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# **SOURCE - SINK RELATIONSHIPS IN CROP PLANTS**

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# SOURCE-SINK RELATIONSHIPS IN CROP PLANTS

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## ABSTRACT

In crop plants, the physiological basis of dry matter production is dependent on the source-sink concept, where the source is the potential capacity for photosynthesis and the sink is the potential capacity to utilize the photosynthetic products. If the sink is small, the yield cannot be high; and even if the sink is large, the yield cannot be high if the source capacity is limited. Several crop plants including rice and wheat have shown changes in source and sink during the course of domestication and evolution into modern cultivars. The modern plant type concept is essentially a blend of improved source and sink where the leaf (source) is short and erectophile to capture greater solar radiation and the sink is expanded by increased grain number and size and by profuse tillering.

A developing leaf is a sink, but when fully grown it becomes a potential source. Instances of a single organ playing the roles of both source and sink are discussed, as well as the nature of additional sinks and metabolic sinks. Sink size is the potential capacity for maximum production of a crop. The intensity and capacity of sink dynamics, the mechanics of source and sink, and the factors influencing them are reviewed with examples.

In tropical and subtropical climates the source appears to be the major limitation to higher yields in rice because of the wide gap between the number of spikelets and the number of grains. In temperate climates, and particularly with japonicas, the sink is the limiting factor, as nearly all spikelets become grains.

Examples of crop plants are reviewed, focusing on the limitations of their sources and sinks.

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# SOURCE-SINK RELATIONSHIPS IN CROP PLANTS

Plateaus in productivity have been reported in all cereal crops as well as in cotton, sugarcane, tomato, and potato; and some oilseeds and pulse crops are approaching that position. The sustainability of modern agricultural breakthroughs is being questioned, as further research seems not to enhance yield potentials. This situation calls for analysis. Crop improvement programs must have the specific objective of improving yield potentials.

Generally speaking, the organ or site that synthesizes food materials is called a *source*; in crop plants the mature leaf is always a *source*. The site of accumulation of synthesized food materials is known as a *sink*. The source is the potential capacity for photosynthesis (Po) and the sink is the potential capacity to utilize the photosynthetic products of the source.

The major part of the starch in rice grains at harvest is the photosynthetic product of the leaves, which is translocated from the leaves directly to the growing grains after flowering. The ripening of rice grains can be considered a process of accumulation of contents in a container. The grain yield may be limited by either the size of the container or the amount of its contents (52). If the container is small the yield cannot be high. On the other hand, even if the container is large, the yield cannot be high if the contents are limited.

While the relationships of sink and source, and their limitations, are not fully understood, their mechanics and dynamics appear to determine the nature of crop performance. Beevers (3) and Evans (15) gave some broad indications of the nature of the source and the sink. Molecular level transformations involving volume flow of assimilates, phloem loading and unloading, general assimilate pools, and metabolic steps in multiple enzyme systems with coupled biochemical processes were covered in a very basic way by Gifford et al (17), Hendrix et al (21), Koch et al (28), Wyse and Saftner (73), and Lafitte and Travis (31). The scope of this review is limited to structural and productivity levels of source and sink.

The following lines of inquiry are relevant for clarifying questions in crop improvement programs:

- the nature of sources and sinks, including their mechanics and dynamics;
- their interactions and interdependence; and
- research directions for crop improvement.

These lines of work envisage an imaginative action plan of intensive basic research and system studies in these areas. It is hoped that this review of the vital systems in crop plants will be useful to researchers in appraising current knowledge and will clarify goals in plant improvement programs.

## SOURCES AND SINKS

The continued growth of any plant depends primarily on photosynthetic activity in the leaves and the transport of organic compounds from the leaves to heterotrophic cells. The source supplies assimilates (C compounds) to the sink. The sink accepts and consumes the assimilates for its own growth or accumulates them for a certain period. The sink-source relationship resembles the demand-supply relationship in economics (52). In general, any plant part that has photosynthetic ability is considered a source, and nongreen cells, tissues, and organs are considered sinks. Thus, leaves are typical sources; and stems, roots, and tubers are typical sinks. The sink and source functions of any plant part may change depending on its developmental stage. For example, in rice, before flowering, the leaf sheath and culm accumulate sugars and starch, i.e., act as sinks (79). After flowering, most of the accumulated carbohydrates move into the spikelets (10).

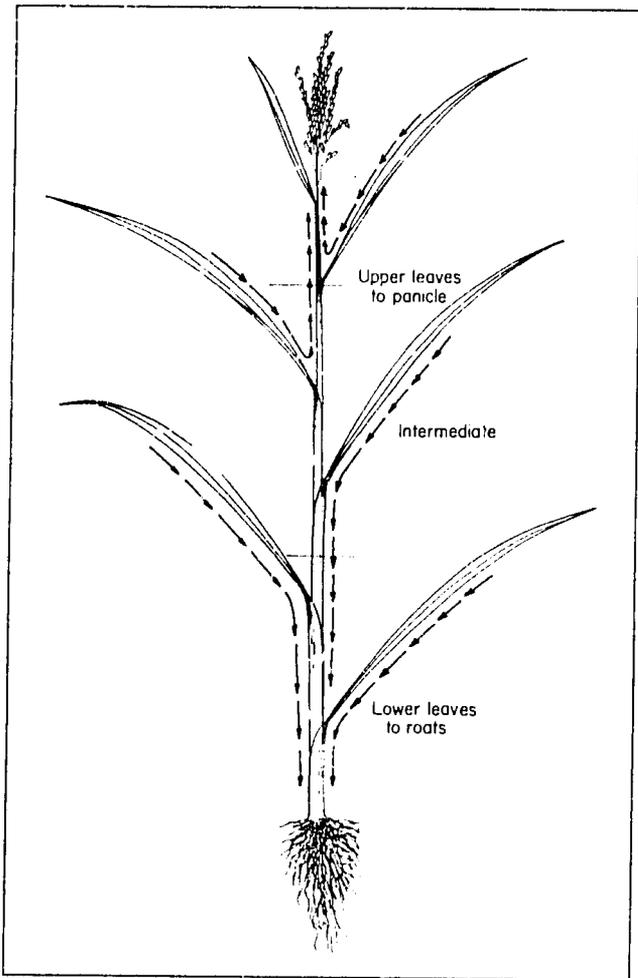
Developing organs, tubers, nongreen aerial plant parts, buds, flowers, fruits, and most of the cells in stems and petioles also constitute a drain on photosynthetic products and are thus sinks. Even within leaves there are many cells without chloroplasts, and the autotrophic cells themselves consume photosynthate in their own growth and respiration.

Developing buds and meristematic regions in roots place demands on the available assimilates and compete successfully as sinks with developing leaves (3). The onset of flowering and subsequent fruit development have a marked effect on the redistribution of assimilates; fruits develop at the expense of vegetative growth, and at this time the growth of roots may be restricted.

In a vegetative plant the developing green leaves are sinks not only for their own photosynthate but also for that produced in the older leaves. The oldest leaves near the base of the plant, provided they receive adequate illumination, export sugars to the roots. Wardlaw (70) reported that once a leaf is mature, it is no longer a sink, even when it is made heterotrophic by natural or experimental shading.

## DIVISION OF FUNCTION

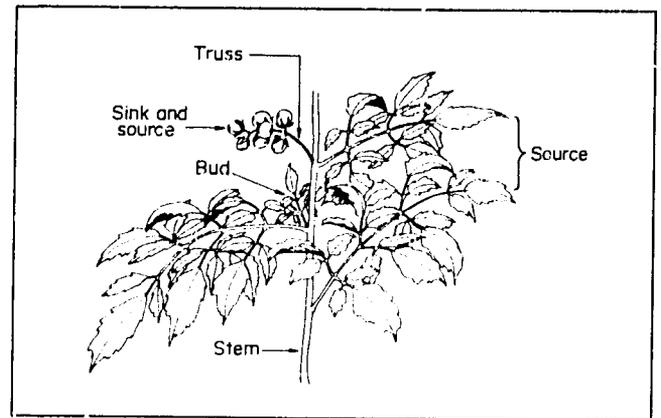
In several crop plants, and particularly in rice, there is a division of function among the leaves on a culm after the elongation of internodes. The sink for photosynthates from the upper two to three leaves is the panicle (Fig. 1); that for the lower leaves is the root system (51). Leaves in an intermediate position may send assimilates in either or both



1. Division of function. Upper three leaves translocate to panicle and lower leaves to root system, while intermediate leaves mobilize toward both ends, but mainly to roots.

directions (75). In maize, the source for ripening grains is the leaves above the ear, and the source for roots is the leaves below the ear (43). Except for several leaves at the base of the stem, which send their photosynthates to the roots, the tomato plant is composed of several units, each of which has three leaves, a truss, and a bud (54). This unit is the source-sink unit (Fig. 2), and the photosynthates of the leaves of a unit go preferentially to the sinks within the unit. However, this source-sink unit is not an absolute one. There is an interunit translocation of photosynthates, the extent of which depends on the conditions of the plant. There are source-sink partnerships between certain leaves and organs, as in tomato, where several trusses containing fruits are fed by specific leaves positioned around them, e.g., for leaf 5, the roots; for leaf 9, truss 1; for leaf 2, truss 2; for leaf 14, truss 3; and for leaf 16, truss 3 (56).

Such a system is hardly seen in higher animals because assimilation is organ-oriented. There are no special storage structures, but fat deposits are concentrated at some vulnerable points like the stomach, chest, and hips. However, animals like camels store some items like water for use



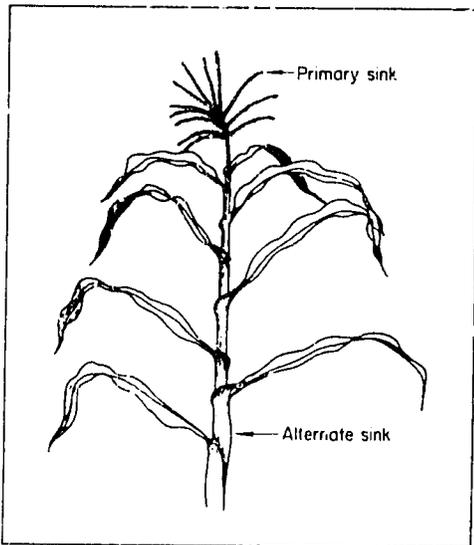
2. A source-sink unit in tomato. The young fruit can be a source because it remains green for some time.

in times of need. While in a developing plant embryo, the embryo is the sink and the endosperm is the source, in a chicken egg, the growing chick is a sink. Sources and sinks are highly interdependent.

