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CONTROL OF PARTITIONING AND EXPORT OF CARBON IN LEAVES OF HIGHER PLANTS¹

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Within source leaves, partition of assimilated carbon and export are regulated in response to both leaf and plant ontogeny and to environmental conditions. System goals, adaptive responses, control mechanisms, and information flow are developed from the viewpoint that a well-adapted plant is an integrated system. Regulation of partitioning and export involves both feedforward control and feedback homeostasis. Export is controlled by regulation of metabolism which supplies assimilated material to be translocated, by control of efflux into the free space of material destined for export, and by regulation of phloem loading. Control of export by the latter two processes depends on responsive metabolic processes that can supply sucrose and other transport molecules upon demand. An integrated model incorporating these features posits that control of export by mechanisms located in the source leaves is an important means of regulating translocation.

Introduction

Translocation under various environmental conditions and at different stages of plant development shows a remarkable degree of regulation of partition and export of material derived by photosynthesis. Control of initiation of export and regulation of partition of metabolites are evident during plant development (FELLOWS and GEIGER 1974; TURGEON and WEBB 1975). Environmental conditions and experimental manipulations which alter carbon economy within the plant produce marked changes in rates of export and in patterns of distribution between regions of the plant (THORNE and KOLLER 1974; GEIGER 1976; BODSON et al. 1977; BORCHERS and SWANSON 1977).

WELL-ADAPTED SYSTEMS

A successfully adapted plant is a finely adjusted system with the capacity to respond to stages of development and changes in environment by well-developed adaptive mechanisms. Export of assimilates is an aspect of plant function which is subject to close regulation. Regulation of export provides a means of maintaining or restoring carbon balance within exporting leaves and between parts of a plant. In addition, it allows a plant to respond to changes in requirements at different stages of development and under diverse environmental conditions. Until we understand regulation of export, we have only a very incomplete understanding of plant function.

Analysis of export and partitioning as adaptive mechanisms which are part of integrated systems of

controls in higher plants may provide new insights into plant function. Analysis and research, based on the concepts of "source strength" and "sink strength," have provided insights and working hypotheses for vigorous research in the area of translocation (WARREN WILSON 1972; WAREING and PATRICK 1975). It is anticipated that an approach based on the integrated nature of plant function will add to the productivity of research on export and partition in the whole plant.

ELEMENTS OF THE PLANT SYSTEM

A well-adapted plant appears to have integrated systems with several key elements:

1. SYSTEM GOALS.—Inherited patterns of adaptation contribute to the adaptive success of the plant within a range of environmental conditions and developmental stages. Balanced allocation of fixed carbon among parts of the plant with retention of adequate carbon reserve in source leaves is an example of such a system goal which likely leads to survival success.

2. ADAPTIVE RESPONSES AND SET POINTS.—These means, on a more limited scale, promote the attainment of system goals. Adjustment of partition of carbon into starch synthesis, thereby providing a certain minimum level of starch that allows export throughout the night, is a possible adaptive response. The sucrose level may function as a set point for helping achieve carbon balance under a given situation.

3. CONTROL MECHANISMS.—Physiological and metabolic functions provide the basic means by which subsystems of the plant carry out adaptive responses or attain and maintain a certain set point. End-product inhibition of an enzyme may serve as a control mechanism that helps attain a certain level of metabolite and thus helps carry out an adaptive response to changing conditions.

4. INFORMATION FLOW.—This involves communi-

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cation of information concerning an environmental condition or of a state within the plant to a control mechanism. The transfer of a hormone between the site of its synthesis and a target organ or transmittal of pressure within a file of sieve elements are examples of information transfer.

Analysis of these control systems not only promises to give insights into plant function but also may help improve crop yield. The hope for increasing yield is based on the belief that adaptive mechanisms of the plant, which are oriented to reproductive success and continuance of members of the species, are not always optimally adapted to humankind's goal of increased crop production.

VARIOUS CONTROL PATTERNS

Observations of patterns of regulation of export lead to the realization that some responses help maintain a given state in the controlled system while others exhibit anticipatory control. ROSEN (1975) compared these two patterns under the headings of feedback and feedforward adaptive mechanisms, respectively. The following is an adaptation of his analysis to the control of partitioning and export within source leaves.

