THE CONTROL AND PATTERN OF MOVEMENT OF CARBOHYDRATES IN PLANTS

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INTRODUCTION

Over the last twelve years, studies on the movement and distribution of organic materials in plants have received considerable impetus from the development and availability of radioactive tracers, particularly the long-lived radioisotope of carbon (C^{14}), which can be used as a marker for carbon assimilated during photosynthesis by the leaves. A consistent pattern of carbohydrate movement, based on these tracer studies, is now emerging, which clarifies and extends deductions made from growth analyses. This information is important in our understanding of how climate and many agricultural practices control growth, and how we might select or manage plants more effectively to obtain maximum yields.

This review is an attempt to integrate the rapidly expanding literature on the movement of assimilates labeled with radioactive tracers, and to assess the relative importance of leaf function and position, vascular connections, and organ development or sink size in controlling the distribution of carbohydrates in plants. With this background, the movement of labeled assimilates under various environmental conditions has been examined to assess the roles of photosynthesis, translocation, and growth in the response of plants to changes in the environment.

There is a considerable volume of work relating to the movement of herbicides (c.f. reviews by Mitchell, Schneider, & Gauch 1960, Mitchell & Linder 1963, Crafts 1964, 1966) and also on the distribution of carbohydrates from leaves, as deduced from patterns of growth and changes in dry weight associated with organ removal or shading (c.f. reviews by Brouwer 1962, Leonard 1962, Van Dobben 1962, Evans, Wardlaw, & Williams 1964). It has been necessary, however, to limit the discussion of these data except where particularly relevant to studies with labeled assimilates.

CONTROL OF CARBOHYDRATE MOVEMENT FROM THE LEAF

Following the build-up of assimilates in the photosynthetic tissue of a leaf, there is a preferential movement of some substances into the conducting phloem tissue (Kursanov, Brovchenko, & Pariskaya 1959). Sugars, generally sucrose, but in some plants stachyose or other carbohydrates, generally constitute the bulk of organic material moving in the phloem, although a considerable range of nitrogenous compounds and even steroids are known to be translocated (Mittler 1953, 1958, Zimmermann 1958, Nelson *et al.* 1961, Webb & Burley 1962, 1964, Clauss, Mortimer, & Gorham 1964, Biddulph & Cory 1965, Trip, Nelson, & Krotkov 1965). Not only are assimilates selectively moved into the conducting tissue, but this occurs against a concentration gradient (Phillis & Mason 1933, Roeckl 1949, Kursanov, Brovchenko, & Pariskaya 1959, Brovchenko 1965, Bieleski 1966), and energy is required for the transfer of assimilates from the photosynthetic to the conducting tissue (Ziegler 1956, Kursanov & Brovchenko 1961, Ullrich 1962). One explanation for the observation that a reduction in light intensity reduces not only the photosynthetic rate but also the proportion of assimilates moved from leaves (Grodzinskii 1959, Shen 1960, Chen 1963, Geiger 1963, Hartt, Kortschak, & Burr 1964, McWilliam & Wardlaw 1965, Hartt & Kortschak 1967), may be related to an alteration in the products of photosynthesis as demonstrated by Burma and Mortimer (1957), but part of the effect may be related to a drop in energy available for the transfer of sugars within the leaf under low light conditions. On the other hand, limiting the rate of photosynthesis (by reducing the concentration of CO_2) has been shown to increase the transfer of assimilates into the conducting tissue (Shiroya *et al.* 1962, Nelson 1963). Although this effect may be related to a failure to divert carbon into storage products with low rates of CO_2-fixation, as suggested by the authors, there is also the possibility that because less energy is required for CO_2-fixation more energy is available for transfer.

With a series of microautoradiographs of cereal leaves at various times after $C^{14}O_2$ assimilation, Pristupa (1964) has demonstrated the movement of assimilates from the photosynthetic tissue into the conducting vessels of small vascular bundles and, within three hours, into the phloem of large bundles. The rate of movement of assimilates out of a fully expanded leaf, however, is not fixed. In tobacco 46 per cent of the carbon assimilated at any one time may have left the leaf in three hours (Claus, Mortimer, & Gorham 1964), and 68 per cent in 96 hours (Jones, Martin, & Porter 1959), a pattern not far removed from that observed by Yamamoto (1967), but Porter and Bird (1962) found a much slower initial loss of assimilates from a tobacco leaf that had been kept in darkness for 48 hours prior to the assimilation of $C^{14}O_2$. Joy (1964) found that about 50 per cent of assimilated carbon was lost from the leaf of sugar beet in 24 hours and about 70 per cent in three days, whereas Mortimer (1965) showed that up to 60 per cent of the assimilated carbon could be exported after only four hours. During grain development in wheat the movement of labeled carbon assimilated by the flag leaf may be almost complete in 24 hours (Shen & Shen 1962, Carr & Wardlaw 1965), or it may take several days (Lupton 1966). In tomato, Khan and Sagar (1966) found that only 20 per cent of the carbon was exported from a leaf 24 hours after assimilation, whereas the work of Balatinecz, Forward, and Bidwell (1966) indicated that less than 30 per cent of the assimilates moved out of a pine seedling branch in three days, although presumably in the latter instance there was actively growing tissue within the branch itself.

