Photosynthesis–nitrogen relationships are intrinsically complex, be-
cause photosynthesis represents the integrated operation of a series of
processes sensitive to environmental factors as well as leaf physiology and
structure. The ecologically relevant measure of photosynthesis is time-in-
tegrated photosynthesis in the natural environment, but this index reveals
little about leaf function. Maximum photosynthetic capacity under opti-
mum conditions may not always scale simply with time-integrated CO_2
fixation, but measurements of photosynthetic capacity are important for
three reasons. They indicate the maximum rates of CO_2 fixation that
occur in nature and also the maximum possible benefits from a given
investment in photosynthetic machinery. In addition, if constructing and
maintaining photosynthetic machinery is expensive, photosynthetic capac-
ities should be tuned to the constraints of the environment, and unusable
capacity should be trimmed by natural selection. Thus, photosynthetic
capacity provides a useful starting point for analyzing the relationship
between photosynthesis and leaf nitrogen.

All of the biochemical and photobiological processes of photosynthesis
require nitrogenous compounds. In addition to the proteins (typically 16%
nitrogen) that catalyze the reactions of CO_2 fixation and the regeneration
of the CO_2 acceptor, photosynthesis requires reducing equivalents
(NADPH) and ATP, produced by light-driven electron-transport and
proton-transport reactions. Nitrogenous compounds that provide the
basis for these reactions include chlorophyll (6% nitrogen), chlorophyll
proteins, electron-transport proteins, and the ATP-synthesizing enzyme.
The nitrogen investment in many of these compounds is not precisely
known, but the proportion of the total leaf nitrogen allocated to photosyn-
thetic reactions is undoubtedly large. As a first approximation, the com-
mitment of leaf nitrogen to photosynthesis in C_3 plants is given by the 75%
of the leaf nitrogen that can be recovered from the chloroplasts (Stocking
and Ongun 1962), minus the probably small proportion of the chloroplast
nitrogen invested in the reactions of nitrite reduction and amino acid
synthesis, plus the nitrogen incorporated in the peroxisome and mito-
chondrial enzymes that recycle the products of photorespiration, plus the
nitrogen in that fraction of the nucleic acids and protein-synthesizing
machinery necessary to produce and recycle the components of the photo-
synthetic reactions. These compounds may account for well over three-
quarters of the total leaf nitrogen.

A number of studies have reported correlations between some measure
of photosynthetic capacity and (a) total leaf nitrogen, (b) the nitrogen
content of some protein fraction, or (c) the activities of particular enzymes,

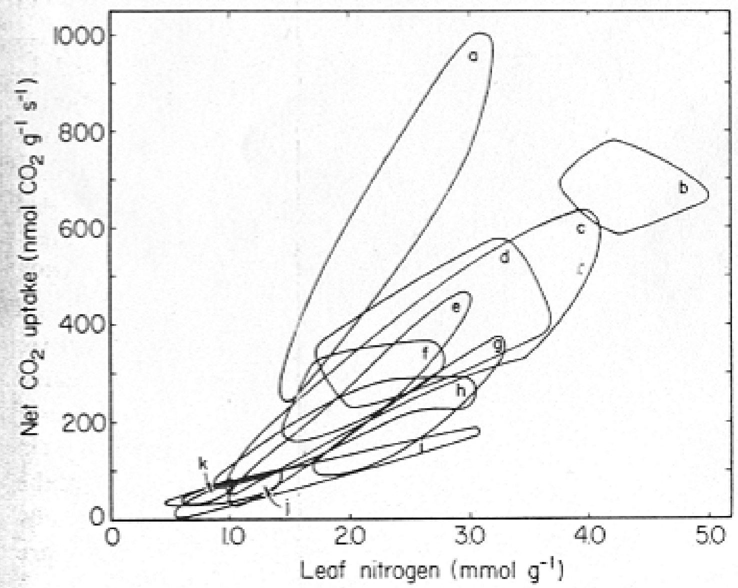

Figure 1.1. A_{max}–N relationships for a wide variety of plant species. Each outline circumscribes all of the data reported in each study. The study species and the experimental conditions are described in Table 1.1. Included are data from 33 C_3 species and 11 C_4 species. Some of the studies present data from naturally grown plants, whereas others report data from plants grown in controlled environments. The experimental variables manipulated to introduce variations in A_{max} and N include nitrogen availability, light availability, and leaf age. Those in group a, with the greatest A_{max} per unit of N, are the only C_4 data in this summary.

Nátr (1975), Yoshida and Coronel (1976), Björkman (1981), and Hesketh et al. (1983) have recently reviewed many of these studies. We approach the photosynthesis–nitrogen relationship in a broader context, examining general trends that cut across taxonomic groups, habitats, and life forms.

To provide an overview of the generality in the photosynthesis–nitrogen relationship, we have summarized a series of studies reporting photosynthetic capacity and leaf nitrogen content on the basis of leaf dry weight (Figure 1.1). In each of these studies, photosynthetic capacity (A_{max}) is the photosynthetic rate measured under saturating light intensity, optimum temperature, relatively high humidity, and the CO_2 concentration typical of normal air. Leaf nitrogen (N) is that measured on the same or matched leaves by Kjeldahl analysis. This procedure is sensitive to all forms of organic nitrogen, of which 70–80% in a typical leaf is in proteins, 10% is in nucleic acids, 5–10% is in chlorophyll and lipoproteins, and the