irradiancies, and at high carbon dioxide concentrations (0,13%), temperature can become an important limiting factor as under these conditions an increase from 20°C to 30°C produces a 50 per cent increase in photosynthetic rate (Gaastoa (1962)).

Increasing plant productivity by increased carbon dioxide supply is frequently employed commercially in greenhouse crops, but because of practical difficulties is not employed in the case of field crops, but these problems are not beyond man's ingenuity. The use of large inflatable plastic canopies would allow crops to be grown year-round in an atmosphere of enriched carbon dioxide and yet retaining limiting water vapour, thus reducing water loss.

The reasons for an increased carbon dioxide external concentration increasing the photosynthetic rate are due to it being limiting at the site of its chemical reduction in the plant, as well as the photorespiratory process being reduced. These processes will be considered below.

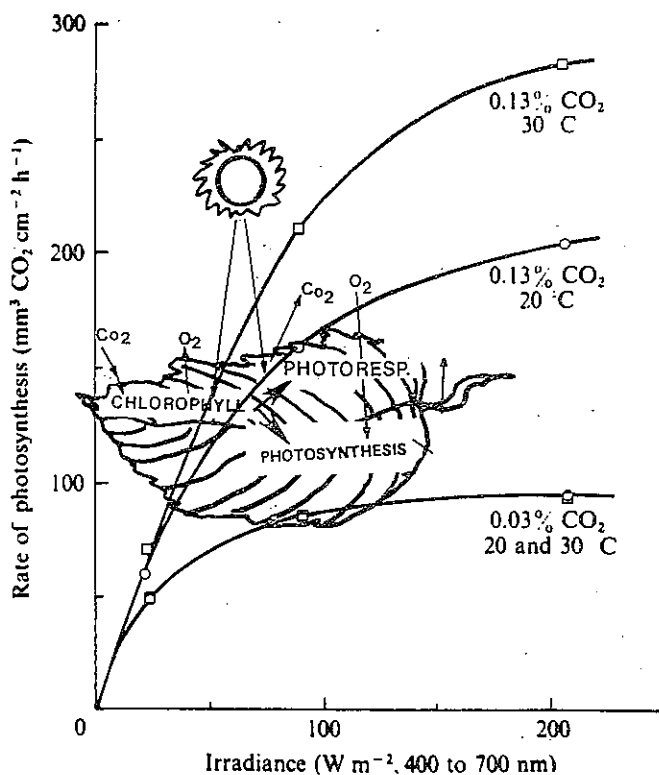


FIG 2 The relationship between photosynthetic activity and light intensity, carbon dioxide concentration, and temperature

Improving photosynthetic efficiency by increasing the carbon dioxide supply in plant breeding programmes

In any plant breeding programme for increased plant production it is necessary to select for specific components of the photosynthetic process; rather than the overall rate. It is therefore necessary to consider the individual processes involved in the dynamic process of carbon dioxide fixation by the plant.

The low concentration of carbon dioxide in the atmosphere (0,03%) means that small concentration gradients exist between the external atmosphere, and the internal site of fixation this is further aggravated by resistances to the diffusion of carbon dioxide along this path. The sites of these diffusion barriers are presented in Figure 3. During photosynthesis the greatest carbon dioxide partial pressure is found outside in a thin boundary layer of air near the leaf (1), the thickness of this layer is dependent upon the size and position of the leaves, the presence or absence of hair on the leaf surface, and on the degree of air movement. In still air the layer may be some millimeters thick, while a strong wind will sweep it away entirely. The thicker the boundary layer, the larger is the boundary layer resistance. If carbon dioxide is taken up into the leaf more rapidly than it is replaced by diffusion, the film of air near the leaf is depleted of carbon dioxide.