The general pattern that emerges is an initial rapid transfer of labeled assimilates out of a leaf, followed by a continuing slower export (Clauss, Mortimer, & Gorham 1964, Porter 1966). Although there is considerable variation in the movement of assimilates out of a fully grown leaf, it is not always clear from the published data as to the cause of this variation. It is dependent not only on factors within the leaf, but also on the ability of other parts of the plant to utilize available assimilates (c.f. Humphries 1963, Hansen 1967, King, Wardlaw, & Evans 1967). Where leaf area is large relative to the growth requirements for carbohydrate the demand for assimilates per unit leaf area will be small. In *Lolium temulentum* L., removal of the upper part of a leaf, thus reducing leaf area relative to growth, stimulated the movement of assimilates from the remaining basal area (Evans & Wardlaw 1966). In sugarcane, however, the opposite effect was obtained, removal of the upper part of the leaf reducing the flow of assimilates from the remainder (Hartt, Kortschak, & Burr 1964). An added complication is the ability of a leaf to temporarily store excess carbohydrate as sugars (Mortimer 1965) or starch (Porter 1966), and thus to modify the pattern of carbohydrate movement from the leaf.

Very young leaves obtain carbohydrates required for their growth from older leaves, and it is not until a leaf has reached between one-third and one-half of its final area that the carbohydrates produced through its own photosynthesis are adequate for its growth requirements and the export of assimilates commences (Thrower 1962, Hoshino, Mishimura, & Okubo 1964, Webb & Gorham 1964, Forde 1965, Evans & Wardlaw 1966). It was suggested by Mokronosov and Bubenshchikova (1961) that the movement of assimilates into the conducting vessels is greater in young than in old fully expanded leaves, and several times leaves have been shown to be most active in exporting assimilates soon after reaching their maximum size, the rate of export subsequently declining with leaf age (Fujiwara & Suzuki 1957, Clauss *et al.* 1959, Shiroya *et al.* 1961, Wanner & Bachofen 1961, Oozeki & Shiozawa 1965).

Diseases, such as rust, affect leaf metabolism and can reduce the rates of both photosynthesis and assimilate export (Grodzinskii 1959, Doodson, Manners, & Myers 1965). It is clear that the outflow of assimilates from a leaf is dependent on factors within the leaf itself, as well as on growth activity and assimilation in other parts of the plant.

LEAF POSITION AND ASSIMILATE DISTRIBUTION

There is a pattern of assimilate distribution that applies to most plants. The lower leaves act as the main source of assimilates for roots whereas the upper leaves perform this function for the shoot apex, and leaves in an intermediate position may supply assimilates in either or both directions. This pattern has been well substantiated for soybean by Belikov (1955, 1957, 1958) and Belikov and Kostetsky (1958), and for cotton by Tuichibayev and Kruzhilin (1965b), as well as for tomato by Bonnemain (1965, 1966). It also applies to grasses and cereals, even though successive leaves may be separated by extremely short unexpanded stem internodes in the vegetative phase (Tanaka 1958, Evans & Wardlaw 1964, Williams 1964). When considering the direction of movement of assimilates from a leaf it should be remembered that a plant is not a static organism and the position of a leaf relative to the shoot apex is continually changing throughout development. Thus the typical pattern of distribution has been shown throughout development for grape (Hale & Weaver 1962), cotton (Tuichibayev & Kruzhilin 1965a), wheat (Doodson, Manners, & Myers 1964), and the perennial grass, timothy (Williams 1964), in that initially a young leaf exports assimilates to the adjacent shoot apex, but with time, as more leaves separate it from the apex, an increasingly greater proportion of these assimilates move to the roots. Defoliation experiments, with soybean (Thaine, Ovenden, & Turner 1959, Thrower 1962, Belikov & Pirsky 1966) and with *Perilla* (Chailakhyan & Butenko 1957), indicate that the pattern of movement from any one leaf is dependent not only on the proximity of the leaf to the growing regions, but also on the supply of assimilates from other leaves on the shoot. One exception to this general pattern is the observation by Khan and Sagar (1966) that, in tomato plants, C^{14} assimilated by the lower leaves moves up, and C^{14} assimilated by the upper leaves goes down the stem. The upward movement from the lower leaves could possibly be related to redistribution of assimilates that have first moved down to the root system and subsequently back into the shoot through the xylem (c.f. Kursanov 1958, Winter & Mortimer 1967). Also, Bonnemain (1965), as will be discussed later, has demonstrated that the vascular traces from a tomato leaf unite with other traces only in the stem at the node below the point of insertion of the leaf, and that assimilates follow the vascular pathway down through one internode before moving up to the top of the shoot. In the work by Khan and Sagar (1966) the flow of assimilates from the upper leaves was very slow and it appears likely that a considerable proportion of these would not have completed their passage through the internode below the leaf by the time the plants were harvested and thus appeared to be moving down through the stem.

The change from vegetative growth to the production of flowers and fruits or of a rapidly developing storage organ will markedly alter the pattern of assimilate distribution. Such developmental changes influence both the intensity of the demand for assimilates and in many instances the position of this demand in relation to the leaves. It is clear from work on peas (Linck & Sudia 1960, 1962), grapes (Hale & Weaver 1962), and tomato (Bonnemain 1966) that a developing fruit has a priority demand on assimilates from adjacent leaves.

