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Metabolic Sinks

Harry Beevers

Purdue University, Lafayette, Indiana

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The continued growth of higher green plants well supplied with water and inorganic nutrients depends primarily on (i) the accomplishment of photosynthesis in the leaves and (ii) the transport of organic compounds from the leaves to heterotrophic cells which constitute metabolic sinks.

I. THE KINDS OF METABOLIC SINKS

Underground parts—roots and a variety of storage organs—are obvious examples of plant parts leading a heterotrophic existence and developing tubers have come to be regarded as the classical sink for products of photosynthesis. Nongreen aerial plant parts—buds, flowers and fruits—and most of the cells in stems and petioles also constitute a drain on photosynthetic products. Even within leaves there are many cells without chloroplasts, and the autotrophic cells themselves consume photosynthetic in their own growth and respiration.

In the literature on translocation to sinks much emphasis has been placed on the storage aspect because massive amounts of photosynthate, more or less unchanged, accumulate. It is emphasized here that wherever in the plant the products of photosynthesis are utilized, we have by definition a sink. Another source, sink relationship, which has not been fully exploited in work on translocation, is the germinating seedling. Here the sink is the rapidly growing embryo and this is supplied by mobile organic materials produced during hydrolytic activity in the source storage organ—cotyledon or endosperm.

The establishment of new sinks during plant growth depends on specific developmental process whose onset may be controlled by environmental influences such as temperature, photoperiod, and light quality; these in turn depend for their expression on internal regulatory compounds. Two further aspects should be mentioned. Most plants are ex-
posed to the activities of microorganisms. Whether the type of relationship established is a tenuous and fleeting one as when organisms in the rhizosphere grow on root exudates, or develops into symbiosis or parasitism, the extra burden constitutes an additional sink which, indeed, can prove to be of lethal consequence. Finally the production of the whole gamut of secondary products—defined here as those compounds having no structural function or readily discernible role in metabolism—represents a metabolic sink. In most plants only a small fraction of the photosynthate is diverted to these compounds but in some, e.g., those extruding resins and latex, the drain is a considerable one.

The extensive literature on translocation (see reviews by Swanston, 1959; Crafts, 1961; Leopold, 1964; Wardlaw, 1968) provides important information on the changing demands of sinks during development. In a vegetative plant the developing green leaves are a sink not only for their own photosynthate but also for that produced in older leaves with appropriate vascular connections, which also support apical growth. The oldest leaves near the base of the plant, provided they receive adequate illumination, export sugars to the roots. Several authors have concluded (see Wardlaw, 1968 for summary) that once a leaf is mature it is no longer capable of importing photosynthate even when it is made heterotrophic by natural or experimental shading. This conclusion is based largely on autoradiography after exposing upper leaves to $^{14}$CO$_2$. The successful models of Duncan (Loomis, Williams, and Duncan, 1967) also suggest that shaded leaves (those below light compensation) do not represent a major sink. However, it follows that if these leaves are not importing sugars they must be consuming their own substance and are therefore incipiently senescent. Presumably a limited importation of sugars, adequate for maintenance but insufficient to survive drying prior to autoradiography, may occur before senescence and loss in dry weight ensues.

The concept has grown that developing buds and meristematic regions in roots place demands on the available assimilate and compete successfully as sinks with developing leaves. The onset of flowering and subsequent fruit development have a marked effect on the redistribution of assimilate; fruits develop at the expense of vegetative growth, and at this time the growth of roots may be restricted.

II. CONCENTRATION GRADIENTS AND SINKS

Most of the metabolic sinks in plants are connected with the source by phloem elements in the vascular strands. In considering the fate of photosynthate at the sinks it is important to take into account what has been established about the material moving in the phloem and the direction of its movement. From the time of the important work of Mason, Maskell, and Phillips (Mason and Phillip, 1937) the idea of sugars moving from source to sink down concentration gradients has become entrenched. Refined experiments with $^{14}$CO$_2$, augmented with analyses of phloem contents have more recently provided much detailed information
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(Swanson, 1959). For our present purposes the following are the most important findings.