#### KINDS OF SINKS AND SOURCES

Several kinds of sources and sinks exist in crop plants. Some plant parts are always sources; some are both sources and sinks; others are always sinks. The following descriptions clarify the types of sinks in crops:

- *Primary sinks.* These are fruits, grains, and sexual organs (Fig. 3).
- *Secondary sinks.* These occur in plants where more than one organ accumulates photosynthates and the other organ takes precedence in filling up before the sexual organs. In most cases secondary sinks also serve as material for vegetative reproduction such as rhizomes and tubers.
- *Alternate sink.* Some plants mobilize their food materials to other organs like the stems, petioles, and sheaths, after filling the main sinks (Fig. 3). Some fiber plants like hibiscus have fiber development in the stem as the primary sink, and the stem and seed as alternate sinks. In cotton, seed and oil are alternate sinks.
- *Additional sinks.* Some organisms grow in the rhizosphere on root exudates, or develop symbiosis or parasitism. The extra burden constitutes an additional sink, which can sometimes be of lethal consequence (Fig. 4). It can be a drain on the growth and productivity of the main host plant. In legume rhizobia, additional sinks can be beneficial to the host plant.
- *Metabolic sinks.* In rapidly growing cells or meristems — whether in vegetative apices, cambial regions, storage organs, floral parts, or embryos — sugar is mainly converted to new cell materials. More than half of the sugar may be diverted to protein, fats, and other cell wall constituents (3). Classical experiments with a drop of kinetin on a senescing leaf resulted in that area

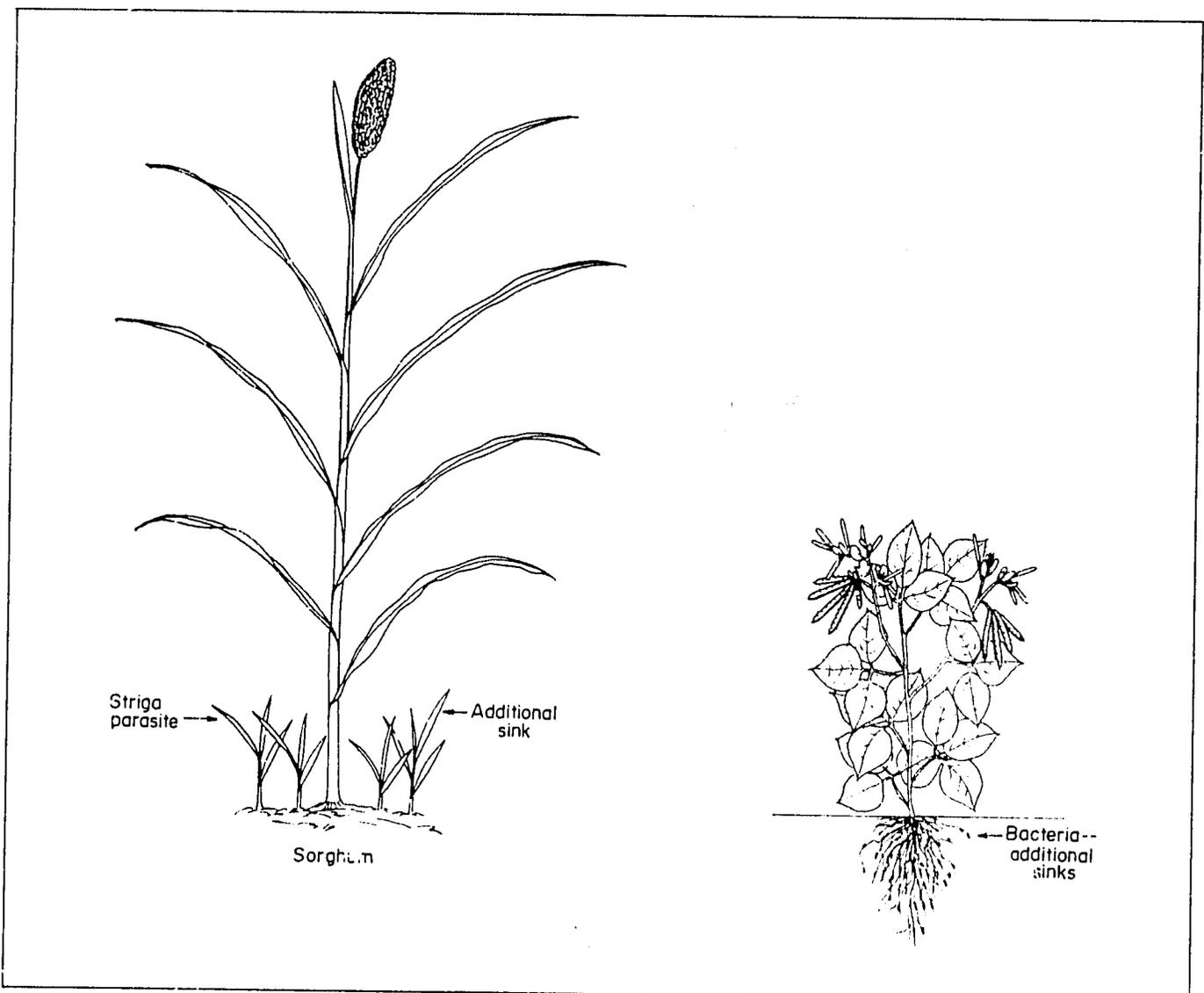


3. Alternate sink: sheath in cereals.

staying green at the expense of surrounding tissues. The kinetin induces a sink in certain cells and influences adjacent tissues to translocate to the sink. Something similar must happen normally with ripening fruits and grain. In cereal plants, the growing and maturing grain forms an intensely active sink. The production of a range of secondary products or compounds having no structural function or readily discernible role in metabolism represents a metabolic sink (3). In most plants only a small fraction of the photosynthate is diverted to these compounds, but in some, e.g., those extruding resins and latex, the drain is considerable

Sinks, then, are cells not only with a high demand for carbohydrate, but also with intensely active mechanisms for moving it across the limiting cell membranes.

The establishment of new sinks during plant growth depends on specific developmental processes whose onset may be controlled by environmental influences such as



4. Additional sinks.

temperature, photoperiod, and light intensity, which in turn depend for their expression on internal regulatory compounds.

Some sources and sinks are dynamic; others are static. Many organs in plants shift from one position to the other based on their location and demands for function.

- *Always sources:* Chlorophyll-containing cells and leaves of green plants are always considered sources.
- *Always sinks:* Tubers, roots, underground stems, developing buds, flowers, some aerial stems, and some fruits act as sinks throughout their existence.
- *Sources and sinks:* Fruits of okra, papaya, tomato, banana, mango, and grape can synthesize food materials by themselves, besides acting simultaneously as powerful sinks. Developing leaves and fruits that are green act as sinks, but when they attain full size they also photosynthesize. They originate as sinks and later function as sources. The tomato fruit might synthesize 15% of its needs and procure the rest from other sources. There is a thin line between source and sink in certain plant organs.

The role as source or sink depends on the utility, growth phase, primary and secondary functions, and simultaneous roles of an organ. The growth of a plant itself is highly sink-oriented. In the early stages all the leaves of a stem work for the growing points of the stem, leaves, and roots (51). Later, when the flower primordia initiate, they start specializing; the upper leaves work for the growing sink, while the lower ones work for the root system.

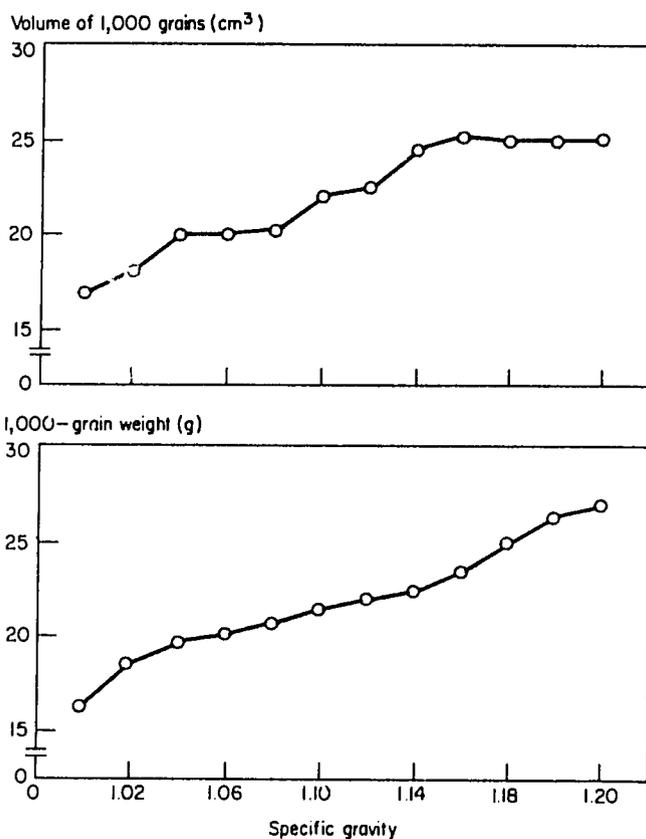
#### MEASURES OF THE SINK

Sinks are measured in terms of carbohydrates, proteins, oils, biological energy, or fresh or dried plant materials — based on the type of crop. In several crops, the sink is measured in terms of number, volume, or weight. But the number of fruits or grains per plant per unit land area does not allow comparison of crops or varieties, because number is influenced by size. When the grain or fruit is small, the number becomes larger, and vice versa. Nonetheless, number of fruits or grains is a useful measure for comparison within a homogeneous group of cultivars, e.g., those having the same growth duration, tillering habit, and grain size. Volume is a better measure than number but suffers from other limitations such as cumbersomeness in determination. Moreover, at a given volume, the packing of starch granules could be different (Fig. 5). Therefore, weight is the most dependable measure of the sink. However, a combination of number and weight helps in making comparisons and evaluations. Quantifying the sink suggests the potential yield of a crop or variety.

