and wheat (Wittenbach 1979), Rubisco constitutes a relatively constant proportion of the total leaf protein. The proportion of total nitrogen in Rubisco appears to decrease late in leaf senescence (Wittenbach 1979; Friedrich and Huffaker 1980; Wittenbach et al. 1980) and may be sensitive to some kinds of source–sink manipulations (Wittenbach 1983).

The correlation between Rubisco and N or protein suggests three interpretations: Levels of other nitrogenous compounds may be adjusted to reflect the limitation of A_{max} by Rubisco, levels of Rubisco may be adjusted to reflect the limitation of A_{max} by other nitrogenous compounds, or A_{max} may be colimited by Rubisco and other nitrogenous compounds. Each of these possibilities is consistent with hypothesis 2: adjustment of nitrogen investment for maximum efficiency of nitrogen allocation. The third possibility represents the merger of functional limitation (hypothesis 1) with efficient investment (hypothesis 2).

Photosynthesis may be limited by Rubisco activity, but it may also be limited by CO_2 transport, CO_2 reduction capacity, or light-driven generation of reducing equivalents and ATP. Rate limitation by CO_2 transport is discussed by Cowan (Chapter 5), who demonstrates that low allocation of N to carbonic anhydrase (the enzyme that catalyzes the interconversion of CO_2 and bicarbonate) can depress A_{max} through effects on CO_2 transport. Rate limitation by either CO_2 reduction or the light reactions can be summarized under effects on regeneration of the CO_2 acceptor, ribulose-1,5-bisphosphate (RuBP) (Farquhar et al. 1980).

Evidence for limitation of A_{max} by RuBP regeneration is beginning to accumulate. The investment of nitrogen in the components of RuBP regeneration is substantial, probably greater than the investment in Rubisco (Kirk and Tilney-Bassett 1978). RuBP regeneration (Evans 1983) and electron-transport capacity (von Caemmerer and Farquhar 1981) are strongly correlated with Rubisco activity. Further, the total concentration of electron-transport components, as indicated by chlorophyll concentration, changes with A_{max} under treatments where rate limitation by Rubisco is unlikely (Terry 1983). Farquhar et al. (1980) summarize a great deal of biochemical information in a model that predicts that photosynthesis is limited by RuBP regeneration at CO_2 concentrations above some critical value. von Caemmerer and Farquhar (1981) argue that nitrogen is efficiently allocated between Rubisco and the components of RuBP regeneration when that critical CO_2 concentration is adjusted to the level at which the leaf normally operates. At this point, A_{max} is colimited by Rubisco and RuBP regeneration.

In summary, strong evidence supports the hypothesis that A_{max} is some-

nitrogenous compounds responsible for RuBP regeneration are certainly adjusted in concert with levels of Rubisco and may be important limitations to A_{max}.

Limitations by physical factors

In C_3 plants, photosynthesis is almost always limited by CO_2 diffusion as well as biochemical factors. Because C_3 plants are typically not CO_2-saturated in normal air (Pearcy and Ehleringer 1984), every step in the diffusion pathway from the bulk atmosphere to the sites of carboxylation in the chloroplasts represents a concentration drop that decreases photosynthesis. The concentration drop across the stomata is typically large, often about 100 μmol mol^{-1} or nearly one-third of the total CO_2 concentration (Wong et al. 1979; Sharkey et al. 1982). Farquhar and Sharkey (1982) provide a simple and elegant method for calculating the proportional limitations to photosynthesis due to effects of stomata. The concentration changes across other components of the diffusion pathway are more difficult to measure, but diffusion limitations imposed by the boundary layer, by the pathway from the substomatal cavity to the photosynthesizing cells (Parkhurst, Chapter 7 in this volume, but see Sharkey et al. 1982 for conflicting evidence), and by liquid-phase transport into the chloroplasts (Cowan, Chapter 5 in this volume; Nobel et al. 1975; Evans 1983) may all present substantial limitations to A_{max} under some circumstances.

These diffusional limitations must be balanced by at least one biochemical limitation. Photosynthetic capacity is completely limited by diffusion only when the CO_2 concentration at the sites of carboxylation drops below the CO_2 compensation point at which respiratory CO_2 evolution equals photosynthetic CO_2 uptake. Though many models have assumed these low CO_2 concentrations at the carboxylation sites, recent evidence indicates that the activity of the carboxylase is sufficient to support observed photosynthetic rates only if the CO_2 concentration at the carboxylation sites is substantially higher (von Caemmerer and Farquhar 1981; Seemann and Berry 1982; Evans 1983).

Each of the segments in the CO_2 diffusion pathway limits photosynthetic capacity, but with proportional magnitudes sensitive to other diffusional and biochemical limitations. In C_4 plants, which may be CO_2-saturated in normal air (Pearcy and Ehleringer 1984), there is no conceptual requirement for multiple limitations to photosynthetic capacity.

Stomatal limitations. Stomatal limitations to A_{max} are generally smaller than predicted by the linear analyses used for the last 25 years-