Feedback homeostats maintain some function of a controlled system at a constant level, helping to maintain constant system quality in the face of environmental changes. A given feedback control mechanism will regulate a particular quantity in the system, responding specifically to error; that is, to the deviation from a set condition in the plant. The control mechanism senses the state of the system directly and the environment only indirectly.

Feedforward controls sense a present state which is related to some future state of the system. For instance, an environmental state, such as a favorable photoperiod, brings about flower initiation, which will often be followed by fruit development. The environmental cue probably brings about the changes in plant function needed to provide for nutrition and development of the fruit. The pattern of response to the state sensed is determined within the genetic makeup of the plant. Similarly, a given daylength, light quality, and light intensity help determine a certain growth pattern of a leaf which is suited to the seasonal conditions ahead. Control is not based on an error signal but on perception of a state which triggers a sequence. The signal event is one that is generally followed by certain events or conditions. In a sense, there is a model of the pattern of the anticipated events built into the plant. Sometimes this sequence takes the form of a developmental process such as source leaf maturation; other times it is a successful pattern of adaptation in response to the onset of an environmental state, as with seasonal responses such as flower development or the initiation of cold hardiness. In feedforward regulation, there is need for some mechanism to sense the

environment. Feedforward control operates off regularities in the pattern of development processes or in successful patterns of response to a given environmental stimulus.

Examination of adaptive responses and control mechanisms dealing with regulation of export, both in the light of feedforward as well as feedback control, will lead to new insights. While the suggested analysis may raise more questions initially than it yields answers, I anticipate that new working hypotheses will emerge and that these will help orient productive future research in the areas of regulation of partition and export.

MEANS TO CONTROL EXPORT

Studies on the control of export provide evidence that there are a number of regulatory processes affecting translocation (fig. 1). There are three groups of processes which regulate export from a source leaf.

The first group of processes (fig. 1, 1-7) results in metabolic control of availability of sucrose and other phloem-mobile molecules for export. Products of carbon fixation may be directed into starch synthesis (1) or may exit from the chloroplast by a transporter mechanism (2). Under certain conditions starch may be mobilized (3) and the soluble intermediates exit through the chloroplast envelope (2). Respiration, photorespiration, synthesis, and growth (4) divert carbon compounds from export. A portion of the fixed carbon is directed into synthesis of sucrose and other phloem-mobile molecules (5). These compounds may be stored (6) to be mobilized at some later time (7). As a group, these metabolic processes control the availability of sucrose and other molecules for export.

The second process (fig. 1, 8) controls the exit of sucrose or other exportable molecules from the mesophyll into the free space. Molecules destined for export move from sites of synthesis or storage via the symplast to the region near the minor vein sieve tubes and companion cells where they enter the free space, possibly from phloem parenchyma cells. This control process regulates export by compartmental isolation from the site of phloem loading.

The third type of control process (fig. 1, 9) directly affects phloem loading by regulating the active uptake of sucrose or other molecules such as amino acids into sieve tubes. Aspects of this model relating to exit of sucrose from the mesophyll into the free space and to phloem loading were discussed by GEIGER (1975). Therefore, only control of partitioning and export will be discussed here.

Metabolic control of availability of compounds for export

SYSTEM GOAL

Metabolic control of availability of compounds able to be exported appears to be particularly im-