Cereals have received special attention in relation to the distribution of photosynthetic assimilates from leaves during grain development. In general, the conclusion reached by Boonstra (1937) from a series of shading and defoliation experiments—that the upper leaves, stem, and ear were responsible for supporting 80 to 90 per cent of the grain growth in wheat—has been confirmed by labeling studies, not only for wheat (Quinlan & Sagar 1962, Stoy 1963, Lupton 1966, Wardlaw 1967) but also for rye (Mayer & Porter 1960) and rice (Fujiwara & Suzuki 1957, Tanaka 1958, Yin, Shen, & Shen 1958, Shen 1960, Lizandr & Brovtsyna 1964). In rice, however, the lower leaves appear to be more important in this regard than in the other cereals. The importance of the leaves in contributing assimilates to the grain of cereals varies with light conditions (Buttrose & May 1965) and variety (Lupton 1966). Also, in barley, and probably other cereals, the contribution of the leaves to grain growth declines as development progresses (Birecka & Skupinska 1963). Grasses show a similar pattern of assimilate distribution during seed formation, in that the top leaf and parts above this supply the required assimilates to the inflorescence (Williams 1964, McWilliam & Wardlaw 1965). Again the pattern of assimilate movement from any one leaf in cereals and grasses, as in soybean, is dependent not only on the proximity of regions of utilization but also on the supply of assimilates available from other leaves (Yu *et al.* 1963, Wardlaw, Carr, & Anderson 1965, Forde 1966b, c, King, Wardlaw, & Evans 1967).

THE ROLE OF VASCULAR CONNECTIONS IN THE PATTERN OF DISTRIBUTION

Although there is still argument as to the mechanism whereby organic compounds are actively moved in plants, there is little doubt that long-distance movement occurs within the living phloem tissue and particularly in the longitudinally orientated sieve tubes (Trip & Gorham 1967). Zimmermann (1961) suggested there may be a strict limitation on lateral movement of translocating sugars away from the phloem, so that in trees this is confined to an angle of less than 1°, or about 1 cm. of lateral movement for every 50 cm. moved longitudinally. Porter (1966) estimated that 12 per cent of the sugars passing through the midrib of tobacco leaves moved laterally into the surrounding cortex; this action was not readily reversible. Also, in the leaf of soybean lateral movement between the veins was found to be extremely limited (Belikov 1961). A similar limitation on lateral movement out of the vascular system has been shown in petioles, stems, and rhizomes of such diverse plants as bracken (Hamilton & Canny 1960), cotton (Ting 1963), peppermint (Rinne & Langston 1960), rape (Wang & Hsia 1962), rice (Asada *et al.* 1960), soybean (Thrower 1962), squash (Webb & Gorham 1964), sugar beet (Joy 1964), tobacco (Shiroya *et al.* 1961), and tomato (McCollum & Skok 1960, Bonnemain 1965). From these data it can be concluded that supply patterns to growing organs will be limited by orthostichy and vascular connections. An interesting example of this is found in sunflower during inflorescence development where cutting leaves from one side of the stem results in the failure of the florets to develop on the defoliated side of the head (Prokofyev, Zhdanova, &

Sobolev 1957, Zhdanova, Lebedyeva, & Chvizh 1961). It was noted earlier by Prokofyev and Sobolev (1957) that P^{32} applied to a sunflower leaf moved only to that part of the inflorescence on the same side of the stem. Similarly in sugar beet each leaf may supply only a particular part of the root system (Belikov & Kostetsky 1964, Gemma 1966).

This restriction of sugar movement, by the pattern of vascular connections, sometimes results in apparently anomalous C^{14} distribution patterns. For example, in sugarcane (Hartt *et al.* 1963), bean (Biddulph & Cory 1965), and tomato (Bonnemain 1965), assimilates entering the stem from an upper leaf first move downward before moving up to the shoot apex. The leaf traces in these instances link with the stem traces further down the stem and it is not until the assimilates have reached this point of union that they can begin their upward movement. In tomato downward movement takes place in the external phloem and return flow in the internal phloem (Bonnemain 1965). In bean plants a low temperature jacket placed round the hypocotyl was shown by Böhning, Swanson, and Linck (1952) to reduce sugar movement from the leaf immediately above the jacket to the shoot apex. This can be explained on the assumption that the leaf and stem traces do not unite at the point of insertion of the leaf on the stem, but further down and hence beneath the temperature jacket. Again, probably because of the vascular arrangement between leaves, the expanding leaf of soybean imports more assimilates from the second leaf below it than from the leaf immediately below, but on the opposite side of the stem (Thrower 1962). The apparent restriction of assimilates to a single vascular pathway is probably a reflection on the comparative velocities of transport in the longitudinal and lateral directions, which may differ by as much as 60 to 100 times in mature tissue, although it may be less than this in young tissue (Webb & Gorham 1964, 1965a).

As with most generalizations, however, there are exceptions, and Peel (1964, 1966) has produced convincing evidence for the tangential movement of sucrose in willow stems in response to a demand by aphids for assimilates. Hale and Weaver (1962) also noted that a fruit spur had a marked effect on the lateral movement of translocated assimilates in grapes, and Joy (1964) found that the phyllotactic distribution pattern in sugar beet could be modified by leaf removal. In wheat there is a direct movement of assimilates between vascular traces at the node of insertion of the flag leaf, eliminating the requirement for assimilates to first move down to the next node, where the leaf and stem traces unite, before going up to the ear (Wardlaw 1965). It appears that assimilates will flow out of the conducting tissue if the lateral demand is high and the demand from areas more directly associated with the vascular system is low. It is interesting to speculate whether the conditions that favor tangential movement of carbohydrates would have similar effects on other substances such as phloem-translocated herbicides or viruses, or whether these would in effect be filtered out of the system.

