Table 1.2. *Potential photosynthetic nitrogen-use efficiency (PPNUE) and nitrogen per unit of leaf weight (N/wt) for the species groups in the VINE survey*[a]

Species group	PPNUE (μmol CO_2[mol N]$^{-1}$ s^{-1})	N/wt (mmol g^{-1})	PPNUE vs. N/wt	
			r	$p <$
Death Valley annuals	142 a	2.9 a	−0.58	0.01
Old-field annuals	130 a	2.2 b	0.31	n.s.
Drought-deciduous shrubs	95 b	1.9 b	0.07	n.s.
California evergreens	46 c	0.9 c	−0.42	0.01
South African shrubs	49 c	0.8 c	0.58	0.05

[a] Within a column, values followed by different letters are significantly different ($p < 0.001$). Values followed by the same letter are not significantly different ($p > 0.05$). In two of the three cases where the correlation between PPNUE and N/wt is significant, the correlation coefficient is negative.

the prerequisites for longevity constrain the options for A_{max}. From this, we can derive two hypotheses. First, Medina (1981) suggested that PPNUE is low in evergreen sclerophylls because the thick or impermeable cell walls required for longevity impose large resistances to CO_2 diffusion. Second, differences in PPNUE may result from differences in nitrogen allocation. Specifically, leaves with high A_{max} may invest a larger proportion of the leaf nitrogen in the primary carboxylating enzyme of C_3 plants, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and leaves with low A_{max} may invest a larger proportion of the leaf nitrogen in compounds required for longevity.

The data from the VINE survey do not provide a direct test of these two hypotheses for the relationship between PPNUE and N or A_{max}, but they do suggest two modifications of the second hypothesis that do not require assumptions about the prerequisites for leaf longevity. For an essentially linear weight-based A_{max}–N relationship, we can write

$$A_{max} = mN + b$$

or

$$\text{PPNUE} = A_{max}/N = m + b/N$$

If the *y* intercept (b) is positive, PPNUE decreases with increasing N, and if b is negative, PPNUE increases with increasing N, reaching a maximum value of m, the slope of the A_{max}–N relationship. This algebraic formulation has two implications. First, PPNUE will increase with N whenever, at least in extrapolation, some minimum nitrogen level greater than zero is

required for a positive A_{max}. Because photosynthesis is only one of many nitrogen-requiring metabolic processes in leaf cells, it is intuitively reasonable that some sort of a nitrogen threshold for photosynthetic competence (A_{max} just greater than zero) does exist, and that this threshold value forces the increase in PPNUE with increasing A_{max} or N. If this hypothesis is correct, low PPNUE may result directly from low leaf nitrogen and is not necessarily mechanistically related to features required to increase leaf longevities.

In the VINE survey, the *y* intercept in the weight-based A_{max}–N relationship is negative. The regression equation suggests that a nitrogen concentration of about 0.5 mmol N g^{-1} is required for an A_{max} just equal to zero. While this value provides a first approximation of the nitrogen content at minimum photosynthetic competence, it must be considered a very rough approximation, because there is little reason to expect a constant threshold value of nitrogen independent of species or leaf type. Consistent with this caveat, extrapolated values for N at $A_{max} = 0$ vary widely among studies (data not shown).

A second implication also concerns the nitrogen invested in reactions unrelated to photosynthesis. When a high LSW dilutes a given A_{max} over a large amount of leaf mass, the nitrogen invested in reactions of intermediary metabolism, biosynthesis, and maintenance of ion gradients may not be diluted precisely in parallel. Because cell viability, independent of photosynthesis, requires nitrogen in proteins and nucleic acids, the nitrogen requirement for reactions not related to photosynthesis may scale positively with LSW. To the extent that this is the case, low PPNUE and high LSW are functionally related, because the proportion of the total leaf nitrogen invested in photosynthetic machinery decreases as LSW increases. This hypothesis not only explains the low PPNUE of evergreen sclerophylls but also is consistent with the pattern in the area-based A_{max}–N relationship (Figure 1.3), where some evergreens contain more nitrogen than would be predicted from the regression with A_{max}.

A third hypothesis is that low PPNUE results from inefficient allocation of nitrogen among photosynthetic compounds, such that some compounds are present in large excess, while the rate-limiting compounds are underrepresented for lack of nitrogen investment. Because photosynthesis is a very complex process, the problems of efficient allocation may be substantial. It is also possible that efficient nitrogen allocation under natural conditions is not efficient under the conditions employed for measurement of A_{max}. For example, shade plants invest large quantities of nitrogen in light-harvesting pigments and proteins, but make only small investments in Rubisco and other