Translocation occurs in the sieve tubes of the phloem and although other sugars and derivatives and also nitrogenous compounds may be found in the phloem exudates, by far the most important and general constituent in the disaccharide sucrose (Kursanov, 1963). At a time when it was thought that sugar movement into plant cells was strictly a downhill diffusion process, concentration gradients between leaves and sinks were given strong emphasis. The concentration of sugars in leaves where they were produced was higher than that in the sinks; the consumption of sugars in roots, meristems, etc., was considered to give direction, if not the driving force, for the movement observed.

Of course the rates of movement—computed from information on cross-sectional area of the phloem connection and the increasing weight of tubers and fruits (see Crafts, 1961)—showed that these were enormously greater than could be expected from simple diffusion, and direct measurements of rate of movement have shown that rates of 50 cm/hr or greater are commonly achieved. Whatever the final solution of this accelerated movement of sugars in the phloem, a further question was raised against the concept of simple diffusion gradients when it was found that the actual concentration of sucrose in the phloem was very high (10-15% or > 0.3M) and therefore considerably higher than in the leaf cells generally.

It thus seems clear that the introduction of sucrose (or its component hexoses) into the phloem cells of leaves is an active loading process, one requiring an expenditure of cellular energy (see Kursanov, 1963; Wardlaw, 1968). Although the mechanism of the process is not established, it should be stressed that this is, after all, only a special aspect of the now well-established ability of plant cells to absorb and concentrate sugars (e.g., Bieleski, 1960; Grant and Beevers, 1964). Glucose and fructose have been shown to be taken up from dilute solutions and concentrated within cells and some cells accumulate sucrose directly (Kriedemann and Beevers, 1966a,b).

The concentration gradient between source and sink is therefore not a simple one, but the representation below is probably close to reality (Fig. 8-1). It is emphasized that detailed information is not available about sugar concentrations in cells adjacent to sieve elements in the loading areas, but the important fact is that, in the confined channels through which it moves out of the leaf and over long distances, the sucrose concentration remains high, and it thus seems that the receiving cells immediately adjacent to sieve elements in the sink may be exposed to solutions of roughly 0.2M sucrose.

At the terminus of a transport pathway, efficiency would seem to be achieved most readily by some finishing reaction which drastically lowered the concentration of the moving component. The reactions described in the next section do indeed have high affinity for sucrose and are thus capable of reducing its concentration far below that of 0.2M. But if the receiving cells are indeed exposed to a continuous supply of 0.2M sucrose its concentration may not be significantly reduced by these reactions.
III. METABOLIC REACTIONS IN SINKS

One of the first reactions to which sucrose moving out of phloem cells is frequently subject is hydrolysis by invertase. This applies both to sucrose moving radially from phloem during transport and that arriving at the termini of transport chains.

A. Absorption of Sugars

As indicated earlier, there is now good evidence that sugar absorption by plant cells is itself a metabolic event. The evidence for this is summarized briefly as follows:

a) Selectivity among sugars and competitive effects.
b) \( O_2 \)-requirement.
c) Uptake rates maintained for long periods.
d) Accumulation against concentration gradients.
e) Inhibition by respiratory inhibitors and uncouplers.
f) Saturation of rate at relatively low concentrations (c 0.01M)
g) High \( Q_{10} \) in 5°-30° range.

Not all of the tissues examined show the same selectivity in uptake. Frequently it is observed that the hexoses, glucose and fructose, are absorbed at the highest rates and when sucrose is supplied, hydrolysis by surface invertases precedes uptake, even though sucrose may be rapidly reformed upon crossing the plasmalemma. However, in some tissues, e.g., castor bean cotyledons, sucrose is absorbed intact as shown by the maintenance of asymmetry of labeling when sucrose-(fructose-\( ^{14}C \)) is supplied, and in this tissue sucrose is absorbed more rapidly than the hexoses (Kriedemann and Beevers, 1966a,b).
Utilization of the absorbed sugar in any metabolic event might be expected to prolong uptake or maintain it at a higher rate, but direct measurements have shown that uptake can continue long after the average internal concentration equals that outside the cells. Sugars can accumulate until the outside solution is virtually depleted. Thus regardless of the fate of the sugar absorbed, the intrinsic capacity for metabolic uptake is emphasized as an important general phenomenon which allows cells in metabolic sinks to deplete the sucrose or hydrolysis products arriving in their vicinity during translocation. Although the mechanism of this process is not understood it is clear that some expenditure of cellular energy is involved; in most theories adenosine triphosphate (ATP) or its equivalent is invoked as an activator or as a maintainer of a hypothetical carrier molecule. The elucidation of cellular accumulation is necessary too for an understanding of the loading process at the source and it may well have a bearing on the mechanism of long distance transport in the phloem.

