higher osmotic potential than adjacent sieve tubes to facilitate loading through a sugar concentration gradient (Troughton and Currie 1977).

At the other end of the translocation process, phloem unloading can also limit the rate at which a sink receives assimilate. Studies on unloading are scarce, so description is difficult (Giaquinta 1980). Some studies have shown that unloading is similar to loading in that the sugars move from the phloem symplast to the apoplast and then are transferred to the symplast of sink cells. However, there are indications that unloading may occur by a direct symplast transfer from phloem cells to sink cells (McNeil 1976). Current indications are that unloading occurs by different mechanisms in different tissues and may vary with the developmental status of the sink (Giaquinta 1980).

ASSIMILATE PARTITIONING

Partitioning of assimilate is generally to the sinks closest to the source. For example, upper leaves export principally to the shoot apex, lower leaves to roots, and middle leaves to both (Wardlaw 1968). Since phloem sieve connections are on one side of the stem, the leaves on one side may be more efficient at exporting assimilate to sinks on the same side. This has been shown for many crops (Wardlaw 1968); for example, the upper, expanding leaves of soybean will import more assimilate from the second leaf below them, which is on the same side of the stem, than from the closest leaf, which is on the other side of the stem (Thrower 1962). Cross-linking of sieve tube elements occurs in most species, but some seem more efficient than others. Grasses have extensive cross-linking at nodes, which essentially eliminates a preferred route by assimilate from any leaf to any particular sink (Gifford and Evans 1981).

Sink-Source Relationships and Partitioning

The movement of assimilate from source to sink is currently believed to occur something like the following (Fig. 3.3). The photosynthetic source cell

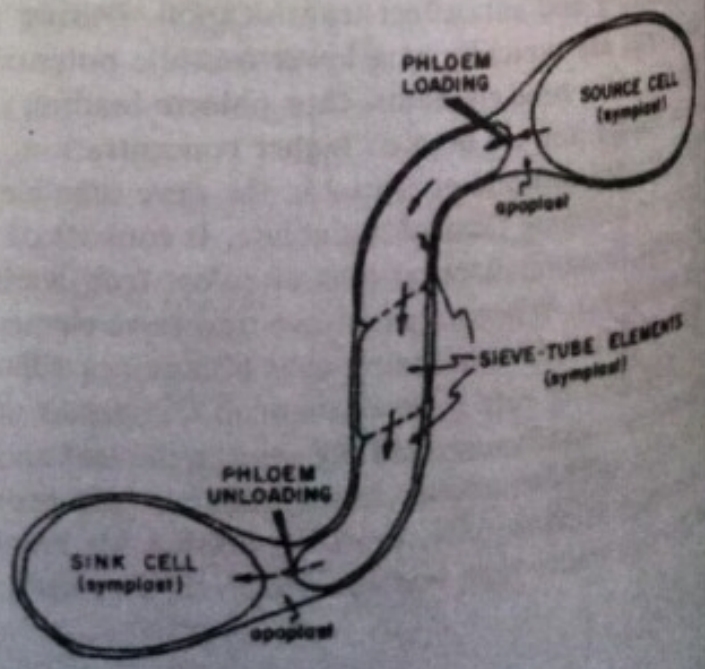

Fig. 3.3. Simplified illustration of assimilate transport from source to sink.

produces the sugars, which can move symplastically to the sieve tubes. Phloem loading increases the sugar concentration of sieve tubes above that of the apoplast.

At the sink, carbohydrates are being absorbed and either actively partitioned into cell constituents (e.g., starches) or changed to other carbohydrates that have little effect on hydrostatic pressure of the phloem. Phloem unloading lowers the concentration of sugars in sieve tubes. The buildup of sugars at the source and the removal of sugars at the sink establish a hydrostatic pressure gradient, which moves water and sugars from sources to sinks.