THE DEMAND FOR ASSIMILATES

During early growth a leaf will require carbohydrate from other parts of the plant for its development; however, once a leaf is fully expanded it is no longer capable of importing assimilates, even when placed in darkness (Rabideau & Burr 1945, Aronoff 1955, Belikov 1955, Fujiwara & Suzuki 1957, Belikov & Kostetsky 1958, Thaine, Ovenden, & Turner 1959, Hale & Weaver 1962, Chen 1963, Doodson, Manners, & Myers 1964, Williams 1964, Lawton 1967). Occasional exceptions appear to involve a redistribution of leaf assimilates back through the xylem (Pristupa & Kursanov 1957, Williams 1964, Eschrich 1966), or occur when movement into the leaf has been specifically stimulated by the addition of growth substances (Booth *et al.* 1962).

Movement of leaf assimilates away from the site of assimilation may continue even when the leaves are detached or isolated by ringing. However, this movement is greatly enhanced and given direction by growing tissues and storage organs (Aronoff 1955, Kursanov 1961, Hartt 1962, Shen & Shen 1962, Humphries 1963, Hartt & Kortschak 1964, Ting & Tseng 1965). Tissues differ in their demand for assimilates and there are a number of mechanisms that can account for these differences. Firstly, there is the ability to deplete the supply of carbohydrate and thus create a concentration gradient that will favor movement to a particular organ. In this respect, either the intensity of metabolism and active unloading of the vein system (c.f. Geiger 1966) or the number of sites of utilization and size of a growing organ may be important. Distance from the site of assimilate production may also be a factor in whether an organ can establish and maintain a favorable concentration gradient. Secondly, growth substances, moving out from a growing organ, may either suppress the development of alternate sites of assimilate utilization (c.f. Leopold 1964) or alternatively stimulate translocation of assimilates through the vascular system to the sites of utilization (Booth *et al.* 1962, Povolotskaya, Rakitin, & Khovanskaya 1962, Davies & Wareing 1965, Müller & Leopold 1966, Hew, Nelson, & Krotkov 1967, Seth & Wareing 1967).

Hale and Weaver (1962) suggest that flowers are a weak "sink" and fruits a strong "sink" in grapes, and Meynhardt and Malan (1963) have shown that fruit clusters in grape will utilize assimilates formed at least 12 feet from the cluster. Chen (1963) showed similar differences between the fruit and flower of soybean. Regrowth of corn following removal of the cob (Loomis 1935, 1945) and the cessation of root growth during fruit development in tomato (Van Dobben 1962) suggest that fruits develop at the expense of vegetative growth (c.f. review by Leonard 1962). Dominance of reproductive over vegetative organs has been illustrated many times by the pattern of assimilate distribution or changes in pattern following leaf or fruit removal (Belikov 1957, Mochizuki 1962, Yakushkina 1962, Maggs 1964, 1965, Wardlaw 1965, Wardlaw, Carr, & Anderson 1965, Ting & Tseng 1965, Belikov & Pirsky 1966, Bonnemain 1966, Hansen 1967, Khan & Sagar 1967), whereas in trees heavy seed production may be associated with decreased secondary thickening (c.f. review by Kozlowski & Keller 1966, p. 339). Although in cereals there may be some movement of assimilates from the ear to the developing stem during the initial stages of grain development (Carr & Wardlaw 1965), this movement ceases as stem development stops and grain growth becomes more active (Buttrose & May 1959, Carr & Wardlaw 1965). Although the same restriction in movement is evident in the pods of bean plants, Wanner and Bachofen

(1961) noted that up to half the assimilates could be exported from a green pod if this was the only part of the plant illuminated, with the exported carbon then moving to other pods on the plant. Storage organs such as the potato tuber (Burt 1964, Nösberger & Humphries 1965), sugar beet (Geiger 1966), and sweet potato (Tsuno & Fujise 1965) also appear to dominate vegetative growth in a manner similar to fruits.

Growth of established shoots appears to have priority over root and bud growth under conditions of assimilate deficiency (Brouwer 1962, Evans, Wardlaw, & Williams 1964). In *Pinus,* Nelson (1963) observed that less assimilate was directed to the roots of plants grown under low light intensity than in those grown under high light conditions. Roots and buds appear to be the poor relations among the plant organs, receiving only material in excess of the requirements of other parts. Anisimov (1959) could find no relation between total root dry weight and the intensity of assimilate movement from the leaves to the roots in wheat, whereas Fujiwara and Suzuki (1961b) found that removing the 5 mm. tip of all roots in barley had only a small effect on translocation of assimilates to the roots. In this latter example, however, growth in the form of cell wall thickening may have been occurring more than 5 mm. back from the root tip. Shiroya *et al.* (1966) found two active periods of translocation of assimilates to the roots of *Pinus,* one in the autumn and a second in the spring, which coincided with increased root respiration. However, this is not necessarily a causal relationship pertaining to a demand by the roots, since root respiration has been shown to be closely dependent on the availability of substrate (Thomas & Hill 1949, Davidson & Milthorpe 1966, Neales & Davies 1966), and this may be a response to an increased supply rather than an increased demand for assimilates. Winter and Mortimer (1967) have shown that the movement of photosynthetic assimilates to roots was not affected by depleting the root media of oxygen or by removing small lateral rootlets, although the work of Starck (1964, 1967) on root removal and defoliation in bean plants does indicate that roots do have some direct effects on assimilate distribution.

