# THE DEPENDENCE OF PHOTOSYNTHESIS ON CARBOHYDRATE SINKS: CURRENT CONCEPTS.

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The process of photosynthesis that leads to reserves accumulating in plants depends primarily on external conditions, especially radiation and temperature, but there is much evidence that internal factors may limit productivity. Thus, fixation of $CO_2$ may become restricted when products of photosynthesis accumulate in leaves because plants lack suitable sinks into which carbohydrate can be diverted and translocation is slowed down. The object of this paper is to consider both our present state of knowledge of this subject and also some of the conditions affecting sink size.

It is by no means a new idea that products of assimilation may limit photosynthesis — it was demonstrated in the latter half of the last century when plant physiology was emerging as a separate subject. Even before Ewart's experiments in 1895 (Ewart 1895) several relevant observations were recorded in the literature. Ewart observed that when mature leaves of *Vitis* were enclosed in an atmosphere of 10% $CO_2$, assimilation ceased after 4 days but was restored after a period of darkness when carbohydrates were used up. Thung (1928) and Barton-Wright and McBean (1932) found potato leaves infected with leaf roll virus photosynthesised less than healthy leaves, presumably because products of photosynthesis accumulated in infected leaves. Kursanov (1933) found that detached leaves of Medlar kept in the dark for 4 days and then illuminated assimilated more than leaves illuminated daily. Leaves with their petioles in glucose solution assimilated less than leaves with their petioles in water. Ringed *Pinus* plants assimilated less than unringed plants. He concluded that accumulation of carbohydrate was probably the chief but not necessarily the sole reason for assimilation being decreased. During the last 20 years many lines of work have suggested a causal relation between accumulation of assimilates and lessening of assimilation, and Muller (1960) reviewed some aspects.

## *Evidence from detached leaves*

Goodall (1945) found that detached tomato leaves assimilated slower than attached leaves and the difference was greater in the afternoon than in the morning. Similarly, Barau (1960) found that photosynthesis slowed in detached leaves of tea and sunflower as the products accumulated, as also did Hall and others (1966) with blueberry leaf disks. Other instances are given by Livingston and Franck (1940).

## *Evidence from removal of plants parts*

More assimilate is likely to accumulate in detached leaves than in leaves attached to plants but there is much evidence that they can also accumulate in the leaves of intact plants that lack adequate sinks for carbohydrate, such as rapid vegetative growth, fruits or storage organs. Nosov (1959) observed that removing cotton bolls halved photosynthetic activity of the leaves in 24 hours. Kiesselbach (1948) similarly found removing maize flowers decreased fodder yield by 27%.

Moss (1962) also examined the effect of barrenness in maize on net assimilation of $CO_2$ ; bagging immature flowers slowed $CO_2$ assimilation and increased sugar content of the tissue. From flowering to harvest dry matter increased only about half as rapidly in barren plants as in plants with normal ears. Moss also found that removing tomato fruits diminished daily assimilation to only 12% of the initial rate. Kheiralla and Whittington (1962) observed that net assimilation rate increased in tomato plants towards the end of their growth period, an effect that might be associated with demands of rapidly developing fruits. Zakhar'yants and Ionesova (1964) infiltrated leaves of cotton and maize with sugar solutions — in both species photosynthesis decreased about 80% soon after treatments but partially recovered later. Vernalisation of *Lolium* seemed not to influence growth in the vegetative stage but speeded growth in the reproductive phase, probably because reproductive tillers grow faster than vegetative tillers because intercalory meristematic tissue functions as a sink for assimilates (Silsbury, (1965). Hartt—K (1962, 1963) concluded that accumulation of sucrose during photosynthesis of sugar-cane leaves inhibited photosynthesis and that a fast rate of photosynthesis required efficient translocation. $^{14}C$ photosynthate moves through detached sugar-cane blades as fast as in entire plants at first but slowed with time when sucrose accumulated at the base. Translocation was increased by supplying a sink as a leaf attached to a 4-joint cutting of stem or by darkening the base of the blade below the fed part. Hartt (1965) showed that when roots are cold $^{32}P$ moved upward in the xylem and the downward movement both of organic compounds of $^{32}P$ and photosynthate was slowed down. Ruck and Bolas (1956) found that the vigorous apple stock Crab C has a greater mean net assimilation rate than Malling IX irrespective of nitrogen supply. Maggs (1958) suggested the increase in net assimilation rate as apple root stock grew larger was because the sites for deposition of synthesised material were relatively larger. Two root stock varieties, Malling XVI and Malling II, showed a different dry weight increase in spite of similarity of leaf development. The dry weight increment distributed in the large root system of Malling XVI resulted in a relatively greater cambial surface than when deposited as thickening in the stem (Malling II). Maggs thought that the more extensive cambial surface provides a larger sink, which makes the foliage above it more efficient. He (Maggs 1963) found that 2-year-old apple trees with flowers or fruits removed produced less total dry matter per unit area of leaf than trees with flowers and fruits. Chandler and Heinicke (1925, 1934) also had evidence that presence of a fruit crop increases leaf productivity.