Where are the limitations for movement of assimilate from sources to sinks? According to the mass flow hypothesis, anything increasing photosynthesis increases hydrostatic pressure and translocation rate. However, this is true only if sinks have the ability to utilize more assimilate. If they are unable to utilize the increased production there would be a steady buildup of sugars in the system, causing a feedback inhibition resulting in reduced photosynthesis (Mondal et al. 1978). Presumably, photosynthetic rate would be reduced to the rate at which sinks could accept assimilate. For leaf photosynthesis to be at maximum potential rates, sinks must be able to utilize all the assimilate produced. Under these conditions partitioning would be controlled by sink strength, that is, sink availability and the rate at which available sinks can utilize assimilate (Gifford and Evans 1981).

Factors that control sink strength also control the partitioning in crop plants. The effect of hormones on enzymatic activity and the elasticity of sink cells can have a dramatic effect on partitioning. Indoleacetic acid (IAA), cytokinins, ethylene, and gibberellic acid, when applied to cut stem surfaces, cause assimilate to accumulate in the region of application (Gifford and Evans 1981). In bean seedlings, the main control over the distribution of sucrose between root and shoot sinks can be attributed to auxin and cytokinin (plant growth regulators, see Chap. 7) concentrations in various sinks (Gersani et al. 1980). Hormonal influences on initiation, development, and abortion of flowers and seeds have a significant effect on the source-sink relationships in crops.

Although there is some evidence that hormones may have a direct effect on translocation rates, most results show an indirect influence through affecting sink demand (Gifford and Evans 1981).

Assimilate Partitioning during the Vegetative Phase

Leaves and other green tissues are the original sources of assimilate. Some remains in the green tissue for cell maintenance and, if translocation is slow, can be converted to starch or some other form of storage. The rest is exported (translocated) to vegetative sinks, which are composed of growth, maintenance, and storage functions.

During vegetative growth, roots, stems, and leaves are competitive sinks

for assimilate. The proportions of assimilate partitioned to these three organs can influence plant growth and productivity. The investment of assimilate in greater leaf area development results in greater light interception. However, the leaves also require water and nutrients, so investment in root growth is necessary. Some crop plants, such as most grasses, have essentially no stem growth during vegetative development and favor partitioning to leaves and roots.

Some meristems are in more favorable positions to intercept assimilate. For example, the intercalary meristems of leaves are in a better position to intercept translocated assimilate than are the peripheral root and shoot meristems (Evans and Wardlaw 1976).

Young developing leaves need imported assimilate to provide the energy and carbon skeletons for growth and development until they produce enough assimilate to handle their own requirements. Thrower (1962) and Webb and Gorham (1964) have shown that the leaves of soybean and squash are largely self-sufficient when 50% of their final area is developed (Fig. 3.4). After full expansion and under good environmental conditions for photosynthesis, leaves may export 60 to 80% of their assimilate to other areas of the plant (Hofstra and Nelson 1969). As the leaf gets older and begins senescence, it may fail to support its own energy requirements because of age or shading or both. Under these conditions the leaf does not export or import assimilate. Instead, cell maintenance requirements (respiration) are often greatly reduced, which allows the leaf merely to survive. Before death, many of the inorganic and organic compounds in the leaf are remobilized and translocated to other parts of the plant.