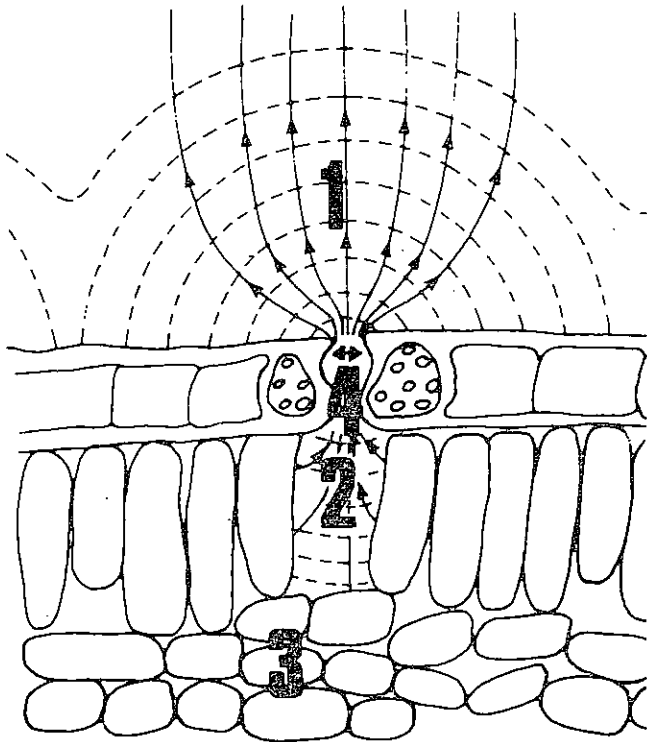


FIG 3 Resistances encountered in the carbon dioxide diffusion path within a leaf

- (1) Boundary layer resistance
- (2) Substomatal cavity where interface resistance is encountered
- (3) Intercellular resistance
- (4) Stomatal resistance

Carbon dioxide can enter the leaf only through regulated pores, the stomata, in the epidermis of the leaf, and this stomatal resistance (4) forms the decisive constraint on carbon dioxide uptake into the leaf. When the pores are closed the stomatal resistance approaches infinity. The carbon dioxide concentration in the substomatal cavity (2) and in the intercellular air is already much lower than that in the outside air, but it is still appreciable. The intercellular air not only serves as a source of carbon dioxide, it also receives carbon dioxide as a result of respiratory processes in the green and non-green cells. The diffusion resistance in the intercellular system (3) is dependent upon the anatomy of the leaf. Two other resistive factors of about the same order of magnitude as the intercellular diffusion resistance are the interface resistance, which is associated with the transition from the gaseous to the liquid phase at the cell walls and the diffusion resistance within the protoplasm and the chloroplasts.

The path of carbon dioxide transport ends in the chloroplast (Figure 4) with its fixation by the carboxylating enzyme on to an acceptor molecule. The rate with which carbon dioxide is carboxylated also affects the steepness of the concentration gradient, and thus the influx of carbon dioxide. The rate of carboxylation may be slow, and thus become the rate limiting step, and therefore be the bottleneck in the overall process, this is then referred to the biochemical carboxylation resistance.

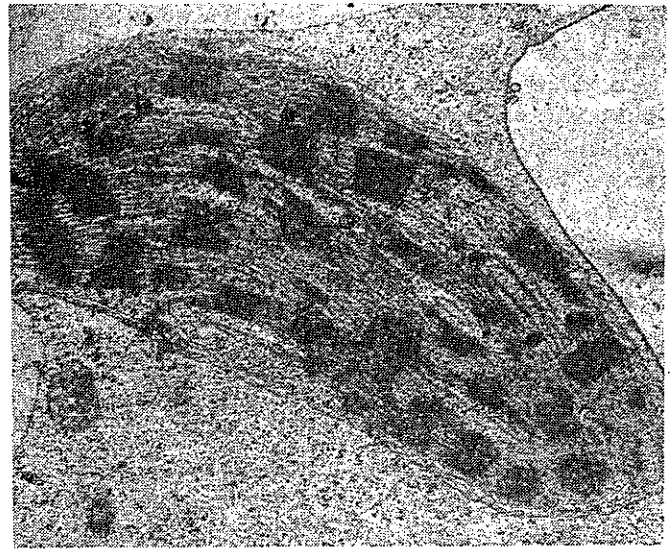
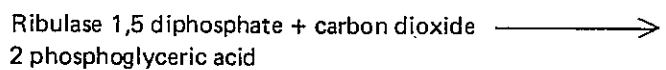


FIG 4 A chloroplast, the site of carboxylation, where biochemical resistances are encountered

The biochemical resistance may be due to the enzyme concerned having a low binding capacity for carbon dioxide, or it also may be due to the presence of a regulator. One of the serious handicaps in breeding crop plants with enhanced photosynthetic capacity is that the internal control mechanisms of the processes in the plant are not well-understood. There is strong evidence that the products of photosynthesis namely sugars are inhibitory to carbon dioxide fixation, however the cases of the "sinks" controlling "sources" have not been adequately explained.