If leaves sometimes function below their full photosynthetic efficiency, removal of a part of them should make the remainder more efficient. Kiesselbach (1948) found removing half of each leaf of maize at time of silking curtailed further increment of dry matter by only 22% of normal. The efficiency of dry matter elaboration by the remaining half leaves was increased by 56% per unit of leaf area. Allison and Watson (1966) also found that, when laminae were removed from maize, less dry matter remained in the stem and the photosynthetic efficiency of the remaining leaves was apparently increased. They suggest that differences in grain yield of maize, for example between varieties, may therefore depend on differences in the capacity of the grain to store dry matter as well as on the size and efficiency of the photosynthetic system. In other words, sink capacity of grains may be an important factor in deciding yield. Maggs (1965) also showed that removing some apple leaves increased the rate dry matter was produced by the remaining leaves. Similarly, Humphries and Dyson (1965) found that removing some potato leaflets or axillary shoots increased the efficiency of remaining leaves. May (1960) suggested that slow translocation in some grasses limited photosynthesis because assimilates accumulated. Preventing photosynthesis for a while at mid-day increased yields by up to 50%, by allowing excess carbohydrate to be removed (Went, 1958). Stern (1965) points out that radiation does not appear to be the primary limiting factor determining cotton yield and emphasises the importance of suitable carbohydrate sinks.

*Evidence from manipulation of sink size*

Experiments in which size of sink is changed also support the idea that sink capacity and photosynthesis are positively correlated. Burt (1964) found that removing potato tubers 21 days after they formed slowed the net assimilation rate and he suggested assimilation by the leaves in bright light may be restricted by their ability to use or store products of photosynthesis. Burt (1966) further showed that, when tubers developed slowly in the cold, net assimilation rate was less than when tubers developed faster. He concluded that environmental factors may regulate sink strength and plant growth by controlling either the initiation or development of carbohydrate sinks (or both); conditions that favour sink initiation (few nutrients and cold tubers) may differ from those that favour use of carbohydrate by sinks (abundant nutrients and warmth). Nosberger and Humphries (1965) confirmed that removing tubers depressed net assimilation rate of potato plants and increased the carbohydrate content of stems and leaves. Assimilation was depressed still more when lack of nitrogen limited growth. Plants with abundant nitrogen developed secondary sinks, such as second order lateral branches and aerial tubers, so removing the primary sinks—the tubers—had less effect on net assilimation than in plants deficient in N.

Mush (1961) showed that the attachment of the mother tuber depressed photosynthesis; which he attributed to it supplying carbohydrate to the leaves. Bremner and El Saeed (1963) suggested that the smaller food reserves in small potato seed tubers are to some extent compensated by these reserves affecting photosynthesis less than that in larger seed tubers, and may explain the greater efficiency of small seed. Burt (1965) found that spraying potato plants with urea increased the net assimilation rate, which may reflect the greater 'sink' strength of the tubers rather than the direct effect of nitrogen on photosynthesis and translocation. Tsuno and Fujise (1965), who inhibited tuber growth in sweet potato by exposing the tubers to light, found the treated plants photosynthesised less and had more starch in their leaves but they detected no change in the diurnal course of photosynthesis and concluded that the rate of movement from the leaf, and not accumulation of carbohydrates, controls rate of photosynthesis. Wilson (1966) points out that arctic plants have small net assimilation rates probably because sugars accumulate in amounts that depress assimilation. Cold slows respiration and new plant growth more than it slows rates at which assimilates are produced. Thus, the $Q_{10}$ for respiration is of the order of 3 but for net assimilation is about 1.2. Arctic plants also tend to accumulate sugars because they are usually deficient in N.

