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Photosynthesis and nitrogen relationships in leaves of C_3 plants

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Summary. The photosynthetic capacity of leaves is related to the nitrogen content primarily because the proteins of the Calvin cycle and thylakoids represent the majority of leaf nitrogen. To a first approximation, thylakoid nitrogen is proportional to the chlorophyll content (50 mol thylakoid N mol^{-1} Chl). Within species there are strong linear relationships between nitrogen and both RuBP carboxylase and chlorophyll. With increasing nitrogen per unit leaf area, the proportion of total leaf nitrogen in the thylakoids remains the same while the proportion in soluble protein increases. In many species, growth under lower irradiance greatly increases the partitioning of nitrogen into chlorophyll and the thylakoids, while the electron transport capacity per unit of chlorophyll declines. If growth irradiance influences the relationship between photosynthetic capacity and nitrogen content, predicting nitrogen distribution between leaves in a canopy becomes more complicated. When both photosynthetic capacity and leaf nitrogen content are expressed on the basis of leaf area, considerable variation in the photosynthetic capacity for a given leaf nitrogen content is found between species. The variation reflects different strategies of nitrogen partitioning, the electron transport capacity per unit of chlorophyll and the specific activity of RuBP carboxylase. Survival in certain environments clearly does not require maximising photosynthetic capacity for a given leaf nitrogen content. Species that flourish in the shade partition relatively more nitrogen into the thylakoids, although this is associated with lower photosynthetic capacity per unit of nitrogen.

Key words: RuBP carboxylase – Chlorophyll – Thylakoid nitrogen – Nitrogen partitioning

The strength of the relationship between the light-saturated photosynthetic rate in air and the nitrogen content of leaves is widely recognised. When both parameters are expressed on the basis of leaf dry weight, data collected from a wide range of C_3 species cluster around a single straight line, declining to zero at about 0.6 mmol N g^{-1} (Field and Mooney 1986). Field and Mooney have argued that this reflects a fundamental relationship that is independent of species and growth conditions. While this is true in a general sense, it conceals variation that may be of significance for plants that have specialised for particular environments. I wish to consider this variation by analysis of the partitioning of nitrogen between various major components in the leaf.

The variation becomes strikingly apparent when photosynthesis and nitrogen content are both expressed per unit of leaf area (Fig. 1). Numerous other species could have been included, but the feature that should be noted is the 10-fold variation in the CO_2 assimilation rate at, for example, 100 mmol N m^{-2}. It is clear that different types of plant have different relationships. Wheat, rice and *Panicum laxum* (Brown and Wilson 1983, not shown) show the high-

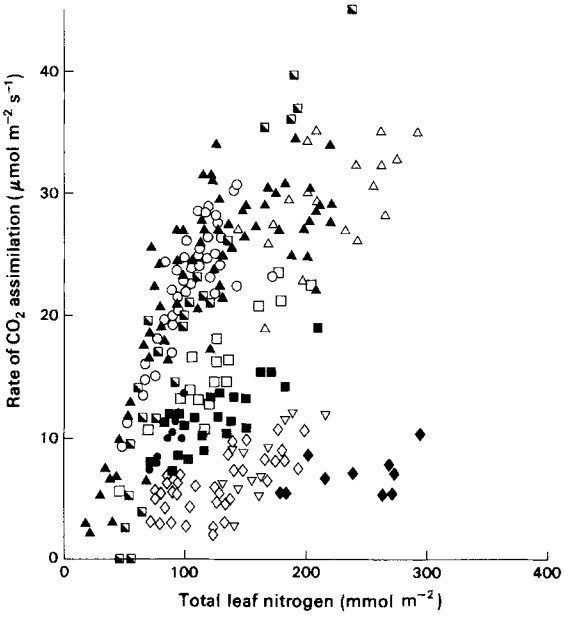

Fig. 1. Rate of CO_2 assimilation at high irradiance versus leaf nitrogen content, both expressed per unit leaf area. ▲ *Triticum aestivum* (Evans 1983, 1985) ○ *Oryza* (Cook and Evans 1983a, b) ◪ *Raphanus raphanistrum* (Küppers et al. 1988) △ Death valley annuals (Mooney et al. 1981) □ Illinois annuals (Mooney et al. 1981). ● *Alocasia macrorrhiza* (Seemann et al. 1987) ■ *Lepechinia calycina* (Field and Mooney 1983) ◇ Californian evergreen trees and shrubs (Field et al. 1983) and rainforest trees (Langenheim et al. 1984) ▽ South African shrubs (Mooney et al. 1983) ◆ *Prunus ilicifolia* (Field et al. 1983)

