

Factors Affecting Photosynthesis, Productivity, and Yield

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Abstract. The rate and efficiency of photosynthesis (PS) is unquestionably one of the primary determinants of crop yield. Yet, as this symposium illustrates, many other factors contribute to plant productivity. Indeed, the exact relationship between PS rate and yield remains undefined. For several years we have now been interested in factors that affect PS rate in both C₃ and C₄ plants, not only within the plant, but also external to it. Internal factors affecting PS that will be discussed include leaf age, leaf canopy, photorespiration, stage of plant development (including both vegetative and reproductive phases), and the occurrence of little-recognized metabolic pathways such as polyol synthesis and transport. External factors that affect PS, in addition to obvious environmental determinants such as temperature, light, and water, include the seasonal growth cycle. While we still do not understand how all of these factors interact to affect yield, we are beginning to understand their singular effects. Control of these factors, once thought to be within reach even before the advent of biotechnology, remains likely, but distant.

Assimilate Partitioning in Relation to Crop Productivity

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Assimilate partitioning may contribute to improvements in crop productivity by:

a) Increasing total biomass production. Watson (99) drew attention to the subsequently well-qualified observation that assimilate partitioning patterns that favor rapid generation of leaf surface contribute significantly to both genetic- and environmentally induced differences in crop growth rates (87).

b) Favoring assimilate transfer to the harvestable portion of the crop. Retrospective physiological analyses have demonstrated that shifts in assimilate partitioning pattern largely account for the evolutionary increase in yield of a range of crop species (for reviews, see ref. 37). Clearly, upper limits exist to the degree to which assimilates may be partitioned to the harvestable portion without jeopardizing the capacity of the plant to support the yield component both structurally and nutritionally. Nevertheless, in these cases, further potential exists for improvement through optimization of yield quality, which, in part, depends on the chemical nature of the assimilate partitioned to the harvested organ.

The bulk of dry matter gain by the harvested portion is supplied as photoassimilate, principally in the form of a single oligosaccharide (sucrose, sorbitol, stachyose, raffinose), the type depending on the plant species. Therefore, not surprisingly, photoassimilate partitioning has received much attention in considerations of crop productivity (21, 37). However, while not contributing directly to biomass gain, partitioning of root-assimilated mineral ions influences crop productivity in a number of ways including: a) determination of total biomass production through effects on leaf growth (24); b) Direct action on processes governing photoassimilate partitioning, such as membrane transport (e.g., potassium; refs. 36 and 89) and cellular metabolism (e.g., phosphorus effects on starch biosynthesis; ref. 88), and these effects contribute to mineral ion efficiencies; and c) determination of the nutritive value of the harvested organ such as protein (49, 78) and phytate (4) levels. These responses to mineral ions depend on their cytoplasmic levels, which, in turn, are determined by root assimilation and subsequent inter-

and intraorgan partitioning.

Based on the arguments advanced above, an attempt will be made to offer an integrated analysis of both carbohydrate and mineral ion partitioning. Further, since phasic development of many crops dictates altered priorities for assimilate partitioning, a broad attempt is made to consider the process during development of the yield organ. These patterns may be altered profoundly by the physical environment, which, if managed, can be exploited in favor of crop productivity. Finally, it is recognized that crop type (vegetative vs. reproductive; annual vs. perennial) will determine the significance of assimilate partitioning patterns. Some attention is paid to this important issue, but not at the expense of seeking out general principles.

ORGAN DEVELOPMENT: SOURCE- OR SINK-LIMITED

Assimilate partitioning is the end result of a coordinated set of transport and metabolic processes governing the flow of assimilates along an array of source-path-sink systems. The activities of these processes are not static, but may change both diurnally and during plant development. Therefore, any attempt to assess assimilate partitioning as a contributing factor to crop productivity must consider the integration of the phenomenon both spatially and temporally. An initial step for such an analysis could be to establish whether biomass gain by the harvest organ (sink) is either limited by assimilate supply (source-limited) or saturated by assimilate supply (sink-limited) (for further definition, see ref. 98).

Assessment of biomass gain in terms of source or sink limitation has been based on two principal approaches. One involves the response of organ biomass gain to increases in assimilate supply. For photoassimilates, the least ambiguous approach is to amplify leaf photosynthesis through exposure to elevated levels of CO₂ (54). Manipulation of photoassimilate supply by removal of competitive sinks or by varying daily irradiance levels may be confounded by changes in correlative hormonal signals. Tissue concentrations of mineral ions can be regulated by varying their soil solution concentration or by foliar sprays. However, long-term experiments can be rendered ambiguous by mineral-ion induced changes in hormonal status (62). An alternative, but more satisfactory, approach is based on the relationship between biomass gain and tissue concentration

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