#### Sink size

Sink size is expressed as:

$$\text{sink size} = \text{sink capacity} \times \text{sink activity}$$



5. Volume and weight of 1,000 grains of Binato at different specific gravities.

Sink capacity is the maximum space available for the accumulation of photosynthetic products. In grain crops it is expressed as number and size of grains. The sink size of rice can be determined easily, as the hull size of the spikelet is the determinant of kernel size. Sink capacity in grain crops is expressed on a unit of land area basis, e.g.,

$$\text{sink capacity} = \text{panicles per unit area} \times \text{spikelets per panicle} \times \text{individual grain weight}$$

In fruit trees, sink capacity can be expressed in terms of fruits per tree or fruits per hectare:

$$\text{sink capacity} = \text{number of fruits per tree} \times \text{individual fruit weight}$$

Sink activity is the inherent capacity of the sink to create a translocation gradient from the source to the center of accumulation. In the reproductive structures, the sink becomes more active and shifts to a higher potential only after fertilization. The process may involve stimulation, hydrolytic conversion, and consequent creation of a moving gradient. The power of stimulation varies and could serve as a starter to determine the dimensions of accumulation. Unfortunately, few investigators have inquired into this area.

Unless both sink capacity and sink activity are fully investigated, we cannot draw complete conclusions about sink size.

### Intensity and capacity

The size of an organ that functions as a sink depends on two factors: 1) *capacity*, which can be expressed by dry weight, and 2) *intensity*, which can be expressed by specific activity. Young growing organs such as very young trusses and the stem can have very high intensity but small capacity (56). The intensity of very young leaves as sinks for the photosynthates of other leaves is not very high, because, most probably, they start to photosynthesize from an early stage of development. The intensity becomes extremely low when the leaves are old. However, their intensity as sinks for their own photosynthates is maintained for a long period. The intensity of fruits or reproductive organs as sinks is high at very early stages of their development and becomes relatively low with growth. However, since capacity increases with growth, the sink size of fruits becomes large.

### MEASURES OF THE SOURCE

The source is generally measured on an area basis despite the interference of factors like thickness, life duration, nutrition, and growth stage. In rice, source activity has been measured as percent N in leaves (62). The leaf area per plant or per square meter of land—called leaf area index (LAI)

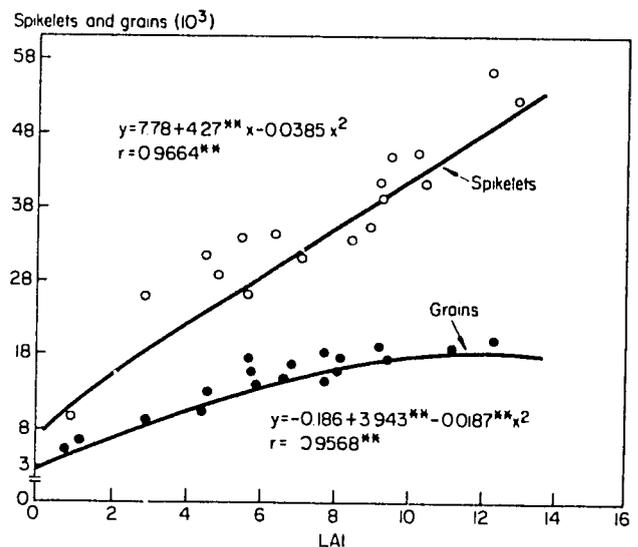
is the usual measure. Functional ability and potential capacity depend upon the crop and cultivar. Thickness, functional ability, and life duration are highly influenced by light, temperature, relative humidity, wind velocity, and nutritional factors. There is a compensatory mechanism between leaf size and leaf weight: the thickness of a leaf is the dominant function at a given leaf area. Thickness is expressed as weight per unit area of leaf and is known as specific leaf weight (SLW). In some situations LAI will not give the proper relationship with sink capacity or productivity. Hence, other leaf measures like leaf weight per tiller or per plant indicate the proper relationship. Leaf area per weight of tiller or per plant, which is known as leaf area ratio (LAR), is a good measure. Unlike the sink, the source is more vulnerable to several biotic and abiotic stresses.

The source is more sensitive to cultural, nutritional, and climatic factors. Nutritional and cultural practices often stimulate the source, making it more responsive. The source is the first organ to respond to management. Therefore, the source may suffer if stress affects its balance with the sink. Many workers (57, 63, 75) have related LAI to productivity and sink capacity (Fig. 6). The source not only produces assimilates but may exert pressure and create a translocation stream to the sink. Although the sink is the starter, it is mainly the source that pushes the assimilates through its capillary mechanism. It is not clear whether the pushing force of the source or the pulling force of the sink determines the flow, but the complementary role of both is apparent.

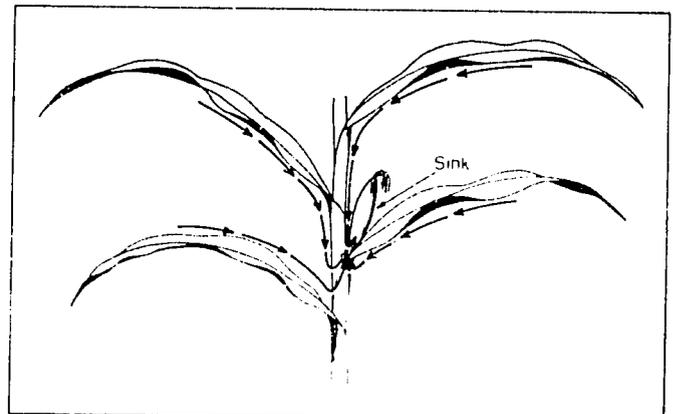
Another view regarding the movement of the assimilates to the respective sinks is that in the primary sink, some hydrolytic activity begins after fertilization and creates a

translocation gradient (67). A third view is that some substance or functional units produced in the sinks migrate to the source and enhance its functional activity, also determining its duration of activity. The production of certain hormones has been projected as a possible mechanism. It is possible that a combination of these processes occurs.

Although chlorophyllous tissue is present in several organs, the nature of its function and its effectivity vary with organ, location, intrinsic life span, purpose, and nutritional, genotypic, and environmental factors. The senescence of a leaf, its pattern of senescence, and the senescence of the sink-bearing structures are all influencing factors. The chlorophyll of culms and panicles is short-lived, but the chlorophyll of panicles, spikelets, and awns is more effective and efficient, perhaps because of its nearness to the sink. Yoshida (75) felt that slow senescence is an advantage for prolonged source-sink efficiency. In rice, however, this has not been clearly established.



6. Relationship between leaf area index (LAI) and sink size (in numbers) (66).



7. Movement of assimilates in maize toward the sink.

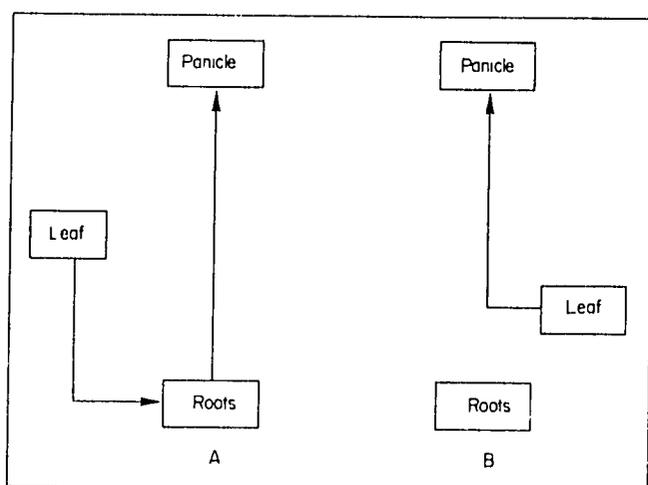
The source is sink-dependent, since the assimilates move from the source to the sink irrespective of its location. In maize, the leaves around the cob supply the cob, the movement being both downward and upward (Fig. 7). The same phenomenon is reported in tomato, pea, cotton, and other axil-borne fruits and vegetables. In tuberous crops like potato, carrot, radish, and sugar beet, the flow is invariably downward, with specific feeding channels for different tubers. Even in cereals like rice, a leaf and a branch of a panicle are partners, although tiller-to-tiller and leaf-to-leaf movements are known. Compensation among the leaves in feeding particular branches of a panicle is also observed (1).

#### TRANSLOCATION FROM THE SOURCE

The source-sink relationship between a leaf and other organs is complex; it is a function of the growth stage of the plant and the position of the leaf. In the vegetative phase, the lower leaves export more C up than down, and the upper leaves export a larger proportion downward (25, 26). In the young fruiting tomato plant, all leaves supply all the trusses, but as the number of trusses increases, groups of leaves come to have primary but not absolute responsibility for supplying single trusses.

Khan and Sagar (26) suggested that photosynthates of the leaves move down to the roots first, and then retranslocate from the roots to the growing organs of the shoots. The sequence *source* → *roots* → *sink* is not necessarily the only possibility. A direct course *source* → *sink* does exist, and is probably the major course (Fig. 8) when fruits or primary sinks are developing (56).

A similar course is known in cereals like rice and wheat among the plants exclusively depending on current photosynthetic contribution to grain yield. In others the sequence is *source* → *temporary sinks* (like culms and sheaths) → *primary sinks* under certain stresses (Fig. 8).



8. Translocation in grain crops. A: assimilates move to roots and then to panicle, B: assimilates move directly to panicle.

Most of the metabolic sinks in plants are connected with the source by phloem elements in the vascular strands. In considering the fate of photosynthate at the sinks, it is important to consider what has been established about the material moving in the phloem and the direction of its movement. The experiments of Mason and Phillis (32) and Swanson (48) have revealed several interesting phenomena.