B. Fate of the Entering Sugar

The fate of the entering sugar in cells of different kinds of sinks may now be examined. In rapidly growing cells at meristems, whether these are in vegetative apices, cambial regions, storage organs, floral parts or embryos, the major fate of the sugar is conversion to new cell material. Figure 8-2 summarizes a few of the reactions leading from sugar to important intermediates. It is meant to emphasize that the breakdown sequence comprising familiar respiratory pathways is at the same time the source of carbon for the monomeric units—amino acids, fatty acids, uridine diphosphate (UDP) hexoses and pentoses—which are, respectively, the precursors of proteins, fats, and cell wall components. In actively growing cells more than half of the sugar may be diverted to these constituents.

The rest of the sugar introduced into the sequence is oxidized to CO₂ and water in providing the ATP and reduced nucleotides required to drive the synthetic events, to allow the cell to accumulate ions, and to reduce NO₃ and SO₄ to forms appropriate for introduction into the metabolic sequence. It follows that the pace of the synthetic events, by draining off intermediates and regenerating the acceptors adenosine diphosphate (ADP) and nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP), determines the pace of sugar breakdown. Superimposed upon this general regulation are various other controls such as end-product inhibition and allosteric effects which apparently ensure the harmonious coupling of degradative and synthetic processes in cell growth. These latter controls have not, as yet, been searchingly examined in plant tissue.

The onset of cell division which initially defines the various sinks, and its subsequent regulation are, of course, other problems. However, insofar as this continues at growing points, the sink for photosynthate is maintained. In expanding and fully mature cells the demand for sugars is less, but even here respiration continues. It is not suggested that the gearing between respiration rate and useful deployment of the
respiratory products is absolute—there is probably a low idling rate—and even in mature cells there is turnover of protein and other constituents whose resynthesis and maintenance consume ATP.

C. Accumulation of Sugars and Starch at Sinks

Major sinks for photosynthate occur at a variety of storage sites. After cell division and expansion some parenchymatous cells (e.g., of tubers, internodes, seeds, fruit, and roots) become repositories for organic compounds which are mobilized subsequently when other sinks appear during development. Two aspects of this accumulation will be considered.

1. Absorption of Sugars at an Accumulating Sink

In an important series of papers, Australian investigators have studied sugar accumulation in the internodes of sugarcane (Saccharum officinarum L.). (Bieleski 1960, 1962; Hatch et al., 1963; Hatch and Glasziou, 1963; Sacher et al., 1963). For our purposes the major findings are as follows.
In the mature internode the sugar concentration (almost exclusively sucrose) is roughly 20%, in the young internode it is 4-10%, and in the leaf 2-3%. No starch appears in the storage tissue. In this example it should be noted that there is no apparent downward gradient between source and sink, and although the concentration of sucrose in the phloem supplying the storage cells is not given, it seems that sugars are more concentrated in the receptor cells. Sections of internode of the appropriate age retain the remarkable capacity for sugar accumulation even when removed from the intact plant. Glucose and fructose are actively absorbed and sucrose accumulates as a result. When sucrose is supplied it too is absorbed but apparently only after hydrolysis at the cell surface or in the outer (free) space. Sugar uptake continues from dilute solutions until the concentration inside the cells exceeds that outside by a factor of 50-200. It was calculated that in the accumulation process itself less than 10% of the sugar was consumed in energy yielding reactions, and it was shown that, regardless of which sugar was supplied, sucrose accumulated in the vacuole. Invertases, one of which was deduced to be associated with the wall, were shown to be concerned with sucrose absorption, and the various enzymes bringing about sugar transformations and sucrose synthesis from hexose were shown to be present in the tissue. It was deduced, as shown in Fig. 8-3, that synthesis of sucrose or a derivative occurred in the metabolic or protoplasmic compartment and that free sucrose accumulated.

The major difference observed in absorption by castor bean (Ricinus communis L.) cotyledon (Fig. 8-4) was that sucrose was absorbed intact; virtually no free hexose exists in this material, or in the exudate obtained on excising the radicle. (Kriedemann and Beevers, 1966a,b).