Substituting a more efficient sink for a less efficient one can also increase net assimilation. Thus, when Thorne and Evans (1964) grafted tops of spinach beet plants, which have poorly developed tap roots, on to roots of sugar beet, the spinach beet leaves assimilated more presumably because the sink was greater. Sweet and Wareing (1966) also found manipulating the sink in *Pinus radiata* seedlings by removing the plant apex below expanding leaves influenced net assimilation; after 8 or 16 days net photosynthesis had decreased, more in bright than in dim light. However, this could have happened because the sink for assimilates was smaller or because the decapitated plants contained less auxin. The possibility that auxin may affect rate of photosynthesis will be discussed later.

Restricting root growth in cotton (Taylor and et al 1963) and in sugar beet (Wheeler, 1966 pers. comm.) affected growth and yield, but whether because leaf efficiency was impaired by diminishing sink size, or for other causes, is not certain. Humphries (1963a) varied the rate of root growth of detached rooted leaves of *Phaseolus* either by use of growth substances or by varying the temperature around the roots. These rooted leaves do not produce buds and the roots are the main sink for carbohydrates produced in the lamina. Net assimilation was contolled by the rate carbohydrate moved from source to sink, which in turn depended on the growth of the root system. Experiments with rooted leaves of two species of *Phaseolus* (Humphries, 1967) showed that one species rooted more freely than the other in the cold and then assimilated faster than the species that rooted less well. At warmer temperatures, the root growth and net assimilation rates were similar in both species. CCC lessened assimilation in *Sinapis alba* (Humphries, 1963b) either because it directly inhibited photosynthesis or because the dwarfed stem of treated plants provided only a small sink for photosynthates. By contrast in sugar beet CCC did not affect net assimilation possibly because the roots provide a large sink (Humphries and French, 1965). In potato, CCC increased leaf efficiency (Dyson and Humphries, 1966) possibly because treated plants tubered earlier. In total the evidence suggests that CCC does not act directly on assimilation but indirectly by altering sink size.

When all the assimilate which would normally accumulate in a sink can be accomodated in stems, e.g. Nosberger and Thorne, (1965); Allison and Watson (1966), assimilation rate is not altered.

Brougham (1961) suggested that plants with large storage organs have an evolutionary advantage. In the same way, production of bulbils which occurs in isolated genera of several plant families, may be an important means of isolating surplus carbohydrate (Burkhill, 1960).

### *Effect of environment on sink development*

Mineral nutrition greatly affects sink size. Thus, Watson and Russell (1943a, 1943b) and Woodman and Paver (1944) showed that nitrogen increased the ratio of roots to tops in mangolds and turnips, which Aaney (1952) suggests is because the meristem activity of the leaf primordia is less affected by nitrogen than the cambial activity of the roots. Potassium increases tuber yield of sweet potatoes without any corresponding effect on the growth of tops, and Tsuno and Fujise (1965) suggest potassium acts by accelerating translocation of carbohydrate from leaves. Austin (1962) found lack of nitrogen increased amount of sugar in red-beet leaves possibly because it limited assimilation by slowing translocation of sugars from the leaves.

Other environmental factors are important in determining growth of sinks especially in plants like *Solanum demissum, Dahlia* and *Helianthus tuberosus* where exposure to short days is necessary for storage organs to form. It would be instructive to compare the net assimilation rates of such plants under long and short days. Differences in assimilation rate in different photoperiods were noted by Bode (1942): short-days increased it in *Kalenchoe,* which may indicate a diurnal decline in which assimilatory efficiency is large at the beginning of the light period but less when assimilates accumulate. Diurnal variations in dry weight accumulation have been noted by other authors (e.g. Goodall, 1945). Went and Engelsberg (1946) suggested that photosynthesis stops when sucrose reaches a concentration of 20% of the fresh weight.