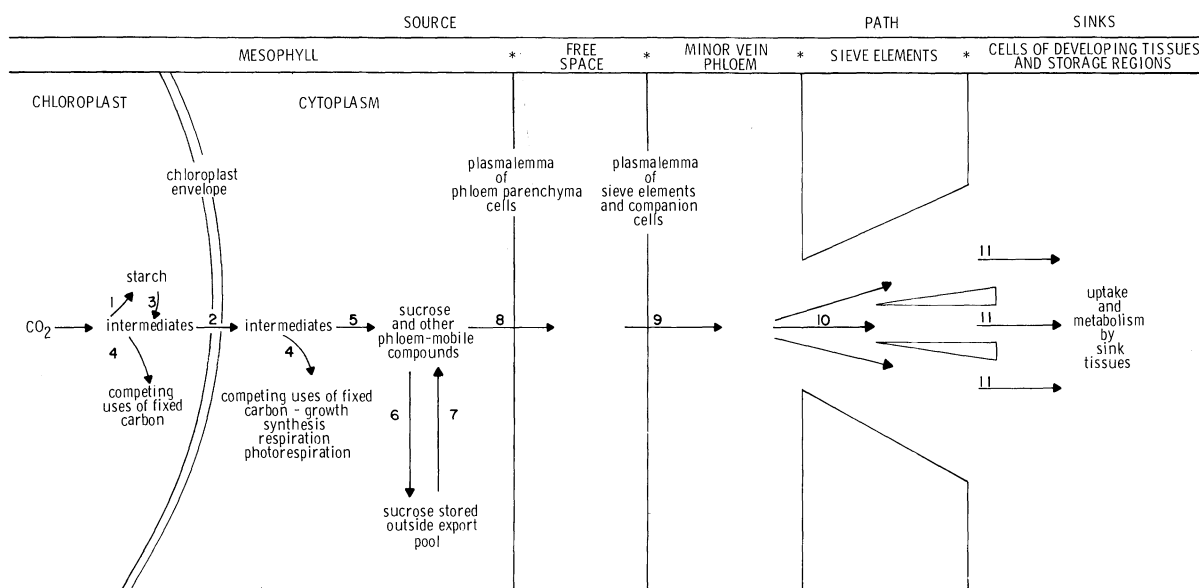


FIG. 1.—Possible control points for regulating the partitioning of assimilated carbon and the export of phloem-mobile compounds. Steps 1–9 are discussed in the text; step 10 is the control exerted by the structural features of the path of translocation; step 11 is the control exerted by transport out of the sieve tubes and conversion of transport molecules in sink regions.

portant for achieving the general system goal of maintaining carbon balance under various levels of nutritional status. Plants are able to adapt to a wide range of daylengths and variations in photon flux densities. Under these various conditions, steps 1 through 7 (fig. 1) provide balanced allocation of carbon within source leaves and between them and the sink regions. Leaves differ in the pattern of carbon metabolism during development and in the allocation of carbon for various pools and processes under different environmental conditions. It is necessary to maintain carbon balance in the midst of leaf-metabolism changes which occur in response to environmental conditions and developmental stages. In nature, success in meeting this goal of balanced carbon nutrition is gauged by competitive and adaptive ability leading to survival and dispersal. In agricultural practice, success in relation to this system goal is measured in terms of a favorable harvest index and yield under a range of conditions.

ADAPTIVE RESPONSES AND SET POINTS

Recent data enable us to identify several adaptive responses related to this system goal. For a source leaf with a given nutrient status and at a given developmental stage, export of recently fixed carbon is linearly related to the rate of net carbon exchange except at photon flux densities near the light compensation point (SERVAITES and GEIGER 1974; Ho 1976, 1978). Leaves with a higher carbon status export at a higher rate for a given net carbon exchange rate and also at a higher rate in the dark (Ho 1977). Plants accommodate to shorter photosynthetic periods by storing, during the day, a

larger proportion of the fixed carbon for export at night (BODSON et al. 1977; CHATTERTON and SILVIUS 1979). Under some conditions part of the stored assimilated carbon is exported during the subsequent light period (PEARSON 1974; Ho 1976; GORDON, RYLE, and POWELL, 1977). Changes in nutritional status or daylength cause changes in the proportion of fixed carbon which is exported, with adjustments occurring over 5–10 days.

While regulation of transport from a leaf is an important means of maintaining or restoring carbon balance for a mature leaf, the nature of set points and adaptive responses is far from clear. It appears that the level of starch at the end of a night period under a given set of conditions is relatively fixed (CHALLA 1976; CHATTERTON and SILVIUS 1979). It is not known whether the level of starch is regulated by a feedback mechanism or is the result of an adaptive feedforward mechanism activated by some environmental cue and related to energy demand during the dark period.