2. Starch Formation

In many storage sinks the entering sugar is converted to starch. The effect of this change is to keep the sugar concentration low and to maintain a higher (less negative) water potential. The biochemistry of

<table>
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<tr>
<th>CONDUCTING TISSUE</th>
<th>PARENCHYMA (STORAGE TISSUE)</th>
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<tr>
<td>OUTER SPACE</td>
<td>METABOLIC COMPONENT</td>
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<tr>
<td>(WALL)</td>
<td>(CYTOPLASM)</td>
</tr>
<tr>
<td>INVERTASE</td>
<td>STORAGE COMPONENT</td>
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<tr>
<td>SUCROSE → SUCROSE → GLUCOSE → [GLUCOSE] → [SUCROSE] → SUCROSE</td>
<td></td>
</tr>
<tr>
<td>+ FRUCTOSE → [FRUCTOSE]</td>
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Fig. 8-3—Sucrose accumulation in sugar cane storage tissue (see text).
starch formation is not yet fully understood. Several enzyme systems are known which could conceivably contribute, including several phosphorylases, starch synthetases bound to starch granules and soluble synthetases (see review by Akazawa, 1965). A good deal of current emphasis is on the synthetases, which utilize nucleotide sugar derivatives; this aspect of starch formation will be considered, and the relation to its origin from sucrose, the transport sugar.

The starch synthetases are able to add glucose units to pre-existing starch or smaller primer molecules when this is provided as uridine diphosphate-glucose (UDPG) or adenosine diphosphate-glucose (ADPG). UDPG, an important glucose donor in the synthesis of sucrose and other derivatives, was the first donor to be discovered in the synthetase reaction but most recent emphasis has been on ADPG, since it is a superior donor in some systems and highly purified enzymes have been obtained which utilize ADPG almost exclusively.

The overall reaction is as follows:

\[(\text{Glucose}_n) + \text{ADPG(UDPG)} \rightarrow (\text{Glucose}_{n+1}) + \text{ADP(UDP)}\]

and this is usually measured by the incorporation of labeled glucose into an insoluble form (starch) or by following the UDP (ADP) released in coupled enzyme reactions.

The sugar nucleotides are made from the appropriate triphosphate and glucose-1-P in a pyrophosphorylase reaction as follows:

\[\text{UTP (ATP)} + \text{glucose-1-P} \rightarrow \text{UDP (ADP)-glucose} + \text{PPi}\]

The enzymes and their products have been detected in several species. The substrate is derived from glucose or fructose by the action of hexokinase and the appropriate isomerases.

The possibility has been raised (see Akazawa, 1965; Slabnik et al., 1968) that a somewhat more direct route to starch from sucrose is possible, since sucrose synthetase (one of two enzymes thought to bring about sucrose synthesis in the presence of ADP or UDP) can bring about the reverse reaction as follows:

\[\text{Sucrose} + \text{ADP (UDP)} \rightarrow \text{ADPG (UDPG)} + \text{Fructose.}\]
The sugar nucleotide could then be used directly in starch synthesis and the fructose utilized as above. In this formulation the expenditure of ATP in starch synthesis from sucrose would be reduced by half, but it should be recognized that in the formation of sucrose itself, ATP is consumed, and no saving would result if the nucleotide sugars which are sucrose precursors were used directly in starch synthesis. The available evidence suggests that, even though sucrose is the form arriving at the sinks, hydrolysis occurs during uptake. If this is so, there would appear to be no advantage in forming sucrose as an intermediate in starch formation, and the formation of sucrose or starch would appear to be alternative fates for the nucleotide-hexoses. It remains to be proved that, even in leaves, sucrose normally intervenes as an intermediate in starch synthesis.

The question of how starch synthesis might be controlled by other metabolites has also received attention. Ghosh and Preiss (1966) showed that the purified starch synthetase from leaves which uses ADPG as a donor was not affected by a variety of glycolytic intermediates but that striking stimulations were observed when PGA and other intermediates were included in the ADPG pyrophosphorylase reaction. Similar, though smaller stimulations have been reported for the enzyme from maize endosperm (Dickinson and Preiss, 1968). If ADPG synthesis is a prime regulatory point in starch synthesis in seeds and tubers as it is believed to be in leaves, a possible control is afforded over the alternative fates of glucose as shown in Fig. 8-5. Active utilization of the glycolytic intermediates in the respiration of growing cells might, by keeping the concentration of PGA low, limit the formation of ADPG and thus of starch. Accumulation of PGA when utilization was slower might then bring about a more rapid rate of starch synthesis.