During periods of stress, e.g. drought, plants grow slowly but when the stress is removed, they often grow and assimilate faster than unstressed plants. The increase in net assimilation when plants are watered after drought, as Owen and Watson (1956) and Orchard (1963) found with sugar beet, could result from increased demand for assimilates by meristems previously retarded by water stress. If this explanation is right it would be necessary to demonstrate accumulation of carbohydrate in the leaves during drought, and Kemper et al (1961) specifically attribute the increased growth rate after relieving soil-moisture stress to accmulation of carbohydrate during the drought.

### *Evidence for sink effects in normal plants*

The evidence for a relationship between sink size, which is often equated to growth of a plant organ and assimilation rate is readily demonstrated when the plant is in some way manipulated or parts amputated, but it is more difficult to show that sink phenomena act as important internal factors controlling photosynthesis in intact plants. Most plants possess a ready means of using excess carbohydrate, namely, by increasing growth of the root system. There is now abundant evidence that the growth of the root system does not necessarily exactly parallel, day to day, the growth of the shoot. It has already been pointed out that the roots of detached leaves provide an adequate sink for carbohydrate produced by the leaves provided conditions favour root growth. The root system of an intact plant can probably accept all carbohydrate the shoot can supply. The root system is an efficient carbohydrate sink because it is potentially of unlimited growth and has many meristems, whereas shoot meristems are limited in number and their production possibly under internal control (Fulford, 1965; Humphries, 1966). Thus, the morphological nature of the root makes it an efficient carbohydrate sink and it can function as a safety valve for surplus carbohydrate from the shoot.

There is considerable evidence that root growth is directly affected by assimilatory conditions. For example, Muenscher (1922), Shirley (1929) and Reid (1929a) all showed that bright light increases root growth proportionally more than shoot growth in cereals and herbaceous plants. Also, the proportion of shoots to roots differs in different seasons, and long days preferentially encourage roots. Wassink (1957) showed there was a close relation between light intensity and root growth which is decreased by shading (Blackman and Templeman, 1940). Removing buds from cotton increased the root system as a percentage of the whole plant from 15 to 30 (Eaton, 1931) and a greater percentage of labelled photosynthate entered the root system of soybean (Nelson and Gorham, 1959) and sweet potato (Sekioka, 1962) in bright light than in dim light. Starck (1963, 1964) concluded that roots affect translocation from shoots because they are important sinks of assimilates. Translocation of $^{14}$C assimilates in pine seedlings with well-developed roots exceeded many times that in plants with a poorly developed root system (Nelson, 1962). Davis and Lingle (1961) suggested that cold diminishes the effectiveness of tomato roots as a sink for phloem-transported material. When photosynthesis is increased by increasing atmospheric-$CO_2$ concentration, root growth increases relatively more than shoots (Reid, 1929b), and White (1937, 1938) concluded that increased net assimilation rate from any cause produced *Lemna* colonies with longer roots.

It seems a general principle for roots to respond more readily than shoots to a supply of carbohydrate. Perhaps variation in root growth rate is usually adequate to deal with fluctuations in carbohydrate supply from the leaves caused by the changing environment without carbohydrate accumulating in the shoot and affecting the rate of photosynthesis. But there is evidence that the root system is not always an adequate sink for surplus carbohydrate; for instance, the fibrous root system of plants with underground storage stems or roots seems unable to grow enough to use all the carbohydrate the shoot can produce. Thus, removing tubers from potato plants, as already mentioned, depresses assimilation (Burt ; Nosberger and Humphries, loc. cit.). Also, preventing grain developing on corn plants increased root weight by only 7% (Kiesselbach, 1948) which did not make them an adequate substitute for the ear as a storage organ. The amount of carbohydrate diverted to the root system will perhaps depend on the distance it has to travel. Thrower (1962) showed that in general the amount of assimilate exported from an expanded leaf to the apex and root is inversely proportional to the distance from those sinks. Fibrous root growth slows or stops when flowering and fruiting begins and the root loses its function as a carbohydrate sink. This may be because of competition for carbohydrates or because, as Resende (1947) and Selim (1956) suggest, auxin is used in the growth of the inflorescence.

