for diffusion. However, as Björkman (1981) pointed out, the ratio of internal volume to leaf area also tends to increase with S_i/S_l, admitting the possibility that increases in A_{max} are more closely tied to increases in the amount of biochemical machinery than to increases in internal surface area. One promising approach to separating these limitations involves comparison of in vitro biochemical characteristics with in vivo photosynthetic rates. Knowing the in vitro kinetic properties of a rate-limiting enzyme, it is possible to calculate the CO_2 concentration required to support observed photosynthetic rates. From this CO_2 concentration, one can calculate the physical limitations to in vivo CO_2 diffusion.

This approach has been best developed for Rubisco. From experiments at low CO_2 concentrations, under which photosynthetic rates can be more accurately related to in vitro Rubisco kinetics, von Caemmerer and Farquhar (1981), Seemann et al. (1981), and Seemann and Berry (1982) all concluded that Rubisco activity is barely sufficient to support observed photosynthetic rates. In these studies, in vivo photosynthetic rates can be explained only by assuming no drop in CO_2 concentration across the liquid phase. Using a similar analysis, however, Evans (1983) found that photosynthesis was less than expected in leaves with the highest photosynthetic capacities, suggesting a drop in CO_2 concentration between the substomatal cavity and the sites of carboxylation. Evans's (1983) conclusion highlights the possibility that liquid-phase diffusion resistance usually imposes relatively small limitations to A_{max} but that when leaves develop exceptionally high biochemical capacities, limitations by liquid-phase resistance become important.

A general, quantitative summary of the magnitude of limitations by liquid-phase diffusion resistance is not yet possible. The very high correlation in the A_{max}–N relationship is consistent with a minor limitation. If the limitation were large but constant, we would expect downward curvature at the upper end of the A_{max}–N relationship, as the diffusional limitation increasingly constrained the gains of additional nitrogen investment. This kind of curvature is apparent in some single-species A_{max}–N relationships (Evans 1983), suggesting that the liquid-phase diffusion resistance is less variable within species than among species. Finally, the A_{max}–N relationship is consistent with large liquid-phase diffusion limitations, if the magnitude of those limitations scales linearly with the limitations imposed by biochemical factors. Unfortunately, the interface of biochemical and liquid-phase diffusional limitations to A_{max} has not been well studied. Correlations between S_i/S_l and A_{max} suggest linear scaling but have not been reinforced by independent measures of biochemical limits to A_{max}.

Integration and conclusions

In C_3 plants, A_{max} is typically limited by biochemical and diffusional factors, with the majority of the total limitation caused by biochemical factors. The biochemical limitations are imposed by nitrogen-containing compounds, and the biochemical capacity for photosynthesis scales with the nitrogen investment in these compounds. Of the nitrogenous limits, limitation by Rubisco is the best-documented case, but limitation by compounds involved in RuBP regeneration and by carbonic anhydrase is also likely. At this point, we cannot distinguish broad colimitation of A_{max} by nitrogenous factors from limitation by one or a few nitrogenous compounds and adjustment to near limitation in others. In variable natural environments, this distinction may be somewhat artificial, as changes in the environment alter the balance among limiting factors.

The mechanisms responsible for adjusting levels of nitrogenous compounds are not generally known. Schmidt and Mishkind (1983) demonstrated that the required 1 : 1 ratio between large and small subunits of Rubisco is maintained by rapid degradation of excess small subunits. They further suggested that similar proteolytic systems could establish and preserve an appropriate balance among a wide variety of photosynthetic compounds by degrading any components not integrated into a functional pathway. Little is known about the ways that environmental signals specifying the appropriate balance among photosynthetic compounds are transduced into controlling mechanisms.

The integrated balance among nitrogenous limitations to A_{max} is, in general, paralleled by a scaling between nitrogenous and diffusional limitations. Neither the mechanisms nor the ecological priorities for this scaling are well known. Is nitrogen investment curtailed when diffusional limitations become too large, or is nitrogen the primary control? This question has no single answer, and priority among multiple constraints is probably sensitive to a variety of environmental and phylogenetic factors (Mooney and Gulmon 1979). When constraints on water loss, the risk of herbivory, or limited light availability decrease the gains expected from high N, plants generally forgo those investments. In these cases, N is the major determinant of A_{max}, but it is not the primary environmental constraint. In other cases, limited N availability may act as both the major limitation to A_{max} and the major environmental constraint. An important implication of the adjustment of biochemical limitations in response to environmental constraints is that A_{max} is not an ecologically meaningless physiological parameter, but is an index of integrated natural constraints