The relative abilities of roots and buds to obtain assimilates depend on many conditions. Roots on intact shoots growing under low light conditions will continue to grow slowly, although bud development is almost totally inhibited. If the shoot apex is removed, however, as can occur with severe defoliation of pasture species, the buds are released from apical dominance and grow at the expense of the root system (Milthorpe & Davidson 1966).

Within the shoot there may be competition for assimilates between the shoot apex, leaves at different stages of development, and expanding stem tissue. The apex, because of its small size, will not have a large absolute demand for assimilates, but the intensity of this demand may be high. If the actual apex is relatively inactive it might be expected to show retarded development in periods of general assimilate deficiency. Although rates of apex metabolism may be relatively low, the observation by Rijven and Evans (1967) that P^{32} applied to the leaf enters the apex of *Lolium temulentum* and is then partly redistributed to other parts of the plant suggests that the apex is well situated to receive available nutrients and carbohydrates. Both Friend and colleagues (1962) working with wheat and Forde (1966a) working with perennial ryegrass and cocksfoot found that differences in light intensity had only minor effects on the development of the apices in these species, although Forde noted marked effects following defoliation. Also, both Langer (1959) and Ryle (1963) have evidence that nitrogen deficiency has only a small effect on vegetative growth of the apical meristem in timothy.

A leaf at the stage of most rapid development appears to inhibit the growth of the next youngest leaf above it (Vyvyan 1924, Thrower 1964, Williams & Rijven 1965). Stem expansion may occur concurrently with leaf expansion and may compete with the young leaves for assimilates. However, the importance of this competition has not been studied. In cereals it was shown by Navasero and Tanaka (1966) that the stem may also compete with the developing ear for available substrate. This competition between ear and stem is also evident in the work of Friend (1965), where he showed that both stem height and ear length increased with light intensity up to 2500 f.c.

Although storage organs actively accumulate assimilates, leaves, stem, and roots also have some capacity for holding excess carbohydrate as either starch, oligosaccharides, or simple sugars. In cereals, temporary storage of assimilates in the stem, at the time of anthesis, is subsequently followed by a redistribution of these materials to the ear and new shoots (Murayama, Oshima, & Tsukahara 1961, Stoy 1965, Wardlaw & Porter 1967).

There are many instances where the demand for assimilates by the developing organs of a plant are matched by those of a parasite attached to it. Thus mistletoe may intercept assimilates moving between the needles and root system of pine (Rediski & Shea 1961). Species of mistletoe differ, however, in their requirements, dwarf mistletoe *(Arceuthobium)* being dependent on the host whereas the leafy mistletoe *(Phoradendron)* is not (Hull & Leonard 1964, Leonard & Hull 1965). In their review of literature on mistletoe, Gill and Hawksworth (1961) infer, from the observation that the presence of a leafy mistletoe on a completely defoliated host prolongs the life of the host, that some transfer of metabolites from mistletoe to host is possible. However, Leonard and Hull (1966) failed to obtain any movement of labeled assimilates from the leafy mistletoe into its host, even when the infected branch was defoliated, but in this instance there was significant redistribution of assimilates into the defoliated shoot from other branches on the host. Also in dodder growing on lucerne there is no evidence, from tracer studies, that photosynthetic assimilates move from parasite to host, even when the host is starved (Allred 1966, Littlefield, Pattee, & Allred 1966). It has been suggested by Okonkwo (1966), when he failed to reverse the movement of eosin into *Striga,* that unidirectional movement may also apply to water.

Melin and Nilsson (1957) demonstrated the transport of assimilates to the mycorrhizal fungi of pine, and Nelson (1964) suggested that there was a stimulation of assimilate transport to the roots of conifers with the development of mycorrhiza. A somewhat similar situation occurs in leguminous plants, where it has been shown that the nitrogen-fixing root nodules obtain assimilates from the host plant (Bach, Magee, & Burris 1958, Pate 1962, 1966, Gibson 1966, Hoshino, Nishimura, & Okubo 1966). In this instance some of the carbon accompanies the fixed nitrogen back into the host plant.

ENVIRONMENT AND ASSIMILATE DISTRIBUTION

It will be evident from a consideration of the previous sections that factors of the environment can control the distribution of assimilates in one or more ways. Effects may be mediated through changes in the rate of growth of developing organs, which in turn may be influenced by hormonal levels, through alterations in the rate of photosynthesis and outflow of assimilates from leaves, or through direct effects on assimilate movement. In addition to these effects, which involve the function and development of existing plant organs, will be changes in plant development, for example from leaf production to flower and fruit formation. Although the following sections on environmental control of assimilate distribution will be discussed on the above basis, it is seldom that a single cause and effect can be clearly isolated.