The early growth of branches and tillers requires importing assimilate

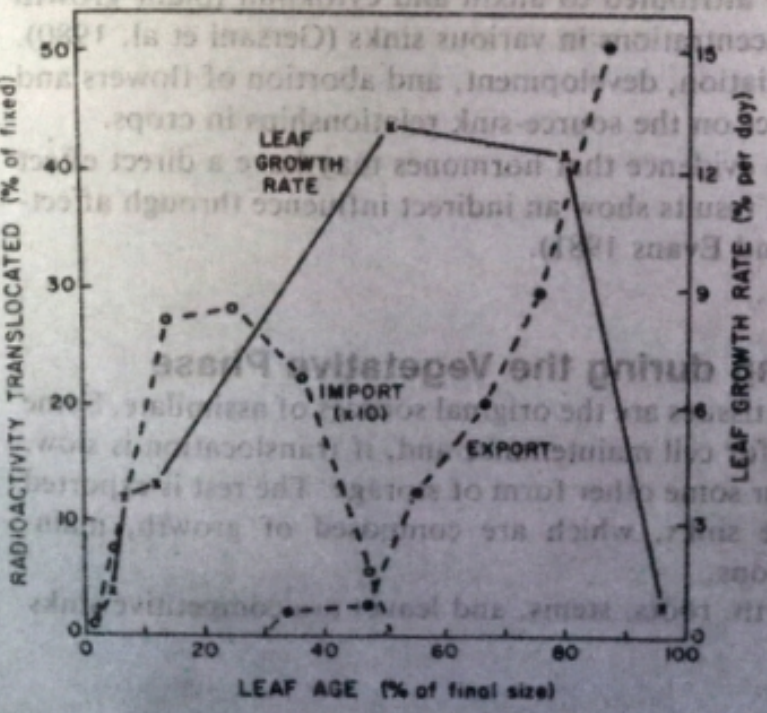

Fig. 3.4. Photosynthesis, import and export of soybean leaf with age (Thrower 1962).

from the main stem or other branches until they become autotrophic. In oats, this usually occurs between the two- and four-leaf stage (Labanauskas and Dungan 1956). Whether a branch or tiller becomes completely independent of the rest of the plant is variable among species. In timothy, the tillers behave as separate units once they become autotrophic (St. Pierre and Wright 1972). Little interaction between timothy tillers occurs even under stress conditions, and roots are supplied only by the tillers to which they are attached. When under stress the autotrophic tillers of some species, such as ryegrass (Marshall and Sagar 1968) and oats (Labanauskas and Dungan 1956), will again start transporting assimilate from the main culm. How partitioning of assimilate among tillers affects total yield is influenced by how much the additional leaf area of the tiller contributes to the total dry weight of the plant and how much the tiller contributes to harvestable yield; for example, tillers of maize do not usually produce grain.

Assimilate Partitioning during the Reproductive Phase

Reproductive growth is often the primary part of the plant harvested for yield. Crops, whose flowers, fruits, and seeds (and their products) are the economic yield, have been selected over time to partition large amounts of their total dry matter into reproductive parts. In such plants a large photosynthetic surface and supporting structure are required prior to fruiting. After flowering the reproductive sink becomes extremely strong, which limits the assimilate partitioned for additional leaf, stem, and root growth. In determinate species, leaf and stem growth cease at flowering (Fig. 3.5), while indeterminate species may have vegetative and reproductive growth occurring simultaneously. Thus indeterminate species are variable in the relative strength of their vegetative and reproductive sinks. If there is much vegetative growth during reproductive development, reproductive yield may be reduced.

