The A_{max}–N relationship suggests that N determines A_{max}, but it does not establish causation. At least three kinds of functional relationships are consistent with the correlation. Nitrogen levels may determine A_{max}; N may be controlled in response to A_{max}; or both N and A_{max} may be regulated by some other factor or factors. To summarize the evidence relevant to each of these hypotheses, we need to state them more precisely.

Hypothesis 1. Photosynthetic capacity is limited by one or more processes that operate at rates determined by their nitrogen contents. As a direct assignment of cause and effect, this hypothesis focuses attention on the physiological basis of photosynthesis. Net CO_2 fixation is potentially limited by CO_2 transport through gaseous or liquid media, by enzymatic reduction of CO_2, or by light-driven generation of NADPH and ATP. Within each process, limiting steps may operate at rates determined by nitrogen levels.

Hypothesis 1 is compatible with the possibility that A_{max} is limited by multiple nitrogenous compounds or by a combination of nitrogenous and nonnitrogenous factors. If multiple nitrogenous compounds limit A_{max}, nitrogen is efficiently distributed among the limiting factors only when all nitrogen redistributions decrease A_{max}. To the extent that inefficient nitrogen distributions decrease A_{max}, hypothesis 1 does require a relatively efficient distribution of nitrogen among limiting compounds. If a combination of nitrogenous and nonnitrogenous factors limit A_{max}, a tight A_{max}–N relationship is still possible, but it requires that the nonnitrogenous limitations be either small or a constant proportion of the total limitation to A_{max}.

Hypothesis 2. Independent of the factors that actually limit photosynthetic capacity, leaf nitrogen content is regulated to reflect photosynthetic capacity. This hypothesis emphasizes potential intraplant competition for nitrogen allocation. To the extent that the whole plant is nitrogen-limited, excess capacity in any enzyme or other nitrogenous compound represents an inefficiency, a diversion of nitrogen away from a rate-limiting step in the same leaf or away from investment in some other part of the plant where the nitrogen could contribute to growth and reproduction. With the maximum efficiency of nitrogen allocation, the level of every nonlimiting nitrogenous compound should be adjusted downward to the lowest activity still above rate limitation. At this level, the distinction between the functional constraint postulated in hypothesis 1 and an adjustment for efficient allocation fades. Hypothesis 2 does not require the assumption that some or all of the limits to A_{max} be imposed by

nitrogenous compounds. If nonnitrogenous factors limit A_{max}, excess capacity in nitrogenous compounds should still be trimmed.

Hypothesis 3. The correlation between photosynthetic capacity and leaf nitrogen is not the result of a functional relationship but arises because both parameters are sensitive to or are controlled by other leaf parameters. This possibility, a null hypothesis with respect to the functional relationships suggested in hypotheses 1 and 2, should be accepted if A_{max} and N are invariant when expressed on the basis of some fundamental unit but are changed in concert when expressed on the basis of some derived unit. For example, if A_{max} and N were intrinsically area-based parameters, and if they were constants on a leaf-area basis, variation in LSW would transform these constants into a perfect correlation between the weight-based measures of A_{max} and N. Such a correlation could reflect nothing more than the differential utilization of leaves for storage, or differential allocation to defensive compounds. In the VINE survey, A_{max} and N both varied over at least a fivefold range, independent of the measurement basis. The magnitude of this variation militates against the acceptance of the null hypothesis but does not eliminate the possibility that some components of the A_{max}–N relationship result from spurious or secondary correlations.

Quantifying the importance of secondary effects resulting from potentially confounding variables like LSW, S_i/S_l, or leaf age is partially amenable to multiple-correlation analysis (e.g., Field and Mooney 1983), but the fundamental nature of the A_{max}–N relationship is too poorly known to allow much confidence in an analysis based on linear or simple curvilinear responses.

To evaluate the relative importance of each of these three hypotheses, we combine an analysis of the VINE survey with results from a variety of studies that have probed the biochemistry of photosynthesis in one or a few species. Because the data required for definitive interpretations of several aspects of the A_{max}–N relationship are not yet available, many of our comments are speculative and are intended as much to identify unanswered questions as to integrate existing information.

Deciding among the three hypotheses

The three hypotheses postulate that the A_{max}–N relationship results from substantially different mechanisms. Though the mechanisms