**IV. INTERACTION BETWEEN SOURCE AND SINK**

In the foregoing a purely passive relation between source and sinks has been implied; we have pointed out where the sinks are and what some of the metabolic reactions are which consume sucrose arriving in the translocation stream. The question of which of several alterna-

![Fig. 8-5—Possible regulation of starch synthesis in sinks by glycolytic rate.](image-url)
tive sinks pre-empts the photosynthate from a given leaf has been raised but not answered. However, it seems that the relationship can not be simply one of different concentration gradients between the source and sinks of different "strength" or metabolic activity.

Another subtle relationship which has been recognized for many years (see King, Wardlaw, and Evans, 1967; Neales and Incoll, 1968 for reviews) is that the size of activity in the sink may have an influence on the rate of photosynthesis in source leaves. The concept has grown that if assimilate is not transported to sinks the rate of photosynthesis is depressed, and if new sinks are provided, the rate is increased. Effects in response to changing status of sinks which suggest control of photosynthesis by the level of assimilate in the leaf are shown in the following table (from summary by Neales and Incoll, 1968):

- a) Decreased rate on detachment.
- b) Fatigue effects: midday depression of photosynthetic rate.
- c) Increased rate in remaining leaves following partial defoliation.
- d) Decreased rate following interference with translocation or removing sink.
- e) Decreasing rate at temperatures suboptimal for growth.
- f) Influence of grafting different sinks.

A sort of mass action is frequently inferred. No biochemical evidence is available which would explain how accumulation of photosynthate would slow down the process, but distortion of the chloroplast by accumulating starch grains is surely not the only possibility, and in any event would not explain declines in rate in leaves which do not produce starch. Nor is it clear that the sugar concentration in the phloem is increased to the point where loading would be reduced, or indeed that inordinately high concentrations of assimilate always accumulate in leaves deprived of sinks.

Neales and Incoll (1968) conclude that although the evidence is suggestive the hypothesis is not proved. Many of the effects are long term and the possibility has been raised that other kinds of feed back from sink to source, including hormonal signals, may be operating. For example, Wareing, Khalifa, and Trehearne (1968) in a recent investigation of the stimulatory effect of partial defoliation on remaining leaves, showed that these had somewhat increased levels of protein, and particularly of carboxylating enzymes. They suggested that a correspondingly increased photosynthetic capacity, rather than increased relative demand by the sink, was responsible for the higher photosynthetic rate of surviving leaves, and favor a dynamic hormonal interaction between sink and source.

However, such an interpretation was shown to be unlikely for results obtained by King, Wardlaw, and Evans (1967). These authors showed that in wheat (Triticum aestivum L.), 2 weeks after anthesis, 45% of the flag leaf assimilates are transferred to the developing ear which is itself photosynthetic. Removal of the ear resulted in a 50% reduction in photosynthetic rate of the flag leaf within 15 hours. Darkening of the other leaves resulted in recovery of photosynthetic rate of the flag leaf, with the assimilate now being diverted to roots and shoots. Under some conditions inhibition of photosynthesis in the ear brought about an increased rate of photosynthesis in the flag leaf. In this sys-
tem then there are relatively rapid interactions, and the photosynthetic rate of the source appears to be closely regulated by the demands of the sink.

LITERATURE CITED


Our topic here is metabolic sinks. Dr. Beevers has clearly outlined the state of our knowledge on the delivery of sucrose to such sinks. The sucrose can be consumed in the biosyntheses which underlie growth, or it can be sequestered in vacuoles or immobilized as starch in plastids. In common, the cells involved must have boundary mechanisms for transport. "Sinks" then are cells not only with a high demand for carbohydrate, but also with intensely active mechanisms for moving it across the limiting cell membranes.

It should be noted that more than sucrose is moved to sinks, particularly to sinks composed of rapidly growing tissues. Essential mineral nutrients flux as well, though not always through the phloem. One of the earliest findings with $^{32}$P applied to roots was that it moved to and became concentrated in active growth centers such as apical meristems and growing fruits. The bounding membranes of these must avidly transport phosphate as well as sucrose. In turn, the transport must "deepen" the sink and keep ions and sugars flowing to it.