It was considered that sugar movement into plant cells was strictly a downhill diffusion process. Concentration gradients between leaves and sinks were given strong emphasis. The concentration of sugars in leaves, where they were produced, was higher than that in the sinks; the consumption of sugars in roots, meristems, etc. was considered to give direction, if not the driving force. Of course, the rates of movement — computed from information on cross-sectional area of the phloem connection and the increasing weight of tubers and fruits (12) — showed that these were enormously greater than could be expected from simple diffusion, and direct measurements of rate of movement have shown that rates of >50 cm/h are commonly achieved.

It thus seems clear that the introduction of sucrose into the phloem cells of leaves is an active loading process, one requiring an expenditure of cellular energy (30, 70).

Australian investigators studied sugar accumulation in sugarcane internodes (4, 5, 19, 20, 47). Sugar concentration (sucrose) was roughly 29% in the mature internode, 4-10% in the young internode, and 2-3% in the leaf. No starch appeared in the storage tissue. There was no apparent downward gradient between source and sink.

#### SOURCE AND SINK DYNAMICS

Nosberger and Humphries (41) discussed the evidence for a causal relationship between the assimilation rate of photosynthetic systems and sink activity. Some outstanding examples were as follows:

- In detached rooted leaves of dwarf bean, the photosynthetic rate (Pr) is related to the activity of the root system (22, 23).
- The nature of the root stock controls the net assimilation rate (NAR) in spinach beet-sugar beet grafts (61).
- The assimilation rate of potato is controlled by tuber activity at least during the bulking period (2, 36, 41).

The evidence allows the conclusion that assimilation by these plants is linked with the size and activity of their sinks.

Lafitte and Travis (31) examined rice genotypes differing in sink-source ratio. Lines with a high sink-source ratio exhibited higher rates of C exchange per unit area and accumulated lower amounts of nonstructural carbohydrates in vegetative storage tissues than other lines. The line with the lowest sink-source ratio accumulated the most carbohydrates in storage tissue. The results suggest that the photosynthetic potential of rice was not fully realized, and that an increase in the sink-source ratio might result in

higher yields. On the other hand, the low source lines had high SLW, which may have been largely responsible for perceived increases in Pr. These observations infer that such manipulations can affect plant yields.

In wheat, when the ear is removed, the Pr of the flag leaf, which is the major source of the ear, decreases rapidly because the major sink is impaired. When the lower leaves of a plant from which the ear has been removed are darkened, the Pr of the flag leaf recovers considerably because those leaves and roots become the sink of the flag leaf (27).

However, an important question arises, viz., How far in the normal growth and development of a whole plant do the sinks determine 1) assimilation rates and 2) the flow of photosynthetic products from photosynthetic areas?

Information on the effect of sinks on assimilation rate during the normal growth and development of a whole plant is available from work on cereals (42, 44, 59), where there is more than circumstantial evidence that excluding light from parts of the photosynthetic system does not depress grain yield in proportion to the darkened-leaf area. Compensation by the remaining photosynthetic area is believed to account for the disagreement between observed and expected values. Hartt et al (18) postulated in sugarcane that some control of the amounts translocated is exerted by the blade itself. Unless compensatory effects merely reflect changed patterns of distribution, observations of this nature imply that leaves often contribute less than their full potential of photosynthates in the normal intact plant.

There is limited evidence on the effect of the sinks on the flow of photosynthetic products from photosynthetic areas during the normal growth and development of a whole plant. The best support comes from the sugar beet-spinach beet grafts of Thorne and Evans (61), where it appears that the NAR of spinach beet leaves is increased by grafting them onto a sugar beet rootstock. Sweet and Wareing (49) also reported increased Pr in pine needles by reducing the photosynthetic area.

#### **Influence of the sink**

In tomato the fruits of a truss develop and ripen by receiving photosynthates from the leaves of the source-sink unit to which the truss belongs. However, if the source exceeds the sink within a unit, the excess photosynthates may translocate to another unit. In this way the photosynthates from a unit go to the other units to a certain extent. Such interunit translocation becomes greater when the leaves or the truss of a unit is removed. Thus, there is a mutual gap-filling device among the units (54).

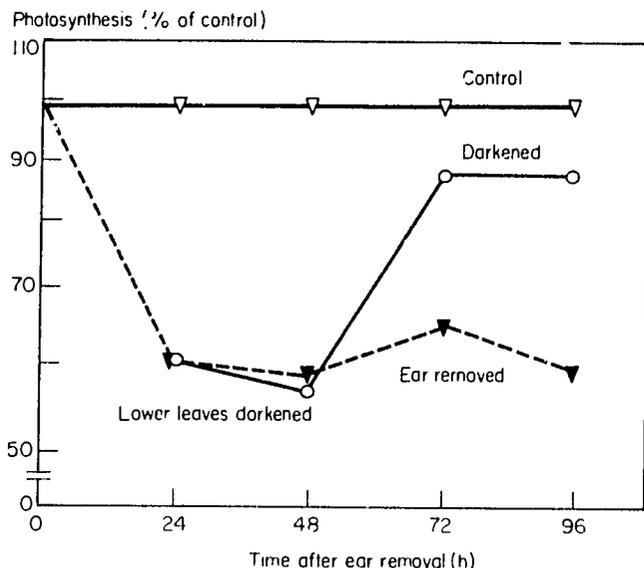
The potential size of a fruit is larger in several situations than under ordinary conditions. However, the flexibility is limited: a fruit can be about 1.5 times larger than normal when the source is extraordinarily large. For example, when T-I (T = truss) was removed in tomato, the photosynthates of the leaves of the unit to which T-I belonged translocated to T-II, and the fruits of T-II became larger, but the weight

of the fruits of T-II under these conditions was much smaller than the total weight of fruits of T-I and T-II under ordinary conditions.

When the major sink of a leaf, i.e., the fruit, was removed, the photosynthates could not leave the leaf, and translocation became as low as 10% (54). Some of the photosynthates that left the leaf accumulated again in the leaves or in the stem, which do not act as sinks under ordinary conditions, and the weight of these organs became heavier. Under such conditions, the leaves became curled and pigmented, and died early.

Pr responds to the demand for assimilates. In wheat, during grain filling, when most of the assimilates from the flag leaf are translocated to the ear, removal of the ear leads to an accumulation of assimilates in the flag leaf and to a fall in its Pr by about half within hours. If the lower leaves are shaded so that the flag leaf has to support the rest of the plant, the assimilates are exported at a high rate, and the Pr rises to its original level (27). Such pronounced feedback effects have not always been found, probably because alternate sinks for assimilates, such as young tillers, were present.

Demand for assimilates can also influence the rate, velocity, and translocation pattern in wheat (45, 69) and presumably in other plants. Another subtle relationship that has been recognized for many years (27, 40) is that the size of activity in the sink may have an influence on Pr in the source leaves. If assimilates are not transported to sinks, Pr is depressed, and if new sinks are provided, Pr is increased. Neales and Incoll (40) summarized the effects of changing status of sinks, which suggest control of Po such as 1) decreased rate on detachment, 2) fatigue effects and midday depression of Pr, 3) increased Pr in the remaining leaves following partial defoliation, 4) decreased Pr following interference with translocation or removing sink, 5) decreasing Pr at temperatures suboptimal for growth, and 6) influence of grafting different sinks. However, other possibilities cannot be ruled out, such as feedback from sink to source, including hormonal signals. Wareing et al (71) showed that the stimulatory effect of partial defoliation on remaining leaves caused increased levels of protein and particularly of carboxylating enzymes. They suggested that a corresponding increase in photosynthetic capacity, rather than increased relative demand by the sink, was responsible for the higher Pr of surviving leaves, and they favored a dynamic hormonal interaction between sink and source. However, King et al (27) showed that in wheat, 2 wk after anthesis, 45% of the flag leaf assimilates were transferred to the developing ear, which was itself photosynthesizing. Removal of the ear resulted in a 50% reduction in Pr of the flag leaf within 15 h. Darkening of the other leaves resulted in recovery of Pr of the flag leaf, with the assimilates being diverted to roots and shoot (Fig. 9). Under some conditions inhibition of Po in the ear brought about an increased Pr in the flag leaf. In this system, then, there are relatively rapid



9. The rate of net photosynthesis of wheat flag leaves after various treatments (27).

interactions, and the Pr of the source appears to be closely regulated by the demands of the sink.

#### Source-sink grafts

The tomato experiments of Khan and Sagar (26) showed that the proportion of current photosynthetic production that is exported in a 24-h period may be increased by reducing the size of the source or by increasing the activity of the sink through growth-regulating compounds. They conducted grafting experiments with potato and tomato. A plant with potato scion on tomato stock produced neither tubers nor fruits, and export from the leaves was very low. Yet when the graft was reversed and both tubers and fruits were formed, the amounts exported were doubled. Therefore, the authors contended that for both tomato and potato leaves, the presence and activity of sinks play a role in determining the rate of export of currently produced assimilates.

In such systems where the sinks control distribution of the photosynthates, competition between sources will occur (18, 25), perhaps leading to accumulation of material in or close to the channels of transport. Nosberger and Humphries (41) reported increases in sugars, starch, and protein in potato stems and leaves following the removal of tubers. Nosberger and Thorne (42) observed similar diversions where sink size was reduced in barley. More research is needed to determine how far the growth and development of plants is controlled by sink activity on the one hand, and by direct and indirect effects of environmental factors on the other.

In an intact plant with numerous sinks, cause and effect cannot always be distinguished (22); it may not be obvious whether increased  $P_o$  is a consequence of greater sink capacity or whether increased growth of the sink is a result of greater assimilation. To clarify this situation, rooted

detached leaves of dwarf bean *Phaseolus vulgaris* were used. This simple system has a photosynthetic surface that changes little in time, and a single sink that can be varied in size. Carbohydrate moves from the lamina in one direction only, because no bud arises to initiate stem growth. Root growth rate controls the rate at which photosynthetic products move from the lamina, and any treatment that increases root growth rate and accelerates translocation rate also increased NAR. Photosynthates accumulate steadily in the leaf, while NAR does not vary; so it is not accumulation of products that inhibits  $P_o$  but the rate of movement of photosynthates from the source that is the important factor.