Temperature

With shifts in temperature there is often a marked change in the pattern of development of plants, much of which is presumably caused by direct alteration of the growth rate of developing organs (Brouwer 1962, Van Dobben 1962). The accumulation of soluble carbohydrate at low temperatures suggests that growth rates are affected more by temperature than are photosynthetic rates (c.f. Evans, Wardlaw, & Williams 1964), although the differences in response may be due, in part, to a limitation of photosynthesis at higher temperatures, through an inadequate supply of CO_2 (Gaastra 1963). Reduced growth due to low temperatures would be expected to reduce the rate of assimilate translocation, as has been shown by Vernon and Aronoff (1952), Whittle (1964), and Hartt (1965a), although translocation being to some extent metabolic may also be directly affected by temperature. Temperature will affect the distribution of assimilates in a plant largely through its effect on the organ with the greater demand for assimilates. For example, where photosynthetic rate does not fall with reduced temperatures, while shoot growth does, more assimilates will become available for the growth of roots and buds. The change in distribution of assimilates with falling temperature is not, therefore, necessarily associated with differences in the optimum temperature for growth of different plant organs. Friend (1966) found optimal temperature for growth of attached roots in wheat to be about 15°C., whereas that for isolated roots in sterile culture was 25°C. Sekioka (1961, 1963) showed that accumulation of C^{14}-sucrose by sweet potato roots was largely controlled by shoot temperature with an optimum again at about 15°C. However, controlling the temperature of two halves of a divided root system indicated that the true optimum for root growth was 30°C. and hence much closer to that of the shoot. Translocation of assimilates from the leaves of sugarcane was found to be more dependent on root than shoot temperature (Burr *et al.* 1958). Part of this effect may be related to the production of tillers from the base of the sugarcane plant, where temperatures will be close to those of the root system. Any alteration in root temperature may also affect nutrient uptake and thus indirectly the pattern of plant development.

Although there is evidence to suggest that movement of assimilates through conducting tissue is associated with metabolically active cells and may be temperature-dependent, there is no conclusive evidence that reduced translocation is ever the primary cause of limiting growth under low temperatures. Fujiwara and Suzuki (1961a) found that the rate of translocation reached a maximum under temperature conditions at which top photosynthesis and root growth were most active. There is little indication in most other work whether the optimum temperature for translocation ever differs from that for growth. Hsia and co-workers (1963) concluded from their work on wheat, in which they lowered the temperature of the ear, stem, and flag leaf separately, that the effect of temperature on the distribution of assimilates from the flag leaf was primarily dependent on the growth of the ear and to a smaller extent on the function of the leaf. Altering the temperature of the stem, from 20° down to 8°C., had no observable effect on assimilate distribution. The effect of temperature on both the region of growth and assimilate movement out of the leaf were presumably related to the energy requirements of these processes (Kursanov & Brovchenko 1961, Ullrich 1962, Geiger 1966). Hsia's failure to find any direct effect of temperature on translocation is at variance with the results of many other workers, who have shown that a local reduction in stem or petiole temperature to between 0° and 5°C. inhibits the movement of applied P^{32} and of C^{14}-assimilates (Swanson & Whitney 1953, Whitehead 1962, Thrower 1965, Webb & Gorham 1965b, Webb 1967).

The effect of temperature on translocation may be transient, as is shown by the work of Swanson and Geiger (1967) and Webb (1966) on sugar beet and squash plants respectively; Whittle (1964) has suggested that the recovery of translocation under low temperatures could be related to a build-up of sugars in the supply regions of the plant and hence the development of a steeper sugar concentration gradient through the cooled zone. However, Ford and Peel (1966) concluded, from their work on the relation between temperature and movement of P^{32} through a willow stem to an aphid colony, that lateral movement out of the sieve tubes is metabolic and dependent on temperature, whereas longitudinal movement down the length of the sieve tubes is independent of temperature. Perhaps temperature effects on cell-membrane permeability and lateral release of assimilates could explain some of the effects of temperature on translocation. It is apparent that this aspect still needs clarification, not only in relation to the effects of temperature on the pattern of assimilate distribution but also in relation to the mechanism of translocation. However, it seems likely that the primary effect of temperature on assimilate distribution is associated with growth rather than sugar conduction, as the shifts in distribution of assimilates with reduced temperature (i.e., to roots instead of shoots) are the reverse of the changes normally associated with a decrease in assimilate supply.

Light

Although the pattern of assimilate movement is influenced by the relative ability of different organs to attract the available carbohydrate, it is also influenced by the rate of assimilate production in photosynthesis, which depends in turn on light intensity and duration. Root and bud growth are inhibited to a greater extent than shoot growth by a reduction in light (Brouwer 1962, Van Dobben 1962), which agrees with the observation by Nelson (1964) that there is a reduced movement of C^{14}- assimilates from the needles to roots in conifers grown under low light. Mutual shading in closely planted wheat was shown by Kravcova (1957) to result in an increased proportion of assimilates moving to the ear from lower leaves on the culm. Also, Navasero and Tanaka (1966) noted that shading the lower leaves of rice intensified the movement of assimilates to the ear from the upper exposed leaves. In rice, Yin, Shen, and Shen (1958) noted that movement of assimilates from non-flowering to flowering tillers occurred under low light.

Although root growth is more restricted than shoot growth under low light, there are several instances where it has been shown that of the assimilates leaving a leaf the proportion moving to the root system is greater in the dark than in the light (Nelson & Gorham 1957, Sekioka 1962, Anisimov *et al.* 1963, Nelson 1964, Hodgkinson & Veale 1966, Tan *et al.* 1966). There is evidence for light stimulation of leaf growth, and Thrower (1964) has shown that a reduction in the rate of photosynthesis of an expanding soybean leaf, due either to darkening or a reduction in the supply of CO_2, results in a smaller demand and reduced import of assimilates into the growing leaf. Such an effect could be responsible for the observed differences in assimilate distribution pattern between light and dark. Translocation of assimilates to the growing organs throughout a normal 24-hour cycle may occur largely in the dark, as Went (1957) has suggested for tomatoes, or largely in the light period, as Mason and Maskell (1928) demonstrated for cotton. However, under low light conditions, with less accumulation of excess carbohydrate in leaves and stems, translocation during the dark period is likely to become far less important than that during the light period. Thus, by reducing movement during darkness, the over-all effect of reduced light intensity will be to increase the relative proportion of assimilates reaching the shoot.