CONTROL MECHANISMS AND INFORMATION TRANSFER

A number of working hypotheses concerning mechanisms which control export in response to the carbon nutritional status of source leaves have been advanced. A key hypothesis—that sucrose concentration in the source leaf mesophyll controls export (Ho 1976)—is another way of stating that metabolic control of the availability of compounds for export is important in controlling export and in achieving the goal of carbon balance, both within source leaves and for the plant. During the light period, net carbon exchange rate and reserve carbon status are major

determinants of sucrose concentration and export rate (Ho 1978). At night, the level of starch, and perhaps other reserves, is the chief factor governing sucrose level and export (Ho 1978). Shortening of the photosynthetic period results in increased partition of fixed carbon into starch during the following day (CHATTERTON and SILVIUS 1979).

Little is known concerning the ways in which carbon status of a leaf controls allocation of fixed carbon among starch storage, growth, respiration, and sucrose storage outside the export pool. Nor is much known about mobilization of starch or stored sucrose in response to leaf carbon status. Regulation of the processes which control the availability of sucrose and other export compounds to leaf carbon status needs to be studied.

Leaf carbon metabolism during leaf development is also the subject of close control (TURGEON and WEBB 1975). Dramatic changes in carbon metabolism occur during leaf development and affect synthesis of sucrose and other compounds (GIAQUINTA 1978). It remains to be elucidated to what extent synthesis and metabolism of exportable compounds control export during leaf development.

Control of efflux of compounds available for phloem loading

SYSTEM GOALS

Control of efflux of compounds utilized in phloem loading appears to help provide the additional carbon required by sink regions under favorable inorganic nutrient status. Availability of adequate to abundant levels of potassium, nitrogen, and phosphorus in various proportions gives rise to various patterns of growth which are recognized in agronomic literature. Above-adequate levels of potassium increase the proportion of assimilated carbon exported to sinks, including fruits and tubers (HAEDER, MENGEL, and FORSTER 1973; MENGEL and VIRO 1974; MENGEL and HAEDER 1977 and literature cited therein).

Integral functioning of a plant necessitates a balance between the availability of inorganic nutrients to growing regions of a plant and the supply of organic nutrients required for growth to these sinks. Mechanisms exist which are oriented to providing adequate export of assimilate to meet the organic nutrient requirements set by a given level and balance of inorganic nutrients.

ADAPTIVE RESPONSES AND SET POINTS

Increased levels of free-space potassium promote export from sugar-beet source leaves (DOMAN and GEIGER 1979). Increased levels of potassium do not increase net carbon fixation but increase allocation of fixed carbon for export. At least for potassium, it appears that adequate to abundant levels promote export of a greater proportion of assimilated carbon to sink regions.

CONTROL MECHANISMS AND INFORMATION FLOW

The results of recent studies (DOMAN and GEIGER 1979) suggest a working hypothesis for regulation of export by potassium. Application of potassium ions to the free space of sugar beet source leaves promotes efflux of ^{14}C -labeled compounds from leaves photosynthesizing in $^{14}\text{CO}_2$ to approximately the same extent that it promotes translocation out of the leaves. The same levels of potassium do not increase the loading and export of ^{14}C -sucrose supplied to source leaves. Potassium increases phloem loading and export by increasing sucrose concentration in the free space. Similar effects for nutrient levels of inorganic phosphorus and nitrogen are suggested by the observation that deficiencies of phosphorus and nitrogen caused a decrease in the efflux into solutions of assimilated carbon from the mesophyll of beet leaves (KAMANINA and ANISIMOV 1977).

The potassium concentration in the source leaf free space likely provides information about the potassium status of the plant. In so doing, the potassium level may help set the rate of export by regulating the efflux of sucrose destined for phloem loading and export. It remains to be established if this mechanism is the basis for increased phloem loading and translocation brought about by an increase in potassium nutrition of plants under field conditions. The mechanism may be part of a feed-forward system of processes which readies the plant for increased growth in response to favorable inorganic nutrient status.

Direct control of the phloem loading process

SYSTEM GOALS

Both the rapid changes in sink demand, associated with changes in environmental conditions, and the gradual changes involved in progressive stages of development help restore or maintain carbon balance. Direct control of phloem loading seems to be instrumental in the response of export to changes in sink demand. Initiation of export from a maturing source leaf appears to occur when phloem loading develops a sufficiently high solute concentration in the minor vein phloem of the leaf (FELLOWS and GEIGER 1974). The increase in phloem loading appears to be part of a feedforward mechanism consisting of a series of events which anticipate the mature state of the leaf as a source of fixed carbon for the sink regions. Phloem loading also appears to adjust rapidly to changes in sink demand occasioned by shading or by loss of source leaves. In both the genetically programmed response and in a precipitous change, the plant appears adapted to restore and maintain sufficient carbon balance, in part, by changing the rate of phloem loading and export in the face of marked changes in sink demand.