May (34) discussed the possibility that  $P_o$  in pasture plants is limited by rate of translocation, causing assimilates to accumulate in the leaf. Brenner (8) found that after peas had begun to flower and fruit, the same assimilating area delivered fewer assimilates per week than before, and he thought that inhibition of growth caused assimilation products to accumulate and to decrease assimilation. Went (72) postulated that in some circumstances Pr might be limited by growth rate; he suggested that translocation of photosynthates out of the leaf cells also controlled Pr.

#### LIMITATIONS IN SOURCE AND SINK

Some studies show that the sink is a limiting factor for achieving higher yields. Other studies suggest that the source limits yields. The source is the powerful system that creates the sink and sustains it. It is therefore natural that the source determines sink capacity and any alternate, secondary, and metabolic sinks. In considering improvements in crop plants, it is necessary to identify whether the yield-limiting factor is the source or the sink.

#### Source as a limiting factor

In several cereals, including traditional unimproved rice varieties, at high N levels, the yield-limiting factor is the source. An improvement of the source through an improvement in plant type can remarkably improve grain yield.

The leaf is the major source in crop plants, although other organs can assimilate C. Leaf clipping and organ shading studies (14, 29, 63) have indicated that the leaf is a major determinant of the nature of grain filling.

In rice, the leaves contribute about 51% of the grain yield (63), while nonstructural carbohydrate contributes 15%, the stem up to 18%, and the panicles up to 16%. In rice the ear contributes less — only 8-23% (14) — while in wheat the ear contributes 10-49% (7, 29). There is hardly any contribution of reserves in wheat under normal conditions, while under stress conditions accumulated reserves are utilized to varied degrees. Thus, the leaf emerges as a major contributing factor that is unfortunately vulnerable to various stresses in the field, like moisture stress, low light intensity, low and high temperatures, mutual shading, insect pests, and diseases. In a shading study (63), stem weight, total dry

matter, tillers, grain yield, and grain filling were severely affected, although change in leaf weight was insignificant (Table 1). Although the leaf is endowed with capabilities, its function is subject to various stresses operating under competitive and isolated systems.

When the source and the sink were varied by adopting different population densities and N levels, the increase in LAI (source) was not reflected in increased grain number. Grain number was far lower than spikelet number (Fig. 10), indicating the possibility of obtaining higher yields with proper support from the source (63, 65). The increased LAI leads to considerable production of spikelets, but a sizable number do not fill. Similar data from other important centers in India (viz., Cuttack, Pattambi, Mandya, and Calcutta) also confirmed that, despite increased LAI, the gap between spikelet number and grain number remains very wide. This is now recognized as a general phenomenon in several modern rice cultivars.

A path coefficient analysis made with LAI, total dry weight (source), spikelet number (sink), and spikelet sterility (39) revealed LAI is the major source component exerting the largest direct influence (negative) on sterility, followed

by sink or spikelet number (positive) (Table 2, 3). Source capacity exerted the largest influence on sterility and hence should be enhanced to realize higher filled grain number.

In several studies in rice in tropical and subtropical climates, the proportion of partially filled grains and chaff was higher, and the gap between spikelets and grains was seen at all LAI levels. The gap was wider at higher LAI levels. Such a situation raises the question of whether sterility is a prefertilization or postfertilization problem. If it is a prefertilization problem, the source is out of the picture, and the factors concerning failure of fertilization are to be blamed. Observations of fertilized and nonfertilized spikelets (Table 4) decisively show there is no apparent constraint operating at the fertilization level irrespective of the N status of the crop (65). In addition, the data on chaff, partially filled grains, and filled grains even at different N levels infer that the former two fractions are high and suggest that photosynthates do not adequately reach the spikelets to convert them to grains. The source is probably unable to meet the demands of the sink in competitive communities.

**Table 1. Effect of continuous shading (40-50% of natural light) on dry matter distribution, tillers, filled grains, and grain yield of rice variety Sona, 1973 dry season (63).**

Character	Control	Shade
Leaf weight (g/hill)	2.5	2.4
Stem weight (g/hill)	13.1	6.5
Total dry weight (g/hill)	45.0	22.3
Tillers (no./hill)	18.0	10.0
Grain yield (g/m <sup>2</sup> )	820.0	275.0
Filled grain (%)	77.0	59.0
Sterility (%)	23.0	41.0

**Table 2. Correlation coefficients of source and sink capacity (39).**

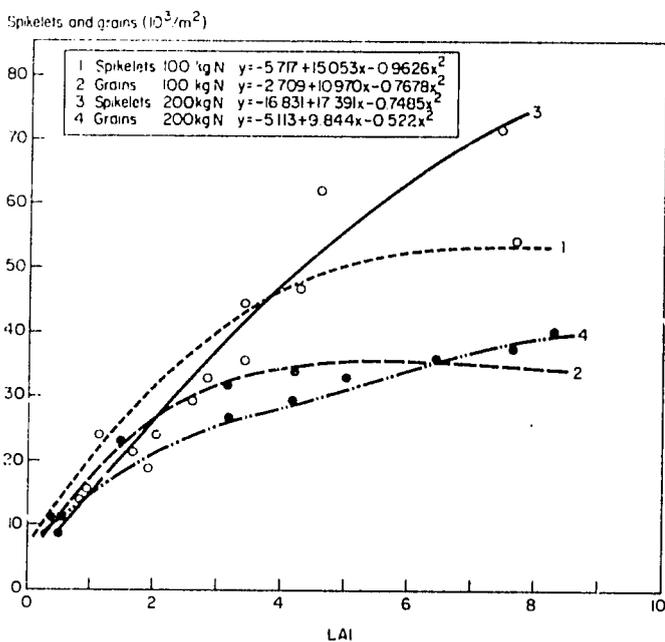
Variable <sup>a</sup>	r-value <sup>b</sup>
YX <sub>1</sub>	0.42*
YX <sub>2</sub>	-0.56**
YX <sub>3</sub>	0.57**
X <sub>1</sub> X <sub>2</sub>	0.44**
X <sub>1</sub> X <sub>3</sub>	0.08
X <sub>2</sub> X <sub>3</sub>	0.15

<sup>a</sup>X<sub>1</sub> = total dry weight at flowering, X<sub>2</sub> = leaf area index at flowering, X<sub>3</sub> = spikelet number, Y = spikelet sterility. <sup>b</sup>\* = Significant at the 0.05 level, \*\* = significant at the 0.01 level.

**Table 3. Direct (diagonal) and indirect effects of source and sink on sterility (39).<sup>a</sup>**

Character	Source		Sink	Total correlation with sterility (%) <sup>b</sup>
	TDW at flowering	LAI at flowering	Spikelet no.	
TDW at flowering (source)	0.28	-0.16	0.02	-0.42
LAI at flowering (source)	0.13	0.38	0.05	-0.56*
Spikelet no. (sink)	0.02	0.25	0.34	0.57

<sup>a</sup>Residual factors = ± 0.74, coefficient of determination = 0.4524. TDW = total dry weight, LAI = leaf area index. <sup>b</sup>\* = Significant at the 0.05 level.



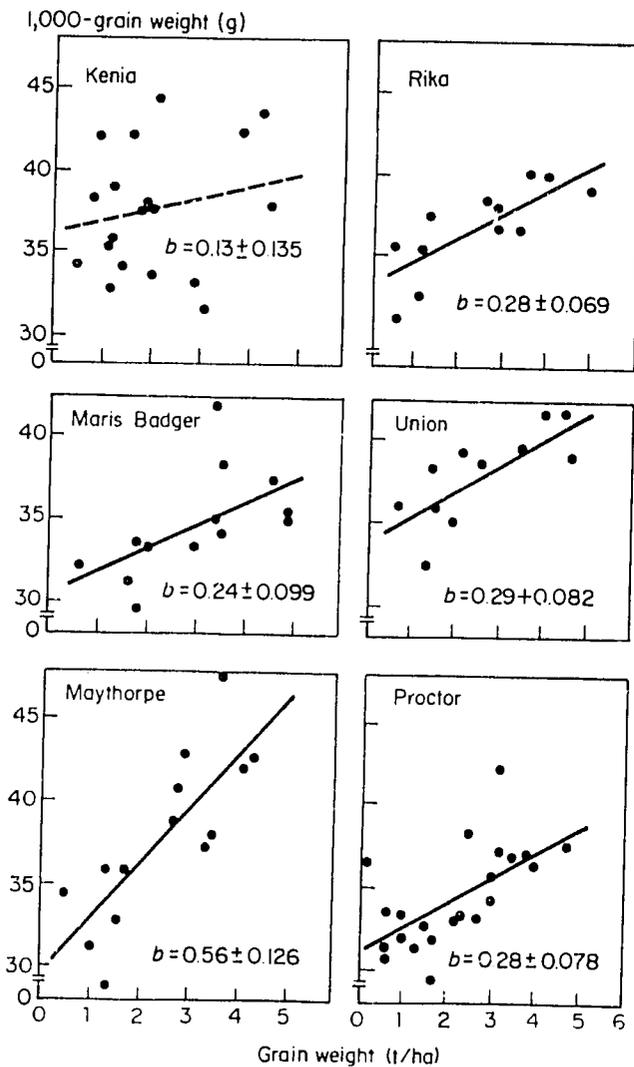
**10. Relationship between source and sink in rice (63).**

**Table 4. Fertilized (F) and nonfertilized (NF) spikelets (%) in short-duration and medium-duration varieties, 1974 wet season (65).**

N level (kg/ha)	Short-duration varieties						Medium-duration varieties					
	Cauvery		IEF1444		RP79-14		Sona		Jaya		RF4-14	
	F	NF	F	NF	F	NF	F	NF	F	NF	F	NF
0	95	5	95	5	93	7	90	10	96	4	93	7
50	92	8	92	8	92	8	92	8	96	4	93	7
100	90	10	94	6	90	10	93	7	95	5	94	6

**Table 5. Effect of shading (45-50% of natural light) during flowering to maturity on sterility and yield components of rice, 1974 dry season (65).**

Parameter	Sona		Vijaya		RP4-14	
	Control	Shaded	Control	Shaded	Control	Shaded
Chaff (%)	20	52	27	41	17	47
Partially filled grains (%)	20	31	17	21	12	14
Filled grains (%)	60	17	56	38	71	39
Panicles (no. / m <sup>2</sup> )	486	440	421	358	595	573
Grains (no. × 10 <sup>3</sup> / m <sup>2</sup> )	30.0	11.1	43.7	18.1	48.1	23.8
Grain yield (t/ha)	9.9	3.8	9.8	4.6	10.1	4.2



11. Regressions of 1,000-grain weight on grain yield for 5 barley varieties, introduced between 1951 and 1963, and for Kenia, introduced in 1934 (Data from trials of National Institute of Agricultural Botany) (60).

