

larger (Comstock and Ehleringer 1984). These relatively large diffusional limitations could affect the A_{\max} -N relationship in three ways. If stomatal conductances were constant as biochemical limitations changed, the A_{\max} -N relationship would curve downward at high levels of N, as stomatal limitation prevented large gains from increased nitrogen investment. If stomatal limitations were large but variable, they should add scatter to the A_{\max} -N relationship. If stomatal conductance scales with biochemical limitations, establishing a proportionally constant stomatal limitation, the A_{\max} -N relationship should have little scatter and should be linear or some other shape set by the response of the biochemistry to changes in nitrogen investment.

An accurate assessment of stomatal limitation requires an analysis of the CO_2 response of photosynthesis (Farquhar and Sharkey 1982), data not available for the VINE survey. At a slightly less sophisticated level, a proportionally constant stomatal limitation is indicated by a linear relationship between A_{\max} and stomatal conductance (g). In the VINE survey, A_{\max} and g are highly correlated ($r = 0.77$), even though the Illinois annuals tend to have high g values in relation to A_{\max} (Figure 1.6).

The scatter in the A_{\max} - g relationship suggests some variation in stomatal limitation to A_{\max} . The five species of California evergreens in the VINE survey provide evidence for this. Field et al. (1983) found that the species with a higher A_{\max} for a given N (a higher PPNU) tended to be from wetter sites than species with lower PPNU. Much of their difference in PPNU values is attributable to higher stomatal conductance in the species of the wetter sites, and these differences generate scatter in the A_{\max} -N relationship.

The mechanisms responsible for maintaining nearly constant limitations by g are not well known. Mooney and Gulmon (1979) argued that investments in photosynthetic machinery should be reduced when drought limits g , a postulate supported by evidence from Ehleringer (1983), who reported that N declines with increasing drought in the desert annual *Amaranthus palmeri*. Alternatively, the value of g may be regulated by the value of A_{\max} , as determined by biochemical factors. Some of the strongest evidence for control of g by biochemical capacity comes from Wong et al. (1979), who demonstrated that stomatal conductance in C_3 and C_4 species is somehow regulated by photosynthetic capacity under a wide variety of treatments, including nutrient availability during growth, nutrient withdrawal, water stress, and chemical inhibition of photosynthesis. This type of coordination tends to eliminate scatter or curvilinearity in the A_{\max} -N relationship that could result from variable stomatal

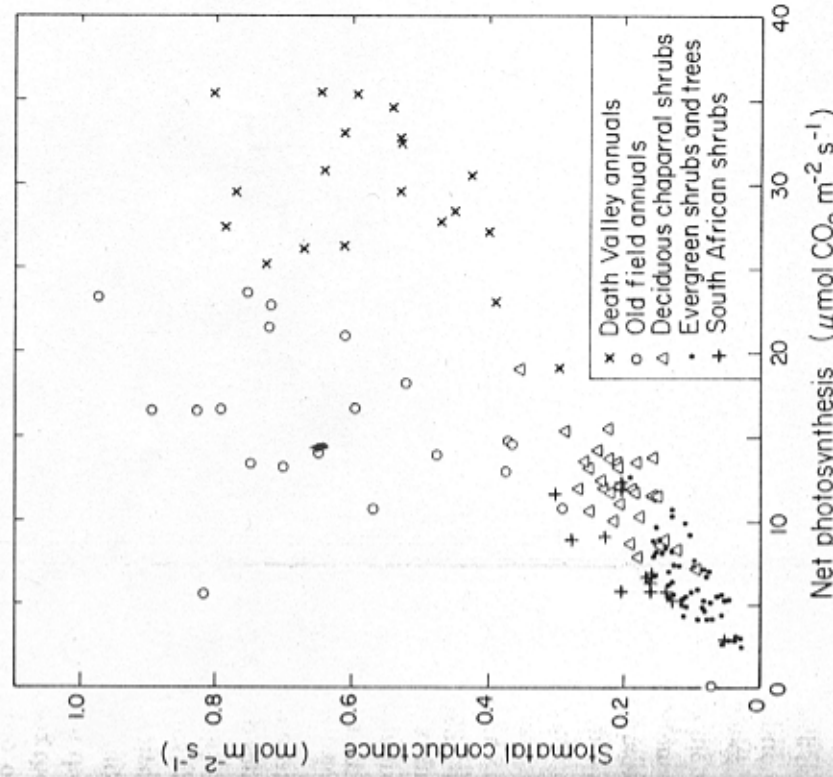


Figure 1.6. Relationship between photosynthetic capacity per unit of leaf area (A_{\max}) and stomatal conductance (g) for the VINE survey. Stomatal conductances were measured simultaneously with photosynthetic capacity. $g = 0.0119 + 0.0215 \cdot A_{\max}$, $n = 135$, $r = 0.77$, $P < 0.001$.

Other physical limitations. Nobel et al. (1975), Raven and Glidewell (1981), and Cowan (Chapter 5) have calculated that A_{\max} typically includes a substantial limitation caused by resistance to CO_2 diffusion between the surfaces of the photosynthesizing cells and the sites of carboxylation. To the extent that this resistance is influenced by the activity of carbonic anhydrase (Cowan, Chapter 5), it acts as both a nitrogenous limitation and a physical limitation to A_{\max} . Experimentally, it is very difficult to separate liquid-phase diffusion resistance from biochemical limitations. Nobel and associates demonstrated strong correlations between a measure of photosynthetic capacity and the ratio of cell surface area to leaf area (S_i/S_l) (Nobel et al. 1975; Nobel 1976, 1977, 1980), indicating that A_{\max} may be limited by the investment in photosynthetic