It is appropriate to ask what sort of impulse or signal quickens the metabolism of sinks. Our best response nowadays is to suggest an involvement of hormones. The experiments of Professor Mothes come to mind in which he places a drop of kinetin on a senescing leaf, with the result that that area stays green at the expense of surrounding tissues. Kinetin has here induced a sink in certain cells, and influences are sent forth (or withdrawn) which command adjacent tissues to senesce in order to nurture the sink. Something similar must happen normally with ripening fruits and grain. In corn plants the growing and maturing grainforms an intensely active sink which derives only half its nitrogen directly from the soil—the other half is mobilized from the senescing vegetative structure.

There is an interesting example of the induction of a sink with sub-
sequent senescence in the use of the auxin herbicide, 2,4-D. It seems to me especially appropriate for this symposium as it provides one of the few instances where we make agricultural use of the induction of sinks.

Dr. Juan Cardenas in our laboratory studied the death of young cocklebur plants (Xanthium sp.) spot-treated on one leaf with 70 µg of 2,4-D (2, 4-dichlorophenoxyacetic acid) (Cardenas, 1968). There were 3 distinct periods in the growth toward death. Between 0-2 days the treated plants showed total growth similar to the control, but distributed in favor of the swelling stem–tap roof axis at the expense of new leaf and root formation. The axis swelled, but the meristems were "frozen." Immature leaves failed to expand properly. Between 2-7 days there was no net growth. However, the axis continued to gain in weight at the expense of leaves which were induced to senesce. In the period between 7 and 10 days the plants collapsed, withered, and died.

Roots were stimulated to greater ion uptake the first day after 2,4-D application, with the major portion of phosphate and potassium delivered to the sink in the swelling axis. Leaves received very little ion and after the second day the supply was virtually cut off.

Photosynthesis was also initially stimulated, but with a drastic decline by the second day. Photosynthate was delivered to the axis, the roots being starved.

Cardenas et al. concluded that the plant died because it failed to be autotrophic. Induction of the axis-sink caused senescence of those organs needed to exploit the environment.

Induction of the sink was ascribed to an accelerated nucleic acid metabolism in the axis, coupled with a "freezing" of nucleic acid metabolism in the apical meristems. There is insufficient time to discuss the evidence here. Key et al. (1966) have made a systematic study of the aberrant nucleic acid metabolism in 2,4-D-treated soybean seedlings (Glycine max L.), and correlated this with cell growth and division. O'Brien et al. (1968) show the induction of RNA polymerase in 2,4-D-treated soybeans.

The principal point to be made is that sinks can be manipulated to agronomic ends. When we know more about hormone action I feel certain that the manipulations can be extended to increasing crop yields. But we must first have more biochemical and physiological fact on the regulation of sink metabolism and on the transmission of signals for mobilization and senescence.

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Cardenas, J., F. W. Slife, J. B. Hanson, and H. Butler. 1968. Physiological changes accompanying the death of cocklebur plants treated with 2,4-D. Weed Science 16:96-100.


It was gratifying to have Professor Beevers dwell on the prospect that a hormonal feed-back may be significant in the determination of the influence of ultimate photosynthetic sinks in the plant on the photosynthetic apparatus. The regulation of metabolic events by mass law considerations is thermodynamically quite untenable, as calculations of the necessary substrate concentrations to effect synthesis of starch or protein by the reversal of hydrolytic processes will readily show. In the last analysis the ultimate metabolic sink is heat. While, with sunlight taken into consideration, metabolic cycles in plants may be taken as an example of a zero sum game—in the systems analysis terms of Dr. M. Clawson—such cycles may be far from a zero sum game in practical terms, when time, and perhaps location, are taken into consideration. A case in point is the role of the ocean as a sink par excellence for at least one critical component of metabolism.