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est rates of CO_2 assimilation for nitrogen contents up to 120 mmol m^{-2}, then *Raphanus*, *Chenopodium album* (Sage & Pearcy 1987, not shown), *Spinacia oleracea* and *Helianthus annuus* (Evans and Terashima, unpublished) dominate around 200 mmol m^{-2}. At the lowest end, Californian evergreen trees, rainforest trees and Australian sclerophylls (see also Mooney et al. 1978) achieve only 10% of the rate of CO_2 assimilation that wheat and rice do for a given nitrogen content. This variation is also evident in the data when expressed on a dry weight basis. A five-fold difference between extremes exists at 2 mmol N g^{-1} (Field and Mooney 1986) and wheat was not included which has a rate of 600 nmol $g^{-1}s^{-1}$ at 2 mmol N g^{-1} (Evans 1983). However, the scatter is less apparent because of the tendency for lower photosynthetic capacity to be associated with high specific leaf weight. Field and Mooney (1986) point out that the correlation coefficient on an area basis (0.53) could be considerably improved by considering life-forms separately. For example, across 10 species of annuals and deciduous perennials, the correlation improved to 0.86. The variation between life-forms is also strikingly obvious when maximum leaf conductance is compared with leaf nitrogen content (Körner et al. 1986), given that conductance is roughly proportional to the rate of CO_2 assimilation (Körner et al. 1979, Wong et al. 1979).

The merits of using weight or area as the basis for expression have been argued extensively (Field and Mooney 1986). Since most of the evidence presented here was obtained on an area basis, I have restricted the discussion to area rather than weight. However, the conclusions reached are not dependent upon this and are as clearly evident had the analysis been made on a weight basis.

For the analysis used here, nitrogen involved in photosynthesis will be divided into two parts. The first is soluble protein, dominated by the enzyme ribulose 1,5-bisphosphate (RuBP) carboxylase. Other chloroplast enzymes of the Calvin cycle, photorespiratory enzymes in the mitochondria and peroxisomes, carbonic anhydrase and ribosomes make up most of the remainder of the soluble leaf protein. The second part is protein in the thylakoid membranes of the chloroplast. These contain the pigment-protein complexes, components of the electron transport chain and the coupling factor. This division into soluble and thylakoid proteins is convenient because it functionally represents the dark and light reactions of photosynthesis, respectively, which can be transposed into the photosynthetic model of Farquhar and Caemmerer (1982). In the model, photosynthesis is separated into the same two parts, most evident in the relationship between the rate of CO_2 assimilation and the intercellular $p(CO_2)$, p_i. At low p_i (<200 μbar) and moderate irradiance, the rate of CO_2 assimilation is proportional to the maximum RuBP carboxylase activity per unit leaf area (Caemmerer and Farquhar 1981, 1984; Caemmerer and Edmondson 1986; Evans 1983, 1986; Evans and Seemann 1984; Brooks 1986, Ferrar and Osmond 1986). Both the rate of CO_2 assimilation and RuBP carboxylase correlate with soluble protein per unit area. At high p_i (400 μbar), the rate of CO_2 assimilation depends on the rate of regeneration of RuBP, which reflects the rate of electron transport (Caemmerer and Farquhar 1981; Evans 1987; Evans and Terashima 1988) and depends on the irradiance. Although the regeneration of RuBP requires the other enzymes of the Calvin cycle, they represent only a small fraction of the protein involved, due to the dominance of the thylakoid proteins. Photosynthesis at high p_i thus correlates with thylakoid nitrogen. In some cases, RuBP regeneration can be limited by the availability of inorganic phosphate in the chloroplasts (Farquhar and Caemmerer 1982; Sharkey 1985), but this can be grouped along with numerous other factors which depress the potential maximum rate of CO_2 assimilation.

In many leaves, the capacities for RuBP regeneration and carboxylation result in similar potential rates in air such that they co-limit the rate of photosynthesis (*Phaseolus* Caemmerer and Farquhar 1981; *Triticum* Evans 1985, 1986; *Spinacea* Brooks 1985; Evans and Terashima 1988, *Pisum* Evans 1987; *Flindersia* Thompson et al. 1988). In these cases, nitrogen is optimally distributed between RuBP regeneration and carboxylation and should therefore operate with greatest efficiency (Caemmerer and Farquhar 1981). The region where colimitation occurs varies with irradiance and temperature, but plants that do not have a co-limitation when measured at high irradiance and normal growth conditions would be expected to have a relatively lower rate of CO_2 assimilation for their leaf nitrogen.