When usual storage of carbohydrate is denied to the plant, by removing storage organs or meristems, carbohydrate accumulates in cells of the stems, leaves and fibrous roots, and this seems to be a pre-requisite for the depression of photosynthesis. Sometimes, however, the plant can isolate carbohydrate by modifying its growth. Thus, detached potato leaves without roots on their petioles produce swellings at the bases of the leaflets where the cells are filled with starch (Humphries, unpublished). Rooted bean leaves use carbohydrate in extension growth of palisade cells (Humphries, 1967 loc. cit.). Dickerson and Edelman (1966) observed that, when tuber initials are removed from plants of *Helianthus tuberosum* grown in short days, the fibrous roots produce tuber-like swellings filled with fructosans.

Little is known about the way in which accumulation of carbohydrate slows down photosynthesis. Possibly more than one mechanism exists. The simplest would be by stomatal control, with stomata closing when sugar contents increase above a certain value. Lee (1965) reported that large amounts of sugar in tobacco leaves closed the stomata, but in most plants slowing of photosynthesis when sinks are lacking seems unrelated to stomatal closing. Wilson (loc. cit.) suggested three ways in which accumulated assimilates depress assimilation. (1) a mass action effect; (2) enzymatic control by the phenomenon of regression or "end product inhibition"; (3) physical obstruction of diffusion or light transmission by accumulation of assimilates in cytoplasm or chloroplast.

The mechanism by which sinks such as growing points, storage organs or fruits accumulate substances is still unknown—it is not definite whether storage organs are passive acceptors of carbohydrate or whether these organs actively pull substances towards them. Watson and Petrie (1940) interpreted the mobilising role of the apex and flowers as a sink into which nutrients flow, but evidence is increasing that the processes of accumulation is under hormonal control. Various authors have demonstrated that applying growth substances to plant organs initiate mobilisation: thus, Marre and Murneek (1953) found very similar accumulation of carbohydrate both in kind and amount in tomato ovaries whether these were fertilised with pollen or treated with auxin. They concluded that auxin acted by mobilising reserves from other regions of the plant. Similarly, Davies and Wareing (1965) showed that, when IAA was applied to decapitated shoots of *Pisum* or disbudded shoots of *Populus*, $^{32}P$ moved towards the treated region. Accumulation of $^{32}P$ by the decapitated second internode of *Phaseolus vulgaris* was stimulated by applying IAA and further increased by kinetin or gibberellic acid (Seth and Wareing, 1964). The strongest hormonal mobilisers are the kinins (e.g. Engelbrecht and Mothes, 1961; Mothes, Engelbreche and Schutte, 1961) and it is probably significant that all fruits so far examined contain kinins (see Crane, 1964), which are not necessarily concerned only with cell division. However, no direct relationship between the ability of fruits to accumulate substances and the content of kinins has yet been demonstrated but a further resemblance between natural accumulation and kinin-induced accumulation is that they are both unselective: for instance, -$\alpha$-aminobutyric acid travels to the kinin-treated region of a leaf but is not used. Phosphate, sulphate and glucose also accumulate in such leaves (Englebreche, 1961). Similarly, miscellaneous substances accumulate in fruits and seeds which have no apparent metabolic function. The phenomenon noticed by Turner and Bidwell (1965) that fluctuations in photosynthesis of a leaf seemed to be correlated with appearance of buds may be connected with hormone-controlled translocation. They also found spraying leaves with IAA increased rate of photosynthesis after 30 minutes; the effect did not reflect stomatol response. When IAA was sprayed on to a bean leaflet, $CO_2$ assimilation in neighbouring leaflets increased. (Bidwell and Turner, 1966). Coulombe and Paquin (1959) obtained a similar response with gibberellic acid.

Knowledge of how storage organs mobilise reserves is of obvious practical importance, because by influencing the amount of substance flowing to a sink, it might be possible to increase photosynthetic efficiency. Varietal differences might be related to the endogenous hormone content of the sink organ.

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