This raises another question — whether the supply or the translocation of photosynthates is a limitation in grain filling in several cereal crops. To clarify this point, data on chaff, partially filled, and filled grains, and grain yield were collected from a crop shaded from flowering to maturity. The chaff and partially filled grain percentages were very high in the shaded crop, the chaff being 52% in Sona and 41% in Vijaya and Prakash (65). The partially filled grain

percentage in the shaded crop was 31% in Sona, 21% in Vijaya, and 14% in Prakash; the partially filled grain percentages were 20% in Sona, 17% in Vijaya, and 12% in Prakash (Table 5). Thus, inadequate leaf support or supply can cause a high proportion of unfilled grains and, therefore, assimilation or support could be more limiting than translocation. Under competitive conditions, mutual shading might still reduce the supply of the photosynthates. However, the environment, particularly a combination of moderate temperatures and moderate light intensity, might enhance the activity of the source and narrow the gap between spikelets and grains.

Thorne (60) showed that the increased grain yield of modern barley varieties is closely correlated with increased grain weight. Obviously at the present level of grain yields and climate in England, yield capacity does not limit the grain yield of these barley varieties, but the activity of the source, perhaps controlled by light intensity during ripening, limits yield (Fig. 11).

#### Sink capacity limits yield

Evans (15) listed evidence that photosynthetic capacity does not limit yield. Leaf size has increased more than  $P_0$  has fallen in the course of evolution, but since ear size has increased even more than leaf size, the supply of assimilates could not have been limiting.

The balance sheets of supply and demand for assimilates throughout grain development for several productive wheat varieties grown under controlled conditions show that even during peak demand, ample amounts of assimilates are available for grain filling (16).

In the field and under controlled conditions, shading or leaf removal have only small effects on grain growth and yield, implying that the supply of assimilates is not limiting. Rawson and Evans (46) reported that increases in flag leaf  $P_r$  and in the mobilization of stem reserves compensate for inhibition of ear  $P_0$ . Another indication of surplus supply of assimilates is the almost linear increase in grain weight per ear during the middle period of grain filling under controlled temperature despite substantial variations in incident daily radiation found in Triple Disk wheat (45) and maize (13).

Treatments involving sterilization of the most advanced florets in ears of Triple Disk wheat at anthesis increased the total grain set and yield per ear by 20% (45), implying that assimilate supply does not limit grain yield.

Lowland rice lends itself to a different, but less conclusive, approach to the question of whether photosynthetic capacity limits yield. Murata (37) found a good correlation between the Pr of the flag leaves of six rice varieties and their crop growth rate, but little correlation between their Pr and grain yield at a given level of N, again suggesting that the supply of assimilates did not limit yield. Yin et al (74) and Murata (38) reported that yield was closely related to spikelet number per square meter, suggesting that storage capacity limited yield.

The CO<sub>2</sub> concentration in the atmosphere is also likely to limit grain yield. Yoshida (76) studied the effects of CO<sub>2</sub> enrichment on grain yield before and after heading. Enrichment before heading increased grain yield 29%, and after heading, 21% (Table 6). The yield increase from CO<sub>2</sub> enrichment before heading was caused by increased grain number and grain weight. Enrichment after heading did not change grain number but increased grain weight and filled grain percentage. Hence, if the yield capacity can be increased by some means, apparently neither photosynthetic capacity of the plant, light, nor CO<sub>2</sub> concentration is likely to limit grain yield, at least in Los Baños (80).

Yoshida (78) further reported a close correlation between grain yield and grain number per square meter. The grain

weight and filled grain percentage were practically constant, suggesting that total grain number limits the yield of IR8 in Los Baños (Fig. 12). Sink size is the limiting factor for grain yield.

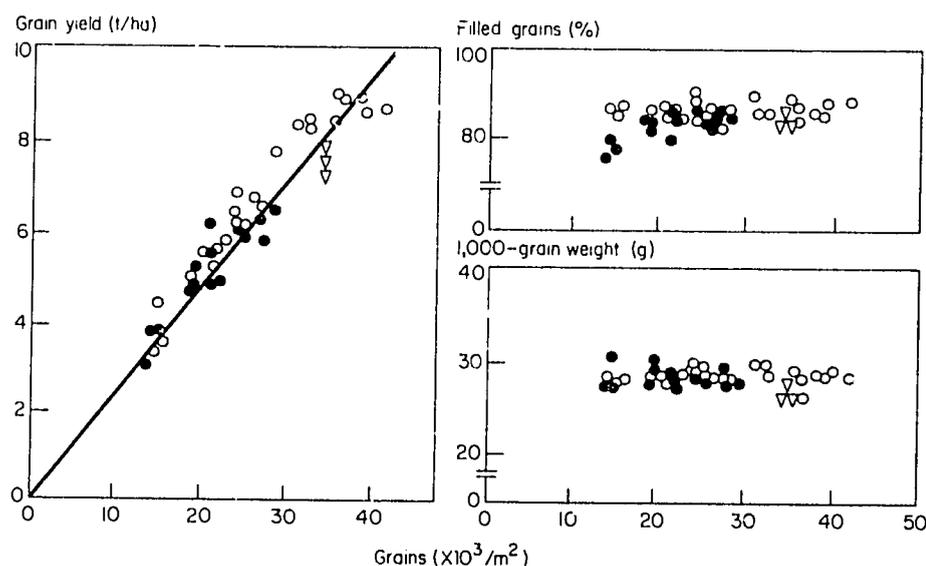
Tanaka et al (55) found that the photosynthetic potential of tomato leaves seems to exceed the requirements of growing organs, and the leaves generally continue to grow even when the fruits are developing rapidly. They also reported a continuous accumulation of carbohydrates in the vegetative organs during rapid fruit growth. In the rice plant, on the other hand, there is apparent retranslocation of accumulated carbohydrates from the vegetative organs to the grains during ripening (51), and a similar phenomenon is observed in maize, although the amount is limited (58). There are also reports that some leaves of tomato can be removed without impairing yield (11). The young developing vegetative organs, such as the apex of the stem or the lateral buds, do not consume a large amount of photosynthate, because these can photosynthesize from early stages of development, unlike in cereals, where the growing points are always hidden by the leaf sheaths (54).

Murata (38) gave three examples for the relative importance of yield capacity and assimilate supply to grain yield: 1) yield capacity (sink) is limiting; 2) assimilate supply

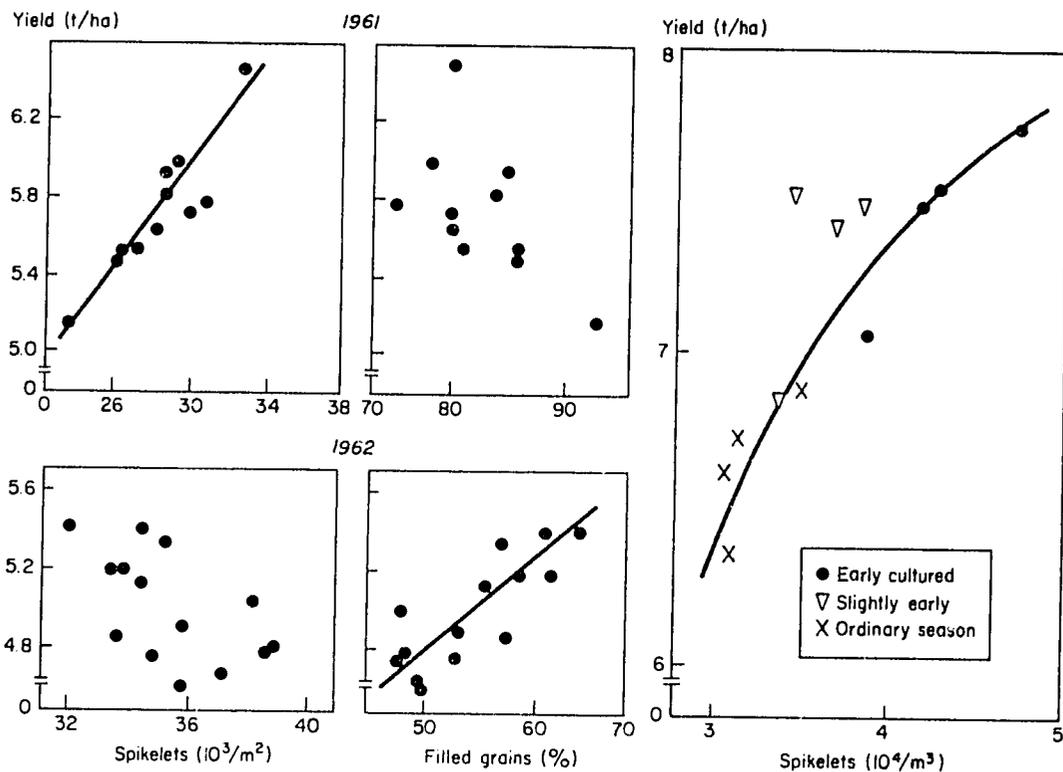
Table 6. Effect of CO<sub>2</sub> enrichment before and after flowering on grain yield components of IR8. IRRI, 1972 dry season (76).<sup>a</sup>

Time of CO <sub>2</sub> enrichment		Yield (t/ha)	Grain no. (10 <sup>3</sup> /m <sup>2</sup> )	Filled grains (%)	Grain weight <sup>b</sup> (mg)
In relation to flowering (d)	Developmental stage <sup>c</sup>				
Control (no CO <sub>2</sub> enrichment)		10.2 c	40.4 c	85.4 b	27.5 d
33 to 24	I	11.3 b	45.0 ab	84.2 b	27.7 d
24 to 14	II	11.4 b	43.4 bc	86.2 b	28.7 c
14 to 0	III	10.2 c	38.9 c	85.8 b	29.1 bc
33 to 0	I-III	13.3 a	48.2 a	87.6 b	29.9 ab
0 to 30	IV	11.5 b	38.9 c	92.4 a	30.2 a

<sup>a</sup>Means followed by the same letter are not significantly different at the 5% level by Duncan's multiple range test. <sup>b</sup>I = neck node differentiation to differentiation of secondary rachis-branch, II = differentiation of spikelets, III = differentiation of pollen mother cell, reduction division stage to flowering, IV = flowering to harvest. <sup>c</sup>Panicles were dried at 75 °C for 48 h, and threshed, then grains were kept at 50 °C for 12 h and weighed.