Carboxylating mechanisms associated with photosynthesis

Up until just over ten years ago it was generally believed that there was a single primary carboxylating mechanism common to all photosynthetic organisms, namely the enzyme Ribulose biphosphate carboxylase which catalysed the following reaction —



The initial product of carbon dioxide fixation was a three carboned molecule, namely phosphoglyceric acid. Plants with this primary carboxylating mechanism are referred to now as C_3 photosynthetic plants, because of the initial three carboned compound. The carbon dioxide fixation pathway found in the so called C_3 plants was elucidated by Calvin for which he received the Nobel prize in 1961. This pathway is referred to as the reductive pentose phosphate cycle and takes place within the intact chloroplasts, see Figure 5. Preliminary photosynthetic studies undertaken by Kortschak, Harlt and Barr, using sugar cane in Hawaii in 1965, and later a more detailed investigation by Hatch and Slack in Australia established that these plants had a different primary carboxylating mechanism.

In this case the initial products of carbon dioxide fixation was a four carbon molecule namely malic acid or aspartic acid, rather than the well-established three carbon sugar phosphate phosphoglyceric acid. With time this phenomenon was then shown to be much more widespread in plants than just sugar cane, namely maize, sorghum, many of our own highveld grasses. This type of photosynthesis is not solely confined to the monocotyledoneae group of plants, but is also found in woody and aquatic dicotyledoneae. In general this type of photosynthesis is confined to plants of tropical and subtropical origin. Plants originating in temperate areas tend to exhibit an initial carboxylation mechanism which gives an initial three carbon sugar, this is the case with the majority of crop plants. It can thus be seen that the initial type of carboxylation has categorised plants into either C₃ photosynthetic plants or C₄ photosynthetic plants: related to the number of carbons associated with the first stable product.

The initial photosynthetic product is not the sole distinguishing feature between C₃ and C₄ photosynthetic plants, they also differ with respect to leaf anatomy, fine structure; and physiological characteristics linked to gas exchange. The C₄ plants exhibit the so called "Kranz leaf anatomy" in which the vascular conducting tissue is

surrounded by a layer of large cells containing chloroplasts, this layer makes up the bundle sheath. The chloroplasts contained in the bundle sheath cells differ markedly from the chloroplasts, found in the adjoining mesophyll cells, see Figure 6, the C₄ plants thus contain dimorphic chloroplasts, in contrast in C₃ plants the Kranz anatomy is usually absent, or if there is a bundle sheath present usually the chloroplasts are completely absent or reduced in size and the leaves do not contain dimorphic chloroplasts (see Figure 6).

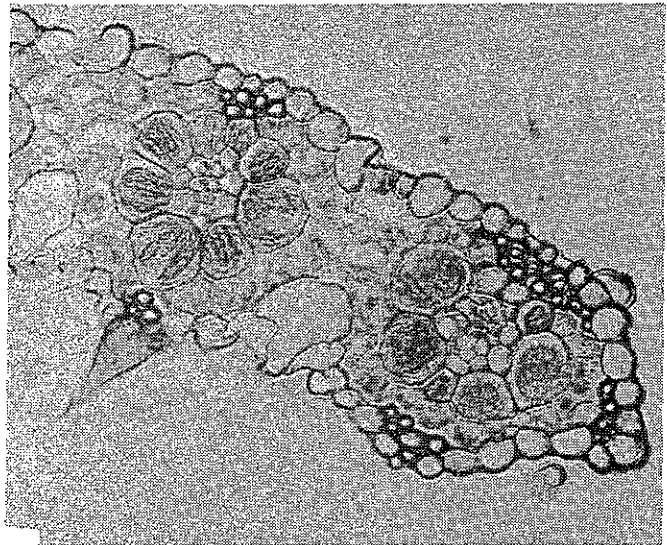


FIG 6 The Kranz anatomy of the leaf of a C₄ grass *Eragrostis curvula* demonstrating the dimorphic chloroplasts of the mesophyll, and bundle sheath cells