While the major elements of photosynthesis are involved in prodigious quantities, they are totally recycled. The over-all constancy of the atmosphere and the level of the oceans attests to the regeneration of oxygen, carbon dioxide, and water. Phosphate, on the other hand, while recycled in metabolism, suffers a constant depletion from the earth's land surface to its underlying layers and particularly to the bottom of the oceans. Retrieval from these ultimate sinks is meager; for practical purposes the traffic is unidirectional. Insofar as the phosphate lost to the ocean bottom is primarily in organic combination, the ocean bottom is a metabolic sink. While other elements as well are lost to the sea (in quantities greater than phosphate) their concentration in the sea permits the visualization of their role in marine agriculture. With phosphate (and with nitrogen as well) the concentration is so low that the energy of retrieval is perforce vast, and biological yields must be limited by the availability of these elements. In short the levels of phosphorus and nitrogen in the oceans do not realistically allow contemplation of the open oceans as a compensation for depleted agricultural potential on the land.

The fixation of carbon in photosynthesis per year over the land surface of the earth is enormous, being some $1.7 \times 10^{10}$ metric tons. Estimates for photosynthesis in the oceans has ranged as high as $14 \times 10^{10}$ metric tons of carbon fixed per year (see Rabinowitch, 1945). There is the prospect, based on the prevalence of $^{18}$O$_2$ in the air, compared with the prevalence of H$_2$O in fresh water and sea water, respectively, that estimates for photosynthesis in the oceans may be several times too
large. (R. Park and S. Epstein. Personal communication.) In any event the turnover of phosphorus on a molar basis is at least three times as great as carbon turnover, simply taking into account that three molecules of phosphate (as ATP) are required for each CO$_2$ fixed into carbohydrate. Respiratory breakdown leads to an even greater phosphate turnover—six molecules of phosphate for each O$_2$ utilized. In brief, the traffic in phosphate is prodigious, coming to some $27 \times 10^{10}$ metric tons of phosphorus turned over in the terrestrial biosphere per year.

While phosphorus is not readily leached on the land (Black, 1965; Fried and Broeshart, 1967), considerable phosphate is lost from the land by erosion. In spite of the fact that the phosphate concentration in the earth's fresh waters is very low indeed, some $14.5 \times 10^8$ metric tons of phosphorus is delivered to the oceans each year by the world's rivers (see Rankama and Sahama, 1950). Withal, the concentration of phosphorus in the ocean is painfully low, ranging from almost nil at the ocean's surface, to but $3 \mu M$ at some $1,000$ m in depth (see Sverdrup et al., 1942). Further, the concentration in the ocean is steadfast, approximately $14.5 \times 10^6$ metric tons of phosphorus being deposited in ocean sediments each year in the form of organic matter in residues of phytoplankton and zooplankton. For practical purposes such phosphorus is irretrievable. Surprisingly, the ocean bottom is not littered with calcium phosphate, and there is evidence that even the phosphorus-bearing concentrations to be found on the ocean floor are not being laid down currently (Personal communication from Dr. I. Kaplan, Professor of Geophysics, UCLA.). Phytoplankton turn over approximately 1% of the phosphorus in the ocean per year, and in turn lose about 1% of what they turn over to the ocean sediments.

In querying the possible jeopardy to our agriculture of phosphate loss from the earth's land mass it is difficult to assign the source of the phosphorus lost by erosion. It seems likely that a disproportionate part of that lost to the oceans comes from arable land—which is currently estimated to be but 10% of the earth's land mass (Pehrson, 1945). In fact, a calculation of the total amount of phosphorus lost from arable land [$11.9$ kg/ha per year (see Black, 1965), $\times 1.4 \times 10^8$ ha (see Pehrson, 1945) = $16.7 \times 10^8$ metric tons] reveals a quantity very close to that lost to the oceans each year, e.g. $13.6 \times 10^8$ metric tons. This quantity represents the loss of roughly 1.0% of the phosphorus in a plowshare's depth of the earth's arable land per year. If an appreciable part of the phosphorus washed into the ocean in fact comes from nonarable land as well, the percent lost to agriculture will of course be less.

Finally, what of mariculture? The phosphorus concentration in the ocean is but $3 \mu M$, and nitrogen no more than $50 \mu M$. Plankton photosynthesis on an acre basis would appear to be but 5% that on land—and if the plankton product is converted to fish, so to speak, with 1% efficiency, the yield would be no more than 0.1 to 0.2% of the edible crop land yield (de Wit, 1967). Thus the prospect of extensive mariculture as a cure for the world's food needs is at best an illusion and at worst, a hoax. Further, with the current trend of ocean pollution, the ocean will unhappily assume an even greater role as an ultimate metabolic sink.
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