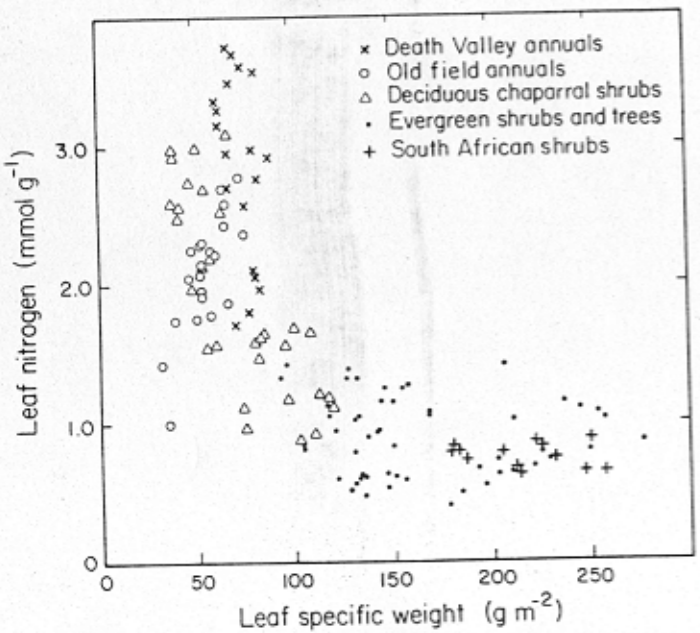

Figure 1.4. Relationship between leaf nitrogen per unit of leaf weight (N) and leaf-specific weight (LSW) for the VINE survey.

lated, and A_{max} per unit of leaf nitrogen is lower for the evergreen sclerophylls than for the other species.

Nitrogen-use efficiency

To simplify discussion of the A_{max} realized for a given level of N, it is useful to eliminate the confounding variable LSW and consider the ratio of A_{max} to N, which we term potential photosynthetic nitrogen-use efficiency (PPNUE). As long as A_{max} and N are both expressed on the same basis, PPNUE is independent of the measurement basis. We can view PPNUE as an index of potential performance under defined conditions that allows direct comparison among species. PPNUE is not an ecologically complete definition of nitrogen-use efficiency, but it is an important component of a more general, ecological definition, as provided by Rundel (1982) or Vitousek (1982). In addition to photosynthesis or growth per unit of nitrogen in tissue, these more complete definitions account for the critical roles in nitrogen-use efficiency played by leaf duration, nitrogen recovery from leaves, and whole-plant patterns of nitrogen allocation

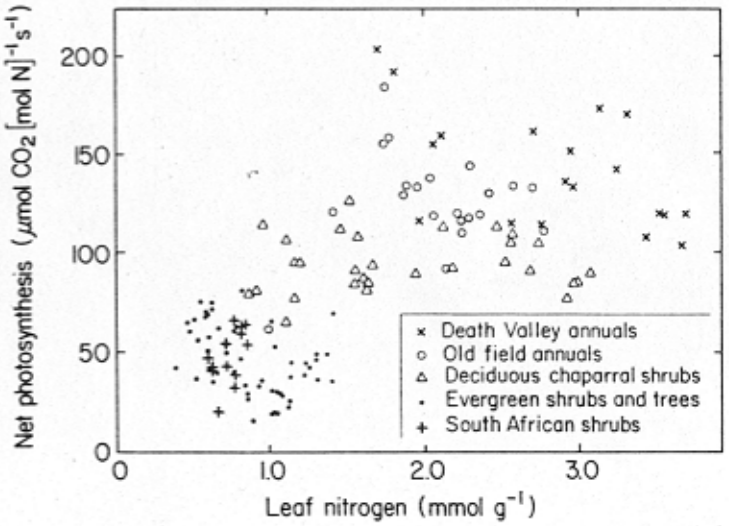

Figure 1.5. Relationship between photosynthetic capacity per unit of leaf nitrogen (PPNUE) and the weight-based measure of leaf nitrogen for the VINE survey.

interpretation of nitrogen-use efficiency. Its potential utility for approaching broader questions about nitrogen and growth will be increased as this index is modified to reflect long-term photosynthesis under natural conditions, and as photosynthetic data are combined with other components of nitrogen-use efficiency.

For the VINE survey, the analysis of PPNUE does provide several insights into the A_{max}–N relationship. PPNUE is lowest in the plants of lowest A_{max}, and increases with A_{max}. From values of less than 30 μmol CO_2 [mol N]$^{-1}$ s^{-1} for leaves of less than 1 mmol N g^{-1}, PPNUE rises to a plateau at around 125 μmol CO_2 [mol N]$^{-1}$ s^{-1} for leaves with nitrogen contents above about 2 mmol g^{-1} (Figure 1.5). Reviewing the data of Medina (1981) and others, Grubb (1984) also reached the conclusion that PPNUE is positively related to A_{max}. In the VINE survey, the relationship can be seen more precisely as a staircase of nearly constant PPNUE within major species types (annuals, deciduous shrubs, evergreen sclerophylls) and stepwise increases between them (Table 1.2). Although not in subgroups within the VINE survey, an increase in PPNUE with increasing N per unit weight is suggested by some studies on individual species (e.g., Gulmon and Chu 1981).

Several hypotheses may potentially explain the increase in PPNUE with increasing A_{max}. Observing that A_{max} and leaf longevity tend to be inversely