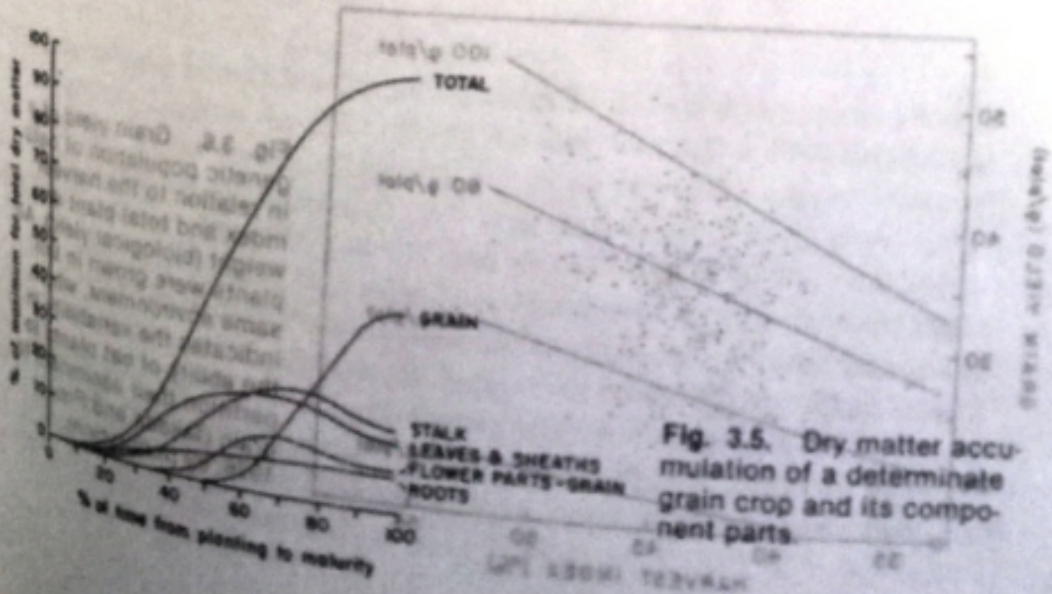

Fig. 3.5. Dry matter accumulation of a determinate grain crop and its component parts.

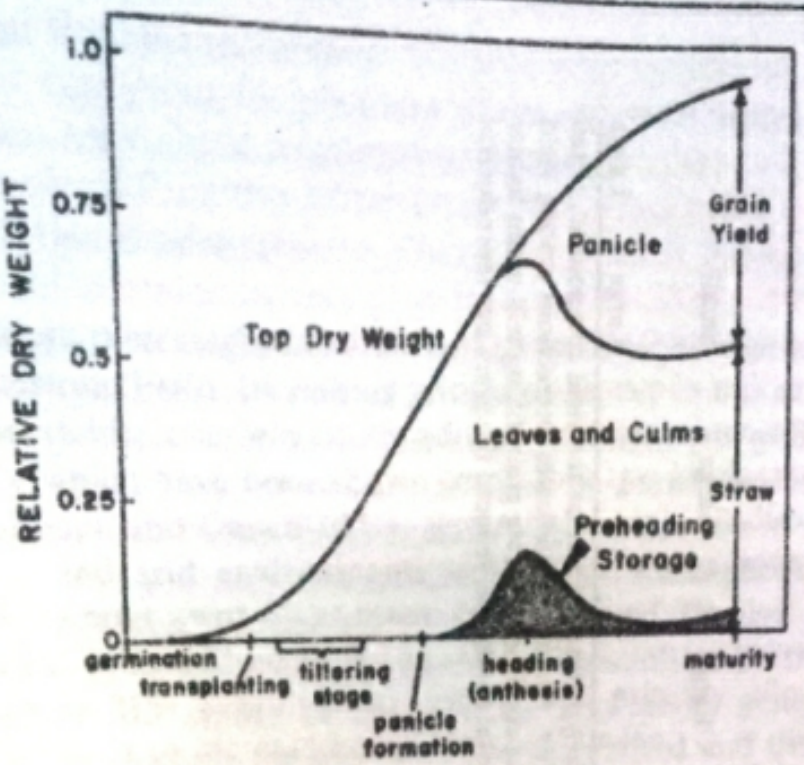

Fig. 3.8. Changes in the amount of temporarily stored carbohydrates (preheading storage) and dry weight of various parts, according to growth stage in rice (Murata and Matsushima 1975, by permission).

An example of remobilization has been shown in rice (Fig. 3.8). During the heading and flowering stage of the plant, the assimilate produced by photosynthesis is more than is required by these processes. The extra assimilate is moved to the stem and stored primarily as starch. However, as the plant goes into grain fill, starch is converted to sugars and translocated to the filling grain.

ASSIMILATE PARTITIONING DURING GRAIN FILL

Photosynthate deposited in grain can come from three major sources: current leaf photosynthesis, current photosynthesis from nonleaf parts, and remobilization of assimilate deposited in other plant organs. How much each of these factors contributes to final grain yield is affected by species and environment.