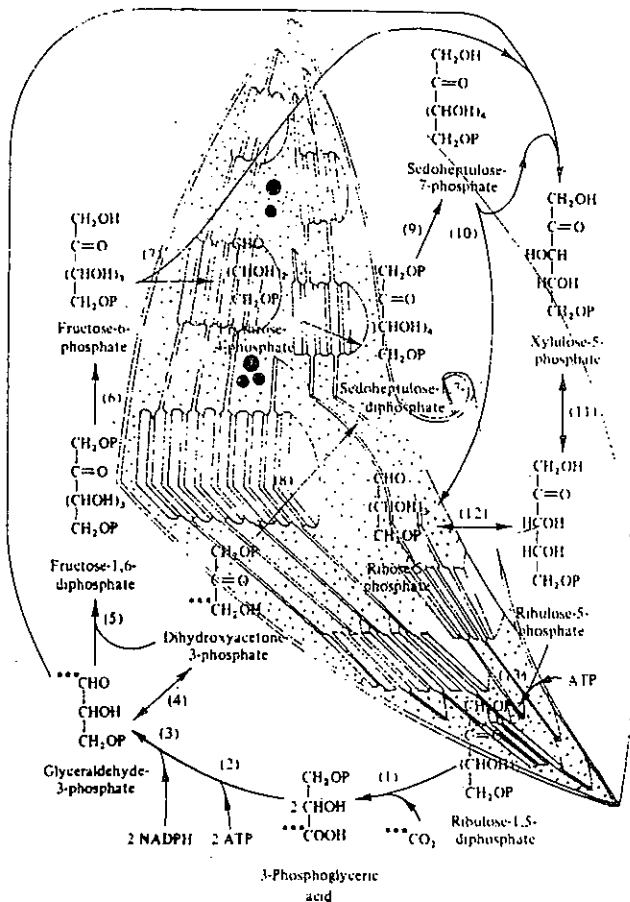


FIG 5 The Reductive pentose phosphate cycle which occurs within intact chloroplasts

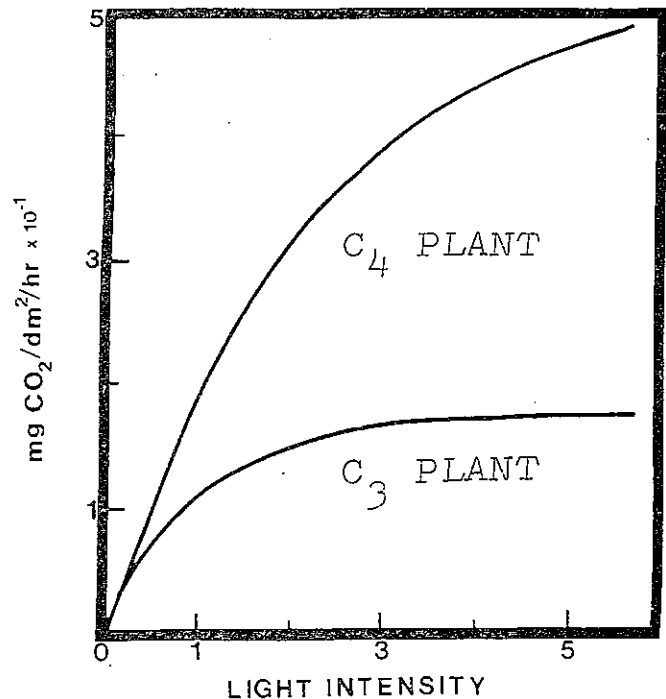


FIG 7 The influence of light intensity on the photosynthetic activity of C₃ and C₄ photosynthetic plants