Soluble protein – RuBP carboxylase

Across a large number of species, Björkman (1981) found a correlation coefficient of 0.96 between the light saturated rate of CO_2 assimilation in air and the fully activated RuBP carboxylase activity. This correlation is also evident within species such as tomato (Besford et al. 1985), rice (Makino et al. 1985, 1988), wheat (Evans 1986) and *Solanum dulcamara* (Ferrar and Osmond 1986). The abundance of RuBP carboxylase protein, reflecting its low catalytic rate and poor affinity for CO_2, results in strong correlations between RuBP carboxylase and total leaf nitrogen (Fig. 2). In all the regressions, the variation in nitrogen contents was achieved by growing plants with different levels of nitrogen nutrition or sampling leaves at different ages but does not include different irradiance during growth. Generally, the straight lines cross the x-axis at positive values of total leaf nitrogen. This means that the proportion of total nitrogen in RuBP carboxylase is not constant, but increases with increasing leaf nitrogen. For example, in spinach it increases from 10 to 19%. Note that at 100 mmol N m^{-2} the proportion ranges from 10 to nearly 30% across species.

Differences in partitioning nitrogen into RuBP carboxylase between species are probably significant. For example, in rice leaves, about 27% of the total nitrogen is present in RuBP carboxylase (Makino et al. 1984) compared with only 20% for wheat (Evans and Seemann 1984; Evans and Austin 1986). The greater proportion of nitrogen in RuBP carboxylase in rice leaves partially offsets the lower specific activity of the rice RuBP carboxylase (Table 1). Rice also has a relatively greater leaf conductance. The net result is that wheat and rice have similar rates of photosynthesis for a given nitrogen content (Fig. 1; Makino et al. 1988). When *Phaseolus* was compared with *Alocasia*, there were differences in both partitioning and specific activity (Table 1). However, *Alocasia* had a lower proportion of nitrogen in RuBP carboxylase and the enzyme had lower specific activity, so that overall it had a photosynthetic rate only one third of that of *Phaseolus*, for a given nitrogen content. The other two examples given in Table 1 show that differences can also arise due to changes in RuBP carboxylase

Table 1. Comparisons between species where the specific activity of RuBP carboxylase and/or the partitioning of nitrogen in RuBP carboxylase vary

	mol CO_2 mol^{-1} RuBPC'ase s^{-1}		E/N[a] %	mmol CO_2 mol^{-1} N s^{-1}
	in vitro	in vivo[b]		
1) *Triticum*	22.9	6.1	23.4	0.24
Oryza	15.5	4.9	28	0.23
ratio	1.47	1.24	0.83	1.04
2) *Phaseolus*	29	9.9	17	0.29
Alocasia	19.7	6.1	9.5	0.10
ratio	1.47	1.62	1.79	2.90
3) *Camissonia*	26.6	6.7	18	0.20
Geraea	22	3.8	18	0.12
ratio	1.21	1.76	1.0	1.76
4) *Spinacia*	26	6.9	15.9	0.19
Glycine	15	3.7	19.5	0.12
ratio	1.73	1.86	0.82	1.52

[a] E/N is the proportion of total leaf nitrogen in RuBP carboxylase
[b] The in vivo rates are measured differently between groups 1–4, therefore only pairwise comparison is possible

1) Makino et al. (1988), intercellular p(CO_2) for *Triticum* and *Oryza* were 225 and 270 μbar, respectively
2) Seemann et al. (1987), CO_2 assimilation measured under CO_2 saturation, RuBPC'ase specific activities from Seemann & Critchley 1985 and Pearcy 1988
3) Seemann et al. (1981), CO_2 assimilation measured in standard ambient conditions
4) Seemann and Berry (1982), CO_2 assimilation measured with 2% O_2 and 100 μl l^{-1} intercellular CO_2. A ratio of 1.36 for the specific activity measured in vitro was also found (Seemann et al. 1984)

specific activity without changes in nitrogen partitioning. The specific activity of RuBP carboxylase from *Camissonia* was 20% greater than that from *Geraea*. Since both species partitioned 18% of total nitrogen towards RuBP carboxylase, the photosynthetic rate per unit of nitrogen of *Camissonia* exceeded that of *Geraea*. In the comparison between *Spinacia* and *Glycine*, both species had a similar relationship between RuBP carboxylase and total nitrogen. However, due to the nonzero intercept (Fig. 2) in combination with higher average leaf nitrogen contents, *Glycine* had a larger proportion of total leaf nitrogen in RuBP carboxylase. The superior specific activity of RuBP carboxylase from *Spinacia* still resulted in a higher photosynthetic rate per unit of nitrogen than *Glycine*. Had it been possible to compare *Spinacia* and *Glycine* at the same leaf nitrogen content, the differences would have been even greater.

The response to different irradiance during growth, in terms of partitioning of nitrogen into RuBP carboxylase, depends on the species. Changing the irradiance during growth did not alter the relationship between RuBP carboxylase and nitrogen for *Phaseolus* or *Alocasia* (Seemann et al. 1987). Growth of spinach under lower irradiance decreased the amount of soluble protein per unit of nitrogen, while RuBP carboxylase: soluble protein remained constant (Terashima and Evans 1988). When *Atriplex patula* was grown at 3% sunlight, RuBP carboxylase as a proportion of soluble protein dropped by 20% (Medina 1971). A drop of 20% was also seen in *Solidago virgaurea* when grown under low light (Björkman 1968).