Partitioning has been extensively studied in small grain crops. Work in wheat and barley has shown that photosynthesis of the flag leaf, stem, and head, which are the closest sources to the grain, is the primary contributor to the grain. Lower leaves supply the needs of lower stem and roots (Lupton 1966; Wardlaw 1968). The strength of the grain as a sink and the relative availability and strength of sources affect the assimilate partitioning. If the top leaves are removed, the lower leaves will supply assimilate to the grain; if the lower leaves are removed, the flag leaf will transport assimilate to roots (Marshall and Wardlaw 1973).

It would be helpful to know just how much each source contributes to grain yield and the variability involved. Early work on shading the head of wheat or barley showed a 20 to 30% reduction in grain weight (Porter et al. 1959). Using shading and measuring photosynthesis, these investigators calcu-

TABLE 3.2. Contribution of preanthesis photosynthesis to the grain yield of wheat and barley under wet and dry growing conditions

Authors	Species	Growing Conditions	Grain Yield ($g \cdot m^{-2}$)	Grain Yield due to Remobilization ($g \cdot m^{-2}$)	Contributions from Preanthesis Photosynthesis (%)
Austin et al. (1980)	Barley	Wet	673	74	11
		Dry	302	133	44
Bidinger et al. (1977)	Barley	Wet	530	65	12
		Dry	384	67	17
	Wheat	Wet	509	64	13
		Dry	294	79	27

lated the contribution of different photosynthetic sources to final grain yield. They estimated that the contribution of preanthesis photosynthesis (remobilized assimilate) was 25%, current leaf and stem photosynthesis was 45%, and head photosynthesis was 30%. These percentages were confirmed by recent studies using more sophisticated procedures (Table 3.2). Drought stress during grain filling reduces grain yield through reduced photosynthesis. Thus the sink demand for grain filling uses more remobilized stored assimilate, which results in a much higher proportional contribution by remobilization (Table 3.2). Although remobilization is an important component of grain yield, photosynthesis during the grain filling period is normally the most important source of weight for grain yield. This is because most assimilate is used for vegetative or flower production before grain filling, whereas during grain filling most assimilate is used for that process (Fig. 3.9).

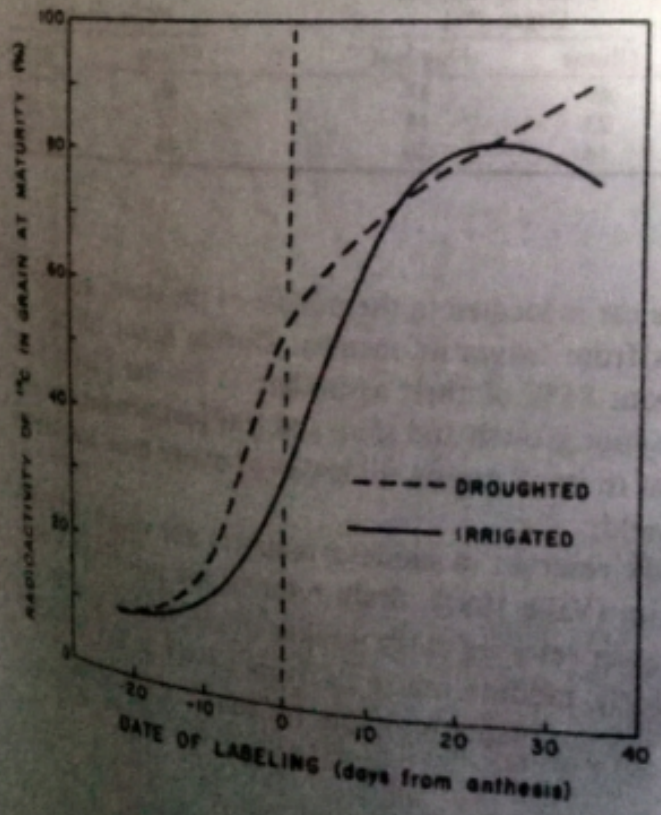

Fig. 3.9. Fraction of ^{14}C found in the grain of wheat and barley at plant maturity as a function of the time (days from anthesis) of assimilation. (From Bidinger et al. 1977)