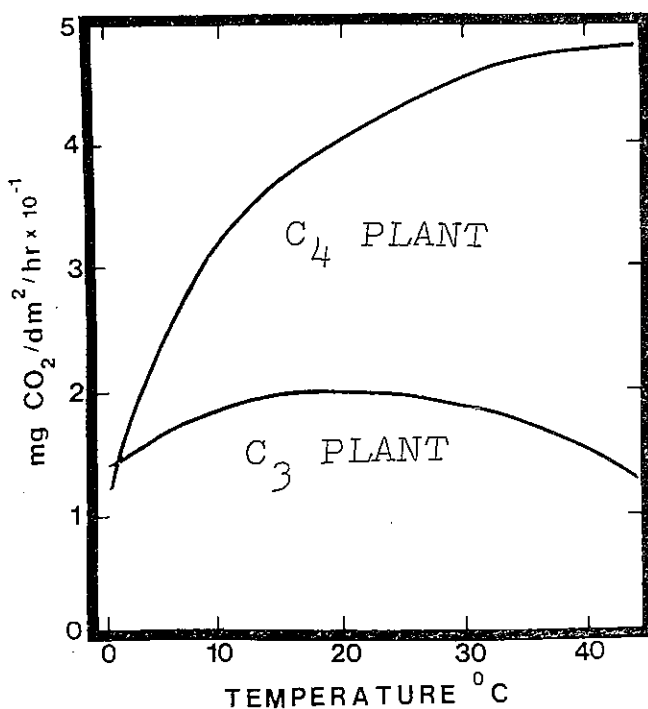
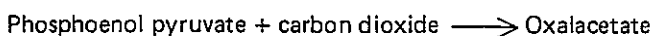
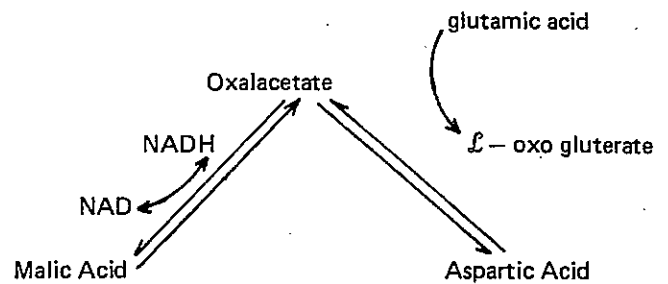


FIG 8 The influence of temperature on the photosynthetic activity of C₃ and C₄ photosynthetic plants

Initially it was thought that all plants that possessed the C₄ photosynthetic characteristics were more efficient photosynthesizers than the C₃ plants, this has been shown not always to be the case as work on C₄ plants has expanded. In general C₄ plants can utilize solar radiation more efficiently in that they have a non-saturating light response, unlike C₃ plants which saturate a comparatively low light intensities (see Figure 7). Also C₄ plants exhibit a higher temperature optimum than C₃ plants (see Figure 8). What is of particular interest is that if C₃ plants are supplied with external carbon dioxide concentrations approximately double that found in the atmosphere, the C₃ plants will exhibit similar light saturating responses as C₄ photosynthetic (Figure 1) plants, thus improving their ability to utilize available solar radiation. This observation supports the general viewpoint that one of the major attributes of the C₄ photosynthetic system is that the plant structure and its primary carboxylating mechanism enable the plant to build up a high carbon dioxide concentration within the leaf, which is responsible for giving C₄ plants their physiological efficient characters. The primary carboxylating enzyme is phosphoenol pyruvate carboxylase which catalyses the following reaction.



The four carbon molecule of oxalacetate is rapidly converted to malic acid or aspartic acid via the enzymes malic dehydrogenase or aspartic amino transferase respectively.



The above reactions take place in the mesophyll cells, and it is generally believed that the above four carbon molecules are rapidly transported to the inner bundle sheath cells, where a decarboxylation occurs, thus the build up of an internal carbon dioxide concentration, and the mechanism responsible for the internal carbon dioxide pump. The fixation of the carbon dioxide by the chloroplasts in the bundle sheath cells is by the identical mechanism found in the C₃ photosynthetic plants, namely the reductive pentose phosphate cycle. The overall mechanisms associated with the fixation of carbon dioxide in C₄ photosynthetic plants, and the importance of the leaf's anatomy to this system is diagrammatically presented in Figure 9. By these biochemical and anatomical adaptations the plant has been able to overcome the limitations of carbon dioxide supply encountered by C₃ photosynthetic plants. If the above biochemical traits could be built into many of our crop plants which are predominately C₃ photosynthetic plants, one could obtain greater efficiency in the utilization of solar energy, and greater production of photosynthate. This is particularly true in areas such as Southern Africa where input of solar radiation is at such a high level, compared to the temperate areas of North America, and Europe.

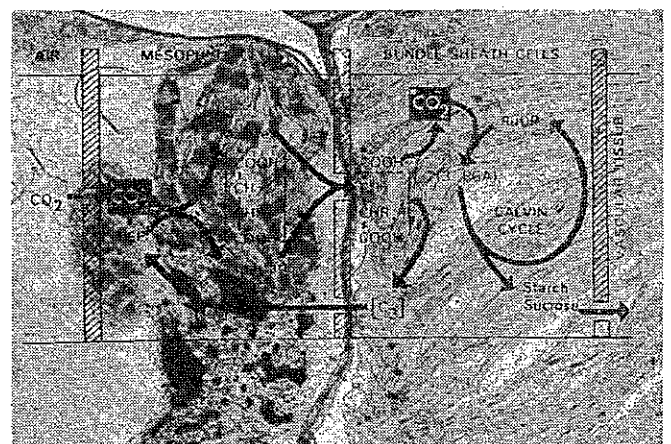


FIG 9 A proposed mechanism for the fixation of carbon dioxide by a C₄ photosynthetic plant demonstrating the spatial separation of the primary carboxylation from the reductive pentose phosphate cycle

