



Figure 1.3. A_{\max} -N relationships for the VINE survey, with A_{\max} and N expressed on a leaf-area basis. Data from *Prunus ilicifolia* are marked by asterisks. $A_{\max} = 0.342 + 0.0814 \cdot N$, $n = 137$, $r = 0.53$, $P < 0.001$.

thetic capacity is strongly regulated by leaf nitrogen, without large effects due to habitat, growth form, or interspecies differences. The linearity, a feature not observed in some single-species analyses (Evans 1983), indicates important constraints on the relationship between nitrogen-based limitations and other limitations to A_{\max} . We shall address both the linearity and the scatter in considering the causal basis of the A_{\max} -N relationship.

The area-based A_{\max} -N relationship (Figure 1.3) is somewhat confusing. The general rankings of species groups are similar for the weight-based and area-based analyses, but with one important exception. Some of the evergreen sclerophylls have high N per unit area, but low A_{\max} (Figure

1.3). The most striking example of these species is *Prunus ilicifolia*, a shrub of the California chaparral. This species is a special case in that its leaves contain cyanogenic glucosides. These nitrogen-containing secondary compounds almost certainly play no direct functional role in determining A_{\max} and may represent allocation of nitrogen away from compounds functionally related to A_{\max} and toward defense. We shall assess the possibility that sclerophylls, in general, allocate proportionally less nitrogen to photosynthesis than do nonsclerophylls when we consider nitrogen-use efficiency. Some of the ecological factors controlling the allocation of nitrogen to defensive compounds have been considered by Bryant et al. (1983) and by Gulmon and Mooney (Chapter 20).

Which basis for expressing the A_{\max} -N relationship is more significant functionally? Compelling arguments can be used to support either expression. Because light capture and CO_2 exchange with the atmosphere are intrinsically area-based phenomena, the area-based analysis provides a resource-harvesting framework for understanding the A_{\max} -N relationship. On the other hand, a weight-based analysis yields more information on the economics of nitrogen and carbon allocation. Each expression gives important information, and the sources of the differences between them can contribute to the elucidation of the functional and ecological controls on photosynthetic capacity and leaf nitrogen.

Differences between the weight-based and area-based relationships result largely from variation in LSW (leaf weight/leaf area). In the VINE survey, LSW varies inversely with the weight-based measure of leaf nitrogen (Figure 1.4). The evergreen sclerophylls have the highest LSWs and also the survey's lowest photosynthetic capacities, either weight-based or area-based. The Death Valley annuals have the highest photosynthetic capacities on both measurement bases and a narrow range of LSW, somewhat above the lowest values. Converting from a weight-based (Figure 1.2) to an area-based (Figure 1.3) A_{\max} -N relationship requires only multiplying each value for A_{\max} and N by the LSW for that leaf. The consequence of the inverse relationship between LSW and N per unit weight is to increase small values and decrease large values of area-based A_{\max} and N, relative to the weight-based parameters. Thus, the transformation from a weight-based to an area-based analysis tends to compress the total range of variation in A_{\max} and N, and to increase the variability among the leaves with the highest LSWs.

The A_{\max} -N relationship is not fundamentally changed by the choice of measurement basis (as long as A_{\max} and N are expressed in the same units), but the choice of units does alter the prominence of various segments of the relationship. On any measurement basis, the relationship between A_{\max} and N is