12. Relationships between total number of grains per square meter and grain yield, filled grain percentage, and 1,000-grain weight (○ = dry season, ● = wet season, ▽ = direct seeding) (78).



13. Relationships of brown rice yield to spikelet number and percentage of completely filled grains of rice plants cultured under various combinations of plowing depth, planting density, and N level (38).

(source) is limiting; and 3) yield capacity and assimilate supply are well balanced (Fig. 13). Such instances are due mainly to the cultivar. It is possible to have all these combinations in other crops. Identifying such varieties helps greatly in formulating cultural and nutrient management for maximizing productivity.

#### SOURCE-SINK MECHANICS

Both source and sink could grow independently, or their growth could be based on some ratio. In crop plants, three different situations can be visualized: 1) the source could be greater than the sink in physical area; 2) the sink size could be greater than the source; and 3) both could be in dynamic equilibrium.

#### Source greater than sink

Traditional varieties in several crop plants possess greater sources than sinks because they are leafy. In the course of crop improvement, leafiness is reduced and sink size gradually increases. Greater source capacity leads to poor crop performance as fertilization and other cultural practices result in greater foliage and poor productivity. The best examples are the cereals, pulses, oilseeds, and a variety of trees, shrubs, and annuals.

Even within a crop or cultivar, there are shifts in source-sink balance based on nutrient availability, environmental conditions, and the soil-water system. Among cereals,

particularly in rice, maize, and wheat, at low N levels, the plant produces enough leaves but poor panicles with unproductive tillers. Nutrient deficiencies (e.g., P, Zn, Mn), toxicities (e.g., Fe, Al), salinity, or alkalinity normally lead to adequate leaves but very poor returns of grain. In all these situations the source is greater than the sink size.

#### Sink greater than source

In some fruit trees (e.g., mango, citrus, guava), vegetables (e.g., cucurbits, tomato), pulses (e.g., pigeon pea, gram), oilseeds (e.g., groundnut, gingelly, sunflower), and cotton, the sinks in terms of flower buds, fruit set, pegs, pods, and bolls are greater than the sources. But they prematurely drop due to inadequate assimilate supply, the formation of an abscission layer, or both. In mango, citrus, and guava, an increase of 1-2% in fruit set may lead to a 50-100% increase in crop yield. Hence, they call for appropriate nutrient and crop management, besides genetic improvement in the capacity of the source.

Even in cereals and other grain crops, breeding has resulted in greater sink size. In several situations, although the sink size is adequate, grain yield is poor. Even in rice, increased LAI is not associated with increased grain production but reaches a plateau (63). The gap that exists between spikelets and grain increases with increased LAI. These cultivars and crops require proper treatment to enhance the functional capabilities of their sources. In some situations, their physical leaf area is adequate and even more than required, but the functional efficiencies are far lower.

### Source and sink in equilibrium

The sink in rice, particularly the number of spikelets formed per square centimeter of leaf, was projected to elucidate the trends between source and sink in physical terms. The number of spikelets formed per square centimeter of leaf at different LAI values was worked out (65); based on those calculations, the possible spikelet production at different LAI levels was determined. The actual spikelet number at the respective LAI levels served as checks. There were varietal differences by duration and genotype. In Jaya (medium-duration type), at 0 N level, the spikelet number per 1 LAI was 8,500, which meant there could be 34,000 spikelets per around 4 LAI; but actually only 23,000 spikelets could be realized, suggesting that at lower N levels, sink size was smaller than the source. But at 50 and 100 kg N levels, spikelet production increased proportionately with higher LAI values (around 4-5), suggesting a tendency for equilibrium between source and sink. Interestingly, when the same analogy was applied for RPW6-17 (late type), source and sink were in equilibrium at all N levels. Obviously, in several irrigated rice varieties grown in nonproblem soil, source and sink are in equilibrium except in situations where nutrients, particularly N, are at lower levels.

Apparently, either a larger source or an increased sink size results in lower productivity; despite full expression of the sink, the realization of yield is lower due to smaller sink size in the former, and to partial realization of sink in the latter. When both are in equilibrium, there is the risk of lower and unstable yields, because the source is more sensitive to climatic, water, soil, nutritional, and biotic factors. However, when the environment and climate are favorable, high spikelet number is associated with high or matching filled grain number. Therefore, instead of large physical dimensions of the source, greater and more stable functional efficiency at moderate source size are more advantageous to realize the potential sink size under field conditions. Thus, based on crop and variety, different situations exist among source-sink combinations. Such analysis can clarify the goals of varietal and crop management programs.

### INCREASING SINK SIZE FOR ENHANCED YIELD POTENTIALS

Higher sink size could be realized through appropriate blending of fertilization and cultural management in a given environment. In cucurbits, fruits like mango and citrus, fiber crops like cotton, and pulse and oilseed crops belonging to the Leguminosae, there is considerable flower, premature bud, and fruit drop. The potential sink size is always high, but the realized sink is lower. Hence, in these crops realization of higher sink or yield depends mainly on sustaining the existing sinks. Cultural practices aimed to retain more buds would give higher yields. Increasing the size of fruits and vegetables also increases yields con-

siderably; in some the sizes could be increased 50%. Moreover, the large proportion of fruits and vegetables below normal size indicates scope for enhancing their possible yields.

In cereals, particularly in rice and wheat, sink size is increased through appropriate combinations of cultural, nutritional, and water management factors. However, the potential has a limit beyond which it is almost impossible to increase sink size in terms of number. The differences are generally attributed to variety. In cereals like rice, potential sink size is based largely on spikelet number, while the realized sink in terms of filled grains is invariably lower.

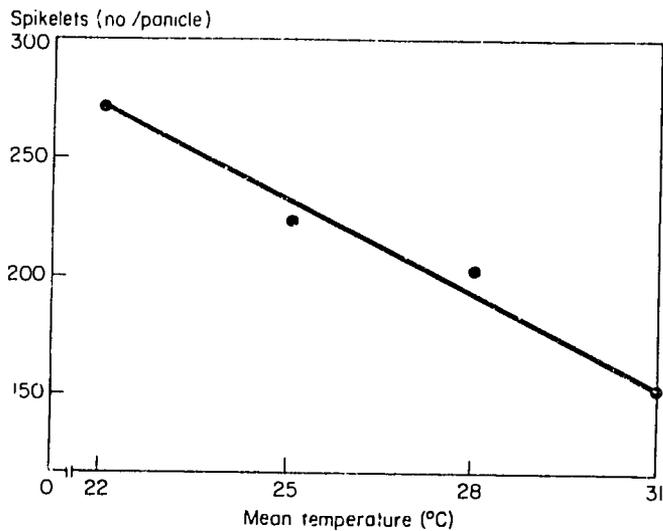
The development of inflorescence of maize, wheat, rye, barley, and oats is well documented by Bonnet (6). For rice, Matsushima's work (33) is most extensive and informative. Differentiation of panicle neck node in rice starts about 32 d before flowering. The differentiation of spikelets proceeds from about 23 to about 15 d before flowering, during which time the maximum number of spikelets is determined. Spikelet degeneration occurs afterwards, during the reduction division stage, which occurs about 11-13 d before flowering and is most sensitive to degeneration. The size of hull is determined 1 wk before flowering. Thus, the potential size of the rice panicle is determined largely during the period from 32 to 15 d before flowering. After this period insufficient nutrition or adverse climate can cause spikelet degeneration.

From the physiological point of view, panicle size may be increased if more assimilates go to developing panicles. This can be achieved in two ways: by increasing total  $P_o$ , or by increasing partition of more assimilates into developing panicles. Nutritional factors increase photosynthesis. Another way of increasing  $P_o$  is through  $CO_2$  enrichment. Yoshida (76) showed that  $CO_2$  enrichment for 33 d before flowering increased grain yield 30%, largely attributable to increased spikelet number and grain weight, i.e., increased sink size.

The combination of light and temperature not only controls spikelet production but conditions the degree of grain filling. Moderate light and temperature are ideal for realizing higher sink levels. High temperatures in association with either low or high light intensities are detrimental, as are low temperatures with low light intensities. Yoshida (77) reported that in a controlled environment and within a temperature range of 22-31°C, spikelet number per plant increased with lower temperature (Fig. 14). However, for vegetative growth, higher temperature was more favorable within the same temperature range. Relatively low temperature around panicle initiation produced larger sink sizes in rice in tropical and subtropical conditions.

