remainder is mostly in free amino acids (Chapin and Kedrowski 1983). For the data summarized in Figure 1.1, correlation coefficients between A_{max} and N range from 0.51 to 0.97, with a median value of 0.90 (Table 1.1). The slopes of linear-regression equations expressing A_{max} as a function of N vary substantially (Table 1.1), but data from all but one of the studies cluster around a single straight line. The outlying data in Figure 1.1 are the results of Pearcy et al. (1982) and represent the only C_4 plants included in the figure. The general comparison provided here confirms the taxonomically limited conclusions of Brown (1978), Bolton and Brown (1980), Schmitt and Edwards (1981), Brown and Wilson (1983), and Wilson and Brown (1983) that for a given investment in leaf nitrogen, C_4 plants tend to realize a higher A_{max} than do C_3 plants. To the extent that environmental conditions permit leaves to operate near A_{max}, the higher A_{max} per unit of leaf nitrogen in C_4 species suggests that selection may favor these plants in nitrogen-limited habitats. This hypothesis is not supported by much of the available data (Pearcy and Ehleringer 1984), but deserves further study. Possible explanations for this difference between C_3 and C_4 plants are discussed by Brown (1978) and Raven and Glidewell (1981).

The fact that all the C_3 plants in Figure 1.1 cluster tightly around a single straight line suggests a fundamental relationship that is relatively insensitive to differences among species or growth conditions. Included in the figure are data from herbs, shrubs, and trees, from evergreens and deciduous species, from leaves ranging in age from a few weeks to more than three years, from plants growing naturally in the field, and from plants maintained under a variety of greenhouse and growth-chamber conditions.

In analyzing these and other reports of A_{max}–N relationships, we consider examples in which both A_{max} and N are presented on the basis of leaf dry weight or leaf area, but we largely ignore the substantial literature in which A_{max} is presented as an area-based quantity and N is presented on a leaf-weight basis. Because leaf-specific weight (LSW) or weight per unit of leaf area tends to change in response to variation in nutrient availability (Loveless 1961; Gulmon and Chu 1981) or variation in light intensity during growth (Björkman 1981), the results of studies reporting A_{max} on an area basis and N on a weight basis can be very confusing.

A survey: the photosynthesis–nitrogen relationship in natural vegetation

For a detailed examination of the A_{max}–N relationship, we restrict our attention to naturally growing C_3 plants. The emphasis on C_3 plants is

able 1.1. *Summary of selected studies reporting a relationship between photosynthetic capacity at light saturation* (A_{max}) *and leaf organic nitrogen (N), both expressed* *r unit of leaf weight*

eference	Species	Equation[a]	r	n	Notes	Label in Figure 1.1
örkman and Holmgren (1963)	*Solidago virgaurea*	$A_{max} = -255 + 195 \cdot N$	0.93	12	Twelve clones grown in growth chambers at high light	*g*
oney et al. (1978)	6 *Eucalyptus* species	$A_{max} = -9.5 + 66.2 \cdot N$	0.97	18	One-year-old nursery-grown plants and 2-month-old phytotron-grown plants	*i*
eld (1981)	*Lepechinia calycina*	$A_{max} = -45 + 161 \cdot N$	0.93	15	Leaf age and shade varied: irrigated plants grown outside	
lmon and Chu (1981)	*Diplacus aurantiacus*	$A_{max} = -82 + 164 \cdot N$	0.96	23	Growth-chamber plants under several light and nitrogen treatments	*c*
dina (1981)	*Nicotiana glauca* and *Eucalyptus camaldulensis*	$A_{max} = -123 + 175 \cdot N$	0.96	32	Excised branches of naturally growing plants	*e*
oney et al. (1981)	5 species of Death Valley annuals	$A_{max} = 171 + 80 \cdot N$	0.64	20	Leaf age series on naturally growing plants	*d*
oney et al. (1981)	4 species of old-field annuals	$A_{max} = 12 + 123 \cdot N$	0.78	21	Leaf age series on naturally growing plants	*f*
rcy et al. (1982)	11 *Euphorbia* species (C_4)	$A_{max} = -180 + 361 \cdot N$	0.90	11	Greenhouse-grown plants: each A_{max} and N represents mean of several leaves	*a*
oney et al. (1983)	6 fynbos species	$A_{max} = -47 + 113 \cdot N$	0.77	13	One-year-old leaves on naturally growing plants	*k*
d and Mooney (1983)	*Lepechinia calycina*	$A_{max} = 8 + 93.8 \cdot N$	0.89	27	Leaf age series on naturally growing plants	*h*
d et al. (1983)	5 species of California evergreens	$A_{max} = 14 + 28.6 \cdot N$	0.51	53	Leaf age series on naturally growing plants	*j*
oney (unpublished)	*Raphanus sativus*	n.s.	0.04	5	Growth-chamber-grown plants	*b*

is in nmol CO_2 g^{-1} s^{-1} and N is in mmol g^{-1}