Efficient utilization of photosynthate

Up until this point consideration has been given to the relationship between solar energy absorption, and its use in the fixation of carbon dioxide. However the overall efficient usage of the photosynthate produced towards plant growth and crop production will ultimately determine the efficiency of the solar radiation absorption. One of the major losses of photosynthate in plants is due to the process of photorespiration, which as the name suggests is light dependent. In this process the photosynthate is oxidised with the release of carbon dioxide, the substrate used in this process is thought to be predominately the identical substrate used in the carboxylation reaction of the reductive pentose phosphate cycle, namely ribulose bi phosphate. Therefore the photorespiratory process is competitive with the carboxylation reaction, as well as being responsible for the loss of carbon dioxide from the plant, and thus markedly reduces the efficiency of solar energy utilization by the plant. The process of photorespiration is enhanced by increasing the temperature, oxygen-concentration, and light intensity, and inhibited by increasing the carbon dioxide concentration. In this manner higher carbon dioxide concentration will again increase productivity, by reducing photorespiratory activity, and it is considered that this may be one of the contributory factors to C_4 plants having a negligible measurable photorespiratory activity, and higher productivity level. The function of the photorespiratory process is still unknown, initially rather simplistically it was considered to be solely a wasteful process, and therefore to be got rid of from crop plants. Work in our own laboratory tends to suggest that photorespiration may be associated with nitrogen metabolism in the light, and some recent work has established that the flag leaf in barley and wheat shows higher photorespiratory activity than any other leaf on these plants. It has been suggested that there may be a link between photorespiratory activity and cereal yield. It is essential that a greater understanding of this process, and its function in the plant be obtained before advocating that it be removed, if that is at all possible anyway.

Another loss of carbon dioxide from the photosynthate is through so called 'dark respiration' in contrast to photorespiration. It is the carbon dioxide balance, between uptake and output and not solely leaf gross photosynthetic rate which determines the production rate of the crop. The overall efficiency of conversion of photosynthate to biomass is dependent on the gross chemical composition of the biomass ie protein lipids, carbohydrates. The energy required for the growth process and the concomitant carbon

dioxide loss is associated with the conversion of photosynthate to structural components of the plant, as well as for the transport of the photosynthate from the site of 'source' in the leaf to the 'sink' either the growing point, or the storage organ, where the interconversions occur. The organs that are growing are generally not the ones which are providing the photosynthate. An improved efficiency in these two processes could be included in breeding programmes for increased crop production.

A third use of respiratory energy is in the building and maintenance of all cell components necessary for metabolism associated with growth and maintenance of life.

In summary respiration with concomitant carbon dioxide evolution is used for two components (1) growth (2) maintenance. Experimental data indicates that crop plants lose about 25 per cent of their net daytime carbon uptake in growth conversions during a 24-hour period. The maintenance losses are in the range of one to four per cent of the carbon fixed during a 24-hour period. These figures will vary with the stage of development, and also with the source of inorganic nitrogen available to the plant for its nitrogen needs, as nitrate nitrogen requires energy for its reduction in order to be incorporated into plant nitrogen components.

The carbon dioxide which the plant generates as respiratory carbon dioxide should be regarded not as a loss, but rather as an indicator of the fact that the essential processes of life are occurring, and therefore from them the rates of growth may be calculated.

Growth and development processes regulate the dynamic behaviour of photosynthetic and respiratory systems and hence the achieved production. Understanding and regulating the possible patterns of growth and development are key problems in the improvement of agricultural productivity.

In conclusion at a meeting such as this one dealing with the utilization of fertilizers, I would like to pose the question why not fertilize selected crops with carbon dioxide, as well as the other accepted nutrient elements? This may not be as impractical as it sounds if large inflatable plastic tunnels were employed such as is now being employed on a small scale with many of our horticultural crops. This would not only enable the carbon dioxide levels to be raised, but would also assist in conserving water, an extremely valuable commodity in Southern Africa as well as extending the growing season in many areas of the country.