in the interest of brevity. The focus on naturally growing plants arises from the hypothesis that an $A_{max}-N$ relationship reflects evolutionary responses to natural habitats and may be altered by growing plants under modified nutrient, water, light, or CO_2 availability. Here we shall consider A_{max}, leaf nitrogen, LSW, and stomatal conductance from four studies. Collectively, these studies reported data from 137 leaves of 21 plant species, including trees, shrubs, and herbs from environments varying widely in nitrogen availability and productivity. Five species are winter annuals of Death Valley, California; four are summer annuals of central Illinois (all described by Mooney et al. 1981); one is a drought-deciduous shrub of the California chaparral (Field and Mooney 1983); five are evergreen shrubs and trees from coastal central California (Field et al. 1983); six are shrubs from South African mountain fynbos (Mooney et al. 1983). In this combined data set, which we refer to as the VINE (vegetation in natural environments) survey, maximum leaf durations vary 50-fold, LSW varies by a factor of 5, and A_{max} varies more than 20-fold in measurements based on a standardized protocol and instrumentation. The desert annuals have some of the highest photosynthetic capacities of any C_3 plants (Mooney et al. 1976), and the evergreen sclerophylls have some of the lowest (Mooney and Gulmon 1979). The VINE survey does not include plants that grow under deep shade, and none of the species has a symbiotic nitrogen-fixing microorganism.

In order to explore the widest range of naturally occurring nitrogen levels, we include measurements from leaves of different ages, ranging from the youngest fully expanded leaf to the oldest nonnecrotic leaf. Leaf nitrogen declines with increasing leaf age in essentially all plants and provides a completely natural source of intraspecies (and intraplant) variation. Though leaf aging is a complex process, many aspects of the gradual changes in leaf physiology following full expansion are consistent with the interpretation that the dominant phenomenon of leaf aging is nitrogen mobilization and export (Field and Mooney 1983), a process that may increase whole-plant photosynthesis when old leaves are increasingly shaded by younger leaves (Field 1983).

Over the 137 leaves in the VINE survey, A_{max} is highly correlated with leaf N. This conclusion applies when both parameters are expressed on the basis of either leaf dry weight (Figure 1.2) or leaf area (Figure 1.3). As observed in other studies (Gulmon and Chu 1981; Medina 1981; Field and Mooney 1983), the correlation coefficient is higher for weight-based measurements ($r = 0.92$) than for area-based measurements ($r = 0.53$). Subsets within the survey, however, show similar weight-based and area-based

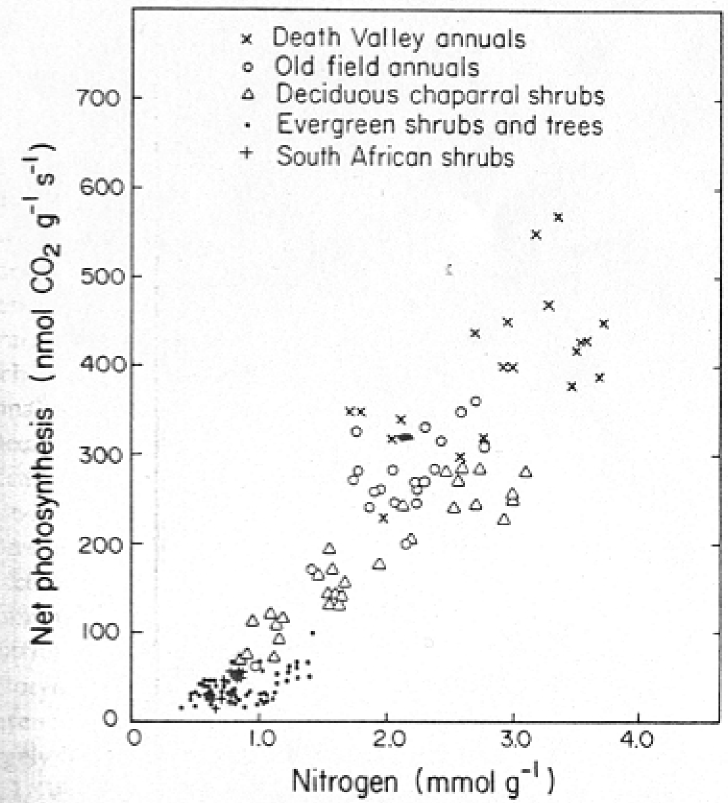

Figure 1.2. $A_{max}-N$ relationships for the VINE survey, representing 21 species grown under natural conditions. A_{max} was measured in the field. N was determined with a micro-Kjeldahl assay on the same leaves used for the photosynthesis measurements. A_{max} and N are both expressed on a leaf-weight basis. $A_{max} = -76.1 + 149 \cdot N$, $n = 137$, $r = 0.92$, $P < 0.001$.

nials), the correlation coefficients are similar for area-based ($r = 0.86$) and weight-based ($r = 0.84$) measurements. For the 11 species of evergreen sclerophylls, the area-based ($r = 0.51$) and weight-based ($r = 0.50$) correlations are also similar. The greater variance in $A_{max}-N$ relationships for sclerophylls than for nonsclerophylls has been reported earlier (Medina 1981; Field et al. 1983) and is an important element in the continuing discussion of the implications of sclerophylly. We shall review aspects of this discussion when we consider nitrogen-use efficiency and the causal basis of the $A_{max}-N$ relationship.

If we focus on the weight-based $A_{max}-N$ relationship, the correlation is striking for both its linearity and its limited scatter (Figure 1.2). The