ADAPTIVE RESPONSES AND SET POINTS

Studies of export under circumstances where relatively rapid changes in sink demand occur have led to several generalizations. A rapid change in sink demand initiated by removal or shading of leaves brings about a rapid compensatory change in export without changing the net carbon fixation rate over the short term, probably 1–2 days (GEIGER 1976; BORCHERS and SWANSON 1977). Export appears to change in a manner which restores and maintains balance in growth. For example, if the source leaf that serves as a major supplier of one-half of a developing sink leaf is darkened or excised, another source leaf that is the primary supplier for the other half of the developing sink leaf rapidly increases export (BORCHERS and SWANSON 1977). The rate of transport from the remaining source leaf maintains export to its original primary sink while increasing export to compensate completely for the loss of material from the other source leaf. This adjustment maintains balanced growth in both halves of the leaf while changing the partitioning of the products of photosynthesis in the source leaf.

Following a rapid change in sink demand, such as that produced by shading or source leaf excision, there is a gradual increase in net photosynthetic carbon fixation in the remaining source leaves over 5–10 days (THORNE and KOLLER 1974; literature cited in GEIGER 1976). Increases in ribulose biphosphate carboxylase or phosphoenolpyruvate carboxylase per unit leaf area support the suggestion that an increase in the photosynthetic apparatus is induced (WAREING, KHALIFA, and TREHARNE 1968; THORNE and KOLLER 1974).

With the systematic changes which are part of the ontogenetic development of a plant, both export and net photosynthetic carbon fixation increase concomitantly with the increased sink demand (FLINN 1974; literature cited in GEIGER 1976) or with source leaf maturation (FELLOWS and GEIGER 1974). Under these circumstances, it seems that adjustments are anticipated, as would be expected for a feedforward response (ROSEN 1975).

MECHANISMS AND INFORMATION FLOW

In ontogenetic development of a leaf, the advent of phloem loading is part of the series of events leading to attainment of source leaf status. The mechanism by which the phloem loading capacity characteristic of source leaves is acquired by the membranes of the minor vein phloem is not known. Possibilities include insertion into the membrane or activation of the sucrose transport system or possibly a modification of symplastic transport by closure of plasmodesmatal connections between minor vein phloem and the surrounding mesophyll. The mechanism for the initiation of phloem loading

and regulation of its onset needs to be investigated further.

The increase in phloem loading and export associated with heightened sink demand is more rapid, occurring soon after the onset of conditions which promote sink demand. A feedback control system responding to a set point is suggested by this type of response. Increased export from the remaining photosynthesizing source leaves, following source leaf removal or shading, is likely to reduce the sucrose concentration of the contents of the sieve tubes and companion cells of the minor veins in these leaves. A decrease in hydrostatic pressure in the sieve elements of the minor veins would accompany the decrease in their sucrose content from the steady-state level associated with the former rate of export. It seems a tenable hypothesis that the sieve tubes respond to the decrease in solute concentration or turgor by a compensatory increase in phloem loading. MILBURN (1974) proposed that a sink induces pressure flow by regulating pressure in the sieve tubes and that solutes are mobilized and loaded rapidly in response to exudation from stem incisions. Information of increased efflux of solutes from a source leaf into sinks would be transmitted to its minor veins by the decreased turgor in the sieve tubes.

Several pieces of evidence support the occurrence of this proposed response of increased loading. The distribution of solute in various cells of sugar beet source leaves (GEIGER et al. 1973), carried out by plasmolysis of tissue followed by electron microscopy gave values for water potential of the minor vein sieve tube contents in excess of those associated with a 1-M solute concentration. Other methods reveal solute concentrations less than half this value for sieve tubes of herbaceous plants (GEIGER, SAUNDERS, and CATALDO 1969; FISHER 1978). Various possible sources of error can be dismissed for the most part, leaving us with the likelihood that the minor veins had loaded sucrose from the mesophyll in a compensatory response to the turgor reduction caused by immersion of the leaf in the mannitol osmoticum.

