This nitrogen allocation pattern may be efficient under low light but inefficient under saturating light. Much work remains to be done in assessing the relationship between A_{max} and the photosynthesis realized in nature.

A final hypothesis to explain the variation in PPNUE is that the kinetic properties of the photosynthesis-limiting nitrogenous compounds are not constant across species and that those plants with the highest PPNUEs have the most active or efficient rate-limiting enzymes.

To date, relatively little evidence is relevant to discriminating among the hypotheses that potentially explain the variation in PPNUE. No analysis based solely on interpretation of gas-exchange experiments can distinguish effects of cell-wall resistance to CO_2 diffusion from effects of nitrogen investment in nonphotosynthetic compounds, or from effects of variation in enzyme or allocation efficiency. However, the available information generally does not support the hypothesis that low PPNUE in sclerophylls results from unusually large internal resistances to CO_2 diffusion.

Three lines of evidence support this position. First, internal resistances should, in general, decrease as the ratio of the internal cell surface area to leaf area (S_i/S_l) increases (Nobel et al. 1975; Raven and Glidewell 1981). Though it is not always the case (Longstreth and Nobel 1980), the S_i/S_l ratio increases with LSW, if cell size and shape are constant. Thus, leaves with high LSWs should typically have low internal resistances. Second, the suggestion that extensive cell-wall development in sclerophylls imposes large limitations to CO_2 diffusion requires that these leaves contain an unusually large proportion of their biomass in cell walls. However, Merino et al. (1984) report that the biomass allocation to cell-wall components in the sclerophyllous chaparral shrub *Heteromeles arbutifolia* is 39.7% (46.7% including ash), comparable to the 38.1% (47.3% including ash) allocated to cell walls in the deciduous shrub *Lepechinia calycina*, and to the 41.4% (47.9% including ash) allocated to cell walls in the deciduous shrub *Diplacus aurantiacus*, after removal of the external resin in the latter species. All these values for leaves of perennials are lower than the 51.0% (56.0% including ash) of the total biomass allocated to cell-wall constituents in young corn plants (Penning de Vries et al. 1974). Neither of these lines of evidence addresses the permeability of the cell walls, but a third does.

Farquhar et al. (1982) argue that because diffusion and the biochemistry of carboxylation discriminate differently against the naturally occurring carbon isotope ^{13}C, then the isotopic composition of plants should reflect the relative importance of limitations to photosynthesis by diffusion and biochemical factors. In experiments where diffusional limitations are controlled, large limitations by diffusion result in high ratios of $^{13}C/^{12}C$. Small diffusional limitations lead to low ratios (Farquhar et al. 1982). For a broad survey of C_3 species, the mean $^{13}C/^{12}C$ ratio is 27.8 parts per thousand less than that in the standard limestone, with a range of 21 to 36 (Troughton et al. 1974). For the five species of California evergreens studied by Field et al. (1983), the mean ratio is 27.9 parts per thousand less than that in the standard limestone (unpublished data). The similarity between the mean values for C_3 plants and for evergreen sclerophylls indicates that the proportional limitations to photosynthesis imposed by diffusion are similar for the two groups. None of this evidence is conclusive in itself, but it all indicates that evergreen sclerophylls do not have proportionally large cell-wall resistances to CO_2 diffusion. The hypotheses favored by elimination are that PPNUE is low in the sclerophylls because proportionally less of their nitrogen is allocated to photosynthetic reactions, or that the sclerophylls have inefficient photosynthetic machinery. We shall review additional evidence concerning these hypotheses in the following section on the causal basis of the $A_{max}-N$ relationship, but quantification of the relative importance of these hypotheses awaits further research.

Correlation or cause

Variation in leaf nitrogen can clearly explain much of the variation in photosynthetic capacity, across a wide variety of plant communities. From a purely predictive viewpoint, the correlation should prove a useful tool in the preliminary characterization of photosynthetic capacities. To understand the ecological controls on photosynthetic capacity, we need to move beyond the correlation to an assessment of cause and effect. This assessment warrants analysis at two levels. At the proximate level, establishing the functional basis of the $A_{max}-N$ relationship will provide the foundation from which to approach a wide variety of ecological questions. How will particular plants or communities respond to changes in nitrogen availability? If nitrogen uptake is increased at the expense of additional allocation of carbon to roots, will the increased photosynthesis more than offset the costs of root maintenance and construction? At the ultimate level, important questions concern the control of nitrogen investment and the efficacy of that control. What controls nitrogen levels? How do actual nitrogen investments compare with the optimal investments for the maximization of growth, yield, or fitness? Here, we concentrate primarily on the proximate analysis of cause in the $A_{max}-N$ relationship, providing a basis for future work at a variety of levels.