Movement of assimilates out of a leaf, as mentioned earlier, is influenced by light energy. Thus, not only is the rate of photosynthesis reduced under low light, but also the proportion of assimilated carbon leaving the leaf. Hartt and Kortschak (1964) and Hartt (1965b) have suggested that there is a light process involved in translocation of assimilates through a sugarcane leaf, with a maximum response at low intensities (approximately 100 f.c.). However, Shan'gina (1965) has reported for tomato that a decrease in light intensity from about 3600 down to 900 f.c.—which has only a small effect on leaf photosynthetic rate—results in a slower outflow of assimilates and an increase in leaf polysaccharides. This response of translocation to decreasing light intensities, at higher levels than those reported by Hartt, is also supported by results from other workers (Shen 1960, McWilliam & Wardlaw 1965), and suggests that either sugarcane leaves respond in a different manner to other leaves or the response may have been affected by detaching the sugarcane leaves.

Daylength, through changes in plant development will have a considerable indirect effect on the distribution of assimilates. Mokronosov and Bubenshchikova (1961) found that the diurnal flow of assimilates from the leaf of potato was affected by daylength through its relation to tuber formation. Similarly, Nelson (1963) noted that movement of assimilates in larch was affected by daylength through effects on shoot and root development. Perhaps the more conspicuous effects of daylength are related to the change from vegetative to floral development, and presumably the greater translocation of assimilates in long-day plants under long days and short-day plants under short days, as suggested by Tsibulko (1962), is the result of these developmental changes. More direct effects of daylength on translocation are difficult to assess because of interactions with growth. Novitsky (1957) observed that as *Perilla* passed from an unfavorable to a favorable photoperiod for flowering, there was a temporary reduction in the flow of assimilates out of the leaf. Although changes at the shoot apex may occur very rapidly following a shift in daylength, detailed work by Chailakhyan and Butenko (1957) on the distribution of assimilates in *Perilla* under different daylengths failed to indicate any variation in movement out of a leaf directly associated with this factor. However, in this instance the autoradiographic techniques may not have been sensitive to small changes in the distribution of labeled assimilates.

Water

Gates (1964) has already pointed out in an earlier review that the effect of water stress on growth and hence on the distribution of photosynthetic assimilates is not fully understood.

Extension growth commonly shows an early response to water stress, whereas photosynthesis and the accumulation of assimilates continue for some time after stress is evident in extension (Iljin 1957). The observation by Slatyer (1957) that dry-weight accumulation ceased earlier than stem elongation in tomato plants under stress is an exception to this rule. Other forms of growth are not so readily altered by stress as is extension. For example, the floral apex of sorghum may continue to develop at a water stress sufficient to prevent leaf expansion (Whiteman & Wilson 1965), and grain development in cereals may be unaffected by a stress that causes wilting of the leaves (Asana, Saini, & Ray 1958, Konovalov 1959, Aspinall 1965, Wardlaw 1967). The response to stress depends on the organ involved, and Iljin (1957) suggested that cells—such as those found in seeds, buds, and storage organs—which generally lack vacuoles and are filled with food reserves will be most resistant to desiccation. It is resistance to desiccation rather than the ability of an organ to function with a low water content that appears to impart ability to withstand stress.

There are often marked alterations in the pattern of distribution of assimilates when plants are subject to water stress. These may be the direct result of reduced growth rates in some instances or of reduced photosynthetic rates in others, although there is some evidence for more direct effect of stress on the conduction of assimilates.

The observation by Hartt (1967) that there is an increase in the sugar content of the stem when sugarcane plants are under water stress appears to fit the suggestion by Iljin (1957) that reduced growth under stress results in the accumulation of sugars. Hartt favors a direct effect of stress on translocation in which sugar accumulation is the result of a reduced velocity of movement through the conducting system. This is somewhat similar to a view expressed earlier by Gates (1955a,b), that changes in the weight ratios of different plant organs, when under stress, were due to a modification of translocation. Zolkevich and co-workers (1958) have carried this a stage further; they suggested that with the inhibition of translocation under water stress there will be a retention of assimilates by the leaf, which in turn could result in reduced photosynthetic rates in the stressed leaf. However, where stress causes an alteration in the distribution of assimilates, with an increased movement in one direction, it seems likely that the response to stress will not have resulted from direct effects on conduction, but rather from effects on photosynthesis or growth. Roberts (1964) observed that water stress increased the upward movement of assimilates in yellow poplar. Also in wheat, during grain development, a water stress that caused reduced photosynthetic activity in the leaves resulted in an increased movement of assimilates from the lower leaves to the ear (Wardlaw 1967); this is typical of the compensation that occurs when assimilation is reduced under low light intensities.