Somewhat more direct evidence of compensatory phloem loading comes from a series of experiments by GEIGER et al. (1974). Application of 0.8 M mannitol to a leaf exporting carbon derived from 20 mM ^{14}C -sucrose which was supplied to the abraded surface of a source leaf caused a temporary decrease in export. By the end of 30–60 min, export increased to the pretreatment rate. The ability of the leaf to maintain a high rate of export of sucrose from a leaf, the free space of which was in contact with 0.8 M mannitol, supports the existence of a mechanism by which the source leaf is able to adjust phloem loading compensatorily. The decreased osmotic potential of the free-space solution appears to have withdrawn

water and reduced the pressure inside the sieve tube-companion cell complex, thereby initiating increased loading of the minor vein phloem and restoring export.

Responses to solute concentration or turgor permit phloem loading to respond to increased sink demand, with information about the level of demand mediated through sieve tube turgor or solute concentration changes. According to this model, the set point value for sieve tube turgor pressure or solute concentration largely determines the actual source strength, with the maximum potential for phloem loading rate determining potential source capacity. Presumably it is the turgor or solute concentration set point or the capacity for active transport, or both, which increases during the maturation of leaves and development of their source status. Experiments are needed to verify these postulated mechanisms and means of information transfer.

Control of export and responses of source leaf metabolism

Mechanisms which regulate export by controlling the availability of sucrose for phloem loading (fig. 2, 1-7) presumably are integrated into the whole of source leaf metabolism. These control processes deal with the partitioning and allocation of the products

of photosynthesis in the source leaf and relate in a special way to the system goal of maintenance of carbon balance in the mature leaves of the plant. Processes in this category respond to leaf carbon status and specifically to factors such as starch level, photoperiod, and net carbon fixation rate.

On the other hand, mechanisms which control phloem loading more directly (fig. 2, 8 and 9) are dependent for their effectiveness upon the ability of source leaf metabolism to respond to the demand for substances to be exported. The results of experiments described in the preceding section show that source leaf metabolism is able to adjust rapidly to meet the demand for increased sucrose synthesis. Furthermore, these adjustments are made without increased net carbon fixation, at least over the short term.

A phosphate/triose-phosphate exchange shuttle in the chloroplast envelope (HELDT et al. 1977) appears to be the key to increased sucrose synthesis in response to the demand created by increased phloem loading. Stoichiometric relationships among synthetic reactions involving CO_2 , triose phosphate, sucrose, and starch (WALKER and HEROLD 1977) appear to provide the basis for responsiveness of source leaf metabolism to a demand for sucrose for export. Particularly important is the balanced stoi-