Characterization of sink potential goes a long way in formulating action plans for their realization. In one study different panicle numbers were created by adopting various plant densities and N levels. Beyond 400 panicles/m<sup>2</sup>, spikelet number either was quadratic or plateaued. Grain number followed suit, with a gap at all levels and particularly

increasing at higher levels (66), inferring that total spikelet number did not vary significantly despite higher number of panicles per square meter. Forty or fifty thousand spikelets are accommodated in 400-800 panicles. Thus, the content is limited and does not respond beyond a limit set by the variety. In such situations nutrient and cultural operations should aim at bridging the gap between spikelets and grains. Studies on sink potential would clarify future goals concerning not only increased grain filling but also enhanced potential sink size.



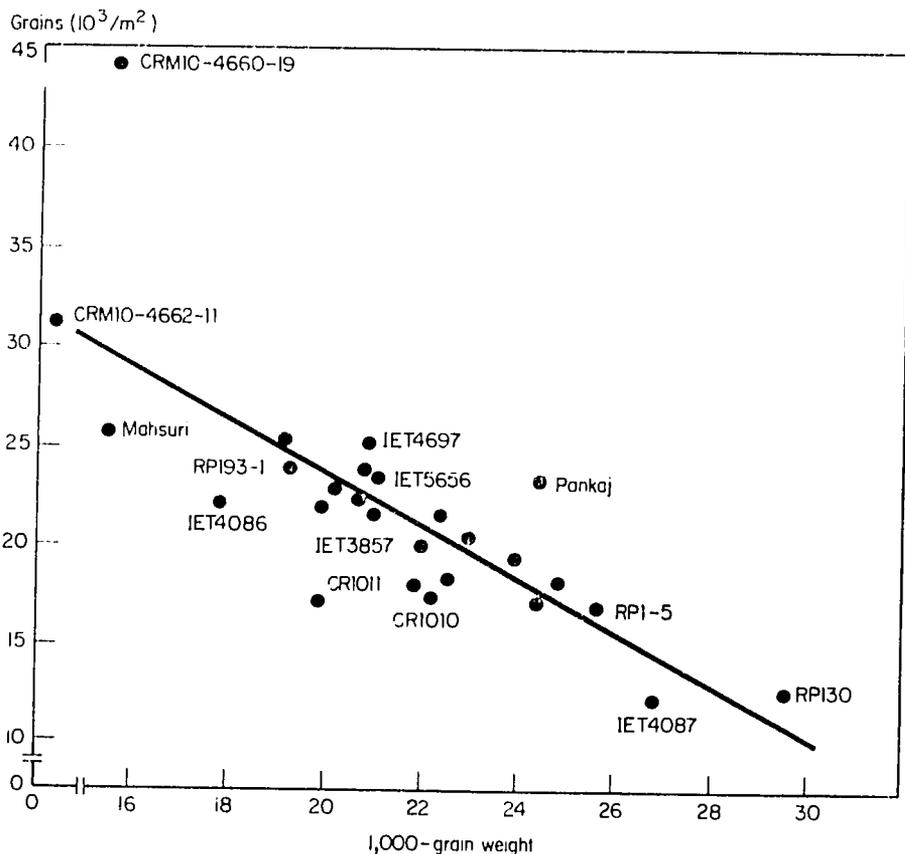
14. Spikelets per panicle vs daily mean temperature, 25 d before flowering (78).

Some studies have indicated that in rice, grain number is compensatory with grain size beyond a 1,000-grain weight of 39 g (24). In another effort (68), there was no compensation in short- and long-duration rice varieties (Fig. 15); it was felt that grain number could be increased at a 1,000-grain weight of 22-24 g. Obviously, increased spikelet number at a given size and enhanced size at a given number would ultimately increase sink size. This situation calls for assessment of genetic materials for number and size.

Growth-regulating substances are used to enhance sink size and stimulate sink activity. Foliar spray of gibberellic acid (GA) at the reproductive stage increased spikelet number and hence grain yield (50). In wheat, injecting chlormequat chloride (CCC) into the stem at anthesis increased grain number but decreased the weight of single grain. In barley, cytokinin activity in caryopses decreased rapidly after pollination during ripening. De-awning or excessive moisture decreased cytokinin activity, which was associated with larger grain size (35). These studies suggest that spikelet number or grain setting can be increased by controlling hormonal activity without any increase in Po.

SOURCE POTENTIAL

In nature, chlorophyll is abundant. The leaf is several times larger than the seed, fruit, vegetable, or tuber. Probably this evolved to make the source-sink system a risk-free enterprise. In several crops, improved cultivars possessed greater leaf area, which was sensitive and responsive to climatic,



15. Relationship between grain weight and grain number in rice (68).

cultural, and nutrient factors. Scissoring of such leaf area brought the revolution in production potentials in modern varieties, particularly in cereals.

Leaf number, size, thickness, position, angle, rate of development, and functional abilities determine the level of crop performance. In modern rice and wheat varieties, excessive leaf area does not lead to lodging or lower productivity as in traditional varieties. However, since it does not enhance productivity or grain filling, efficiency is a more important consideration.

In one study, the leaf area was manipulated to the level of 11 LAI, but the spikelet and grain numbers did not change; increased source size did not help in increasing grain number (66). This means that the source (leaf), even in modern types, is still more responsive than the sink (panicles). The leaf is becoming thinner and probably losing its functional efficiency, as it was compensating through thickness. Promoting functional ability in stress conditions and controlling the responsive and reactive nature of the source would enhance potential yield. The question of whether we should prefer a thicker or thinner leaf has not been conclusively answered, although thinner ones appear to be better in diffused light and thicker ones in bright light. The reflection and absorption of radiation and the sustenance of the leaf in relation to different degrees of thickness have to be worked out before any valid conclusions on the desirability of the nature of the source can be drawn.

Finally, it boils down to determining what is limiting in furthering yield potential. Is it the sink or the source? Experience has shown that in japonica rice, all spikelets are filled in several favorable situations, and therefore many believe that further improvement in the sink would enhance yield potential. In indicas, a clear gap exists between spikelets and grains in several tropical and subtropical climates, suggesting that the source is the limitation. Identification of the yield-limiting factor is the key to the consideration of a rational method to further improve grain yield.

#### AGRONOMIC MANIPULATIONS OF SOURCE AND SINK

Agriculture is the manipulation of the source and the sink for realizing higher productivity. Nutrients are added mainly to enrich and efficiently manage the source. Nutrient application enriches the chlorophyll system and favors functional efficiency, which results in luxuriant growth. Nutrients are also applied around flowering to early grain filling in some cereals, fruits, and vegetables to catalyze the grain- or fruit-filling process, leading to higher productivity. Cultural manipulations involving population density, row orientation, time of sowing, and monocropping all facilitate the efficient functioning of the source. Even the plant type concept mainly concerns the greater utilization of solar energy and nutrients through the functional efficiency of the leaves.

The principles of fertilization in agricultural crops are oriented not only to source efficiency but also to sink productivity. Spraying growth-regulating compounds is meant not only to stop preharvest fruit drop, but also to enhance the size and quality of vegetables, fruits, and fibers. The uses of GA in grapes and guava; naphthalene acetic acid (NAA) in mango, guava, and citrus; and CCC and NAA in cotton are good commercial practices. Sink size is manipulated for higher sink realization. Cultural practices like pruning in grapes and tailoring of cucurbits are efforts to increase sink size. Even selection pressure in crop plants is sink-oriented. Modern technology is concentrating on finer manipulations of sources and sinks for enhancing potential productivity.

Sink size is apparently limiting in cereals because of the existing wide gap between theoretically possible yields (20-24 t/ha in rice) and actual maximum yields with modern plant types (8-16 t/ha). However, one can also argue that at the present level of evolution, both source and sink are limiting; if one is increased the other is likely to decrease, and vice versa. But the main question is whether in contemporary varieties the source or the sink size is limiting. This answer would clarify the level of manipulation required.

Tanaka (55) discussed the following historical sequence in rice improvement:

1. improvement of the sink by making the grain size larger,
2. improvement of the source through an increase in leaf size or improvement of the sink through an increase in spikelet number per panicle,
3. expansion of the sink size through an increase in panicle number by making tillering ability more vigorous, and
4. improvement of the source by making the leaves smaller and more erect to minimize mutual shading among leaves.

A shorter stem was an important change, because this increased resistance to lodging. Thus, improvement meant tailoring of both source and sink. The source (leaf) in its size, thickness, color, life duration, nature of senescence, arrangement, and capacity merits comprehensive study. Field studies (63, 65) have conclusively shown a wide gap between spikelets and grains, which increases with increased LAI. Therefore, improving the capacity of the source goes a long way toward increasing the realization of potential yields, even by 20-40%. Hence, the capacity of the source deserves priority.

But one should also consider the importance of the capability of the sink, i.e., the functional ability to stimulate the production of photosynthetic products and their acceptance, in several crop plants and particularly in a major cereal like rice. It was shown that in wheat (7, 29) the contribution of the panicle to yield (10-49%) is greater than in rice (8-23%) (14, 63). But the sink capacity is more governed by certain enzymes like phosphorylases and

amylases besides the endogenous hormonal level, about which little is known.

It is important to investigate assimilate production during ripening and its partitioning into grain, including studies on the balance sheet, rates of flow, and diversion toward other organs. Obviously, sink components interact differently, calling for inquiry into their interrelationships. As Tanaka (53) stated, improvement of source and sink follows a zigzag path; we move in one direction, get stuck, and divert our route based on the conditions. At every phase we have to assess the organ to be improved in our efforts to attain higher yields.

The information assembled in this review clarifies two important issues:

- The source deserves priority in enhancing the realization of the sink in crops and their modern cultivars. This situation calls for proper evaluation of green energy resources with appropriate characterization.
- Sink capacity and activity deserve equally serious consideration in producing greater sink size. Various components of the sink in different crop plants must be characterized, and the possible ways of improving them deserve priority.

Naturally, strategies to improve both sink and source simultaneously would help to achieve good dividends in crop plants. Recently, Choi (9) found that all sink characters except grain yield are regulated mainly by additive genetic components. Potential kernel size and sink capacity per panicle also showed significant dominance effects and nonallelic genic interaction for sink capacity per tiller. These are promising indications of possible manipulations for furthering yield potentials through source-sink concept. Thus, the source-sink system deserves priority in research pursuits in crop plants.

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