The work of Plaut and Reinhold (1965, 1967), on the movement of applied sucrose in bean plants under water stress, has been interpreted as showing that water stress directly alters translocation. Certainly changes in xylem tension affect pressures within the sieve tubes of the phloem, as Peel and Weatherley (1962, 1963) demonstrated by measuring the exudation of phloem sap through aphid stylets. However, where growing organs are not subject to the same stress as the rest of the plant, as with the ear of wheat during grain development, velocity of movement of labeled assimilates through the conducting tissue was found to be relatively insensitive to stress (Wardlaw 1967). This is evidence, in part, for the suggestion by Nelson (1963) that water stress affects the movement of assimilates into but not through the conducting tissue. There is ample evidence that under water stress there is a reduction in the rate of movement of assimilates out of the photosynthetic tissue (Zolkevich 1954, Zolkevich, Prusakova, & Lizandr 1958, Wiebe & Wihrheim 1962, Roberts 1964, Plaut & Reinhold 1965, Hartt 1967, Wardlaw 1967). The close interaction between growth and translocation makes it difficult to assess the relative importance of these processes in determining the pattern of distribution of assimilates in plants under water stress. In the few instances where growth has been eliminated as a factor it appears that translocation is relatively insensitive to stress. Also, the observation by McWilliam (1968) that there is a significant movement of assimilates from stem to roots and buds (in the perennial grass, *Phalaris tuberosa* L.), when the plant is dormant due to a restricted water supply, suggests that the transport system is resistant to desiccation.

Nutrition

When considering the effect of temperature and other environmental factors on the distribution of assimilates in plants, it is often difficult to decide on the secondary effects that will occur through associated changes in nutrient uptake and distribution.

Many elements are essential for both growth and cell maintenance, and it is not surprising that Anisimov (1962, 1965) found that both nitrogen and phosphorus stimulated the outflow of assimilates from the leaves of wheat and sugar beet; in potato, however, he found decreased translocation when phosphorus was added to plants grown at high nitrogen levels (Anisimov 1966). The accumulation of soluble carbohydrates in the stems of nitrogen-deficient plants (Archbold & Mukerjee 1942, Alberda 1966) indicates that photosynthesis and transfer of assimilates out of the leaf are less affected by nitrogen deficiency than is growth.

Tsuno and Fujise (1964) suggested that, because the distribution of dry material to the tops in sweet potato is relatively greater under low than under high potassium levels, potassium is involved in the translocation of assimilates from the leaves to the tubers. Spanner (1958) has implicated potassium in an electro-osmotic mechanism of translocation, but in the work by Tsuno and Fujise (1964) it is not possible to dissociate the effects of potassium on translocation from those on photosynthesis and growth.

More controversial is the role played by boron in controlling the distribution of assimilates. Gauch and Dugger (1953) and Sisler, Dugger, and Gauch (1956) suggested that boron-complexes with sugar are directly involved in movement through the phloem. However, work by Neales (1959) has indicated that it is unlikely that boron is involved in translocation in this way, and that the effects of boron are on growth, a view strongly supported by McIlrath (1960). Dyar and Webb (1961) found that auxin would stimulate translocation in boron-deficient plants, whereas Weiser, Blaney, and Li (1964) noted that although both boron and aluminum stimulated sucrose uptake by bean leaves, they did not affect the distribution of assimilates, following the fixation of $C^{14}O_2$. It is doubtful if the claim by Lee, Whittle, and Dyer (1966), that boron affects the velocity of assimilate movement, is meaningful in deciding the relationship between boron and translocation, as the rate of growth is also known to affect the velocity of translocation (Wardlaw 1965).

Other minor elements have been implicated in translocation. Brown and co-workers (1958) noted that copper affected the distribution of assimilates in wheat, and Takahashi and co-workers (1966) reported an effect of silicon on translocation in rice. Shkolnik and co-workers (1959) and Shkolnik and Saakov (1964) found that manganese, copper, zinc, and molybdenum, as well as boron, increased both translocation and photosynthesis. Again, effects on translocation have not been adequately separated from those on growth and photosynthesis.

CONCLUSIONS

We have a considerable empirical knowledge of the distribution of photosynthetic assimilates in plants. The supply of assimilates from a leaf is controlled partly by the leaf itself through its photosynthetic rate and its ability to load assimilates into the conducting tissue. However, control of the distribution of assimilates depends largely on the ability of different organs to utilize the available supply. Some curb on the pattern of movement is imposed by the vascular anatomy of the plant, although under conditions of high demand this restriction may be broken. In addition there is an interaction between the position of leaves relative to each other and to the growing regions. Thus we can predict, to a certain extent, from leaf position, leaf area, and the growth rates of individual organs, the likely distribution of assimilates from any one source of supply.

When considering the response of plants to changes in their environment it is often difficult to draw definite conclusions as to what aspect of plant function initiates the response. However, it seems probable that the actual conduction of assimilates is of minor importance in determining their pattern of distribution in response to environmental changes. Temperature would appear to be more directly associated with growth rate than with either translocation or photosynthesis. There are instances where an optimum temperature has been recorded for translocation through short lengths of the vascular system, but this has not been related to other temperature responses in the plant; also, in several situations temperature effects have been shown to be transient in nature. Total light energy will control the level of assimilates available for translocation from a leaf through effects on photosynthetic rate, while superimposed on this will be the effect of light quality and daylength on growth and development. Water stress in some instances, for example during seed development, may result in reduced photosynthetic efficiency prior to any effect on growth, while at another stage of development, for example during leaf expansion, growth may be more sensitive to stress than photosynthesis. However, it seems likely that reduced translocation in plants under water stress is the result of a reduction in growth rather than any direct effect on the conducting system.

The greatest lack in these studies is an understanding of the mechanism involved in assimilate distribution. There is little information on the mechanisms whereby sugars are transferred against a concentration gradient into the conducting tissue, nor on how these sugars are transferred into growing organs. Certainly there is no agreement on how sugars are moved through the conducting tissue.

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