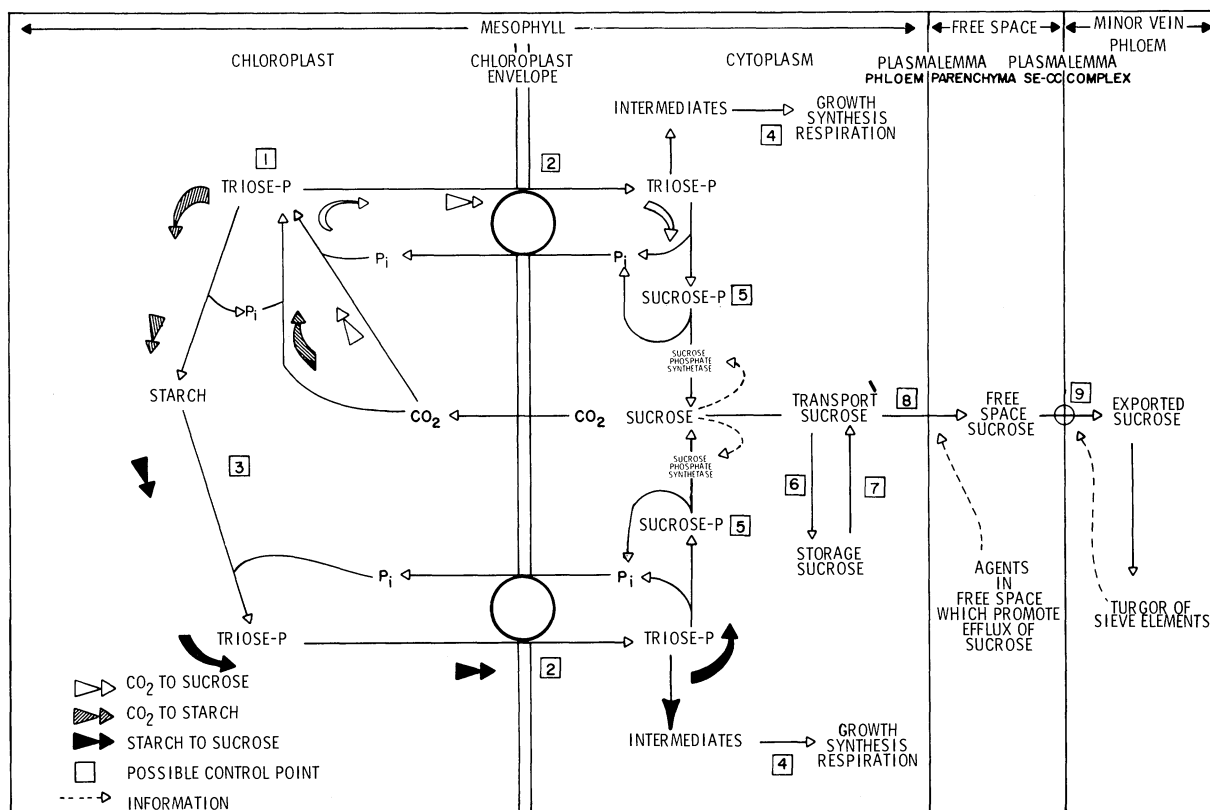


FIG. 2.—Detail of a model for control of partitioning of assimilated carbon and export showing proposed mechanisms for the regulation of phloem loading (steps 8, 9) as well as those involved in supplying sucrose in response to increased phloem loading (steps 5-7).

chiometry between the supply of inorganic phosphate required for the exit of triose phosphate and the release of inorganic phosphate during synthesis of sucrose from triose phosphate. Joined with the feedback inhibition of sucrose phosphate synthetase by sucrose, this balanced stoichiometry permits leaf metabolism to provide sucrose at a rate called for by processes which regulate phloem loading.

Summary

Two major groups of processes regulate export. One group controls the availability of sucrose for export in keeping with the ontogenetic stage of the leaf and in response to factors such as leaf carbon status and net photosynthesis rate. The system goals of carbon balance within the source leaf and between the source leaf and the rest of the plant are served by these regulatory processes.

A second set of processes regulates phloem loading more directly, controlling either the efflux of sucrose destined for loading or the active transport step of phloem loading. These control mechanisms are more responsive to conditions outside the source leaf, such as the inorganic nutrient status and sink demand, and serve system goals related to overall plant carbon balance and allometric growth. A mark of this set of controls is its dependence on responsiveness of source leaf metabolism to supply what is needed for synthesis of sucrose for phloem loading. Certain substances in the free space may promote efflux of sucrose for subsequent loading and export. The transport of sucrose during phloem loading may

respond to the set point of sieve tube turgor or solute concentration, with efflux being promoted by the steepened sucrose gradient. The level of the set point and the rate at which phloem loading can occur constitute the controls for source capacity. Increase in sink demand, which lowers the solute content of the sieve tubes from one or more source leaves, lowers solute concentration and turgor in the sieve tube-companion cell complex of the minor veins and brings about a compensatory increase in loading in the affected source leaf. Both increased efflux of sucrose and increased loading cause increased turnover of cytoplasmic sucrose. As a consequence, the rate at which inorganic phosphate is generated during sucrose synthesis increases, promoting exit of triose phosphate from the chloroplast and, in some cases, the mobilization of starch to triose phosphate.

Clearly these suggestions are based on both a considerable amount of speculation along with considerable data and analysis. More experiments are needed to test the hypotheses advanced. It seems likely that the analyses based on the concept of the plant as a well-integrated, responsive system will be productive.

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