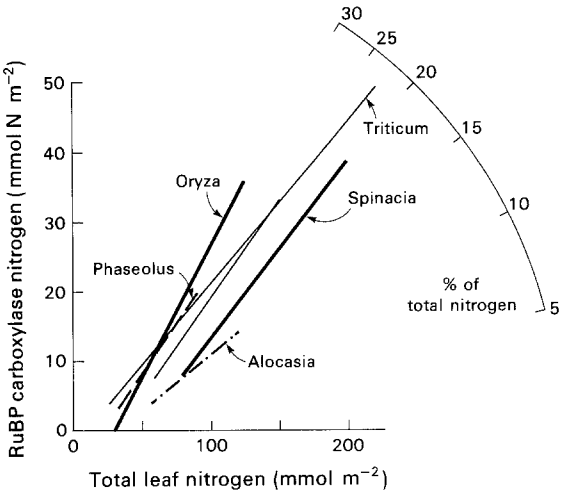

Fig. 2. Nitrogen content of RuBP carboxylase versus total leaf nitrogen. *Triticum* (Evans 1983, 1986), *Oryza* (Makino et al. 1984), *Spinacia* (Terashima and Evans 1988), *Phaseolus* and *Alocasia* (Seemann et al. 1987). RuBP carboxylase N as a percentage of total leaf nitrogen can be derived by joining a straight line from the origin to the curved scale. *Chenopodium album* (Sage et al. 1987) shares the same line as *Spinacia*

Thylakoid protein

The second major fraction of nitrogen directly related to photosynthesis consists of the pigment-protein complexes, photosystem reaction centres, components of the electron transport chain (primarily the cytochrome b/f and ferredoxin NADP reductase complexes) and the coupling factor (ATP synthase). The majority of thylakoid nitrogen (60–85%) is found in the pigment-protein/reaction centre complexes. The nitrogen content per unit of chlorophyll for each component has been estimated (Table 2). A detailed analysis of the components was used as the basis for the estimates in column A, while column B was determined directly from thylakoids following solubilization by digitonin and electrophoresis. The two estimates show reasonable agreement and represent an upper limit. The nitrogen cost is influenced by the irradiance at which the leaves are grown. When grown at high irradiance, the electron transport capacity per unit of chlorophyll is greater than when grown at low irradiance. This is mainly due to a relative increase in the amount of the cytochrome b/f complex and coupling factor (Björkman et al. 1972; Wild et al. 1973; Berzborn et al. 1981; Davies et al. 1987). Consequently, a greater amount of thylakoid nitrogen per unit of chlorophyll is associated with higher rates of oxygen evolution (Fig. 3). As shown in Table 2, approximately 40 mol N mol^{-1} Chl are involved in complexing the pigments (represented by the dashed line in Fig. 3), so the electron transport capacity can be increased by relatively small amounts of additional nitrogen. However, to a first approximation, 50 mol thylakoid N mol^{-1} Chl can be assumed.

While the nitrogen content of chlorophyll is only 4 mol mol^{-1}, because of the large amount of protein that complexes the pigments in vivo, strong correlations are found between the chlorophyll and nitrogen contents in leaves (Fig. 4A, Table 3). The variation was obtained by varying nitrogen nutrition and sampling leaves of different age. Different linear relationships are clear for the four species.

Table 2. The nitrogen cost of the protein complexes in thylakoid membranes for spinach grown under full sunlight

	Proportion of total Chl[c]	Nitrogen cost (mol N mol^{-1} Chl)			
	1	2[a]	1×2	3[b]	1×3
Light-harvesting Chl a/b complex	0.56	25.5	14.3	22.6	12.7
Photosystem II	0.12	69.8	8.4	70.5[d]	8.5
Photosystem I	0.32	40.9	13.1	36	11.5
Chlorophyll			4		4
Sub total for light harvesting			39.8		36.7
Electron transport chain and coupling factor			24.2[e]		31.1[f]
Total thylakoid nitrogen cost			64±3[g]		67.8[h]

[a] Evans (1987)
[b] Picaud et al. (1982)
[c] Evans and Anderson (1987)
[d] corrected to account for the contribution of LHC that reduced the Chl a/b ratio to 4, originally 49.4
[e] by difference, which requires the cytochrome b/f: ferredoxin NADP reductase: coupling factor to be 1:1:1.2
[f] by difference
[g] Terashima and Evans (1988)
[h] Park and Pon (1963) obtained 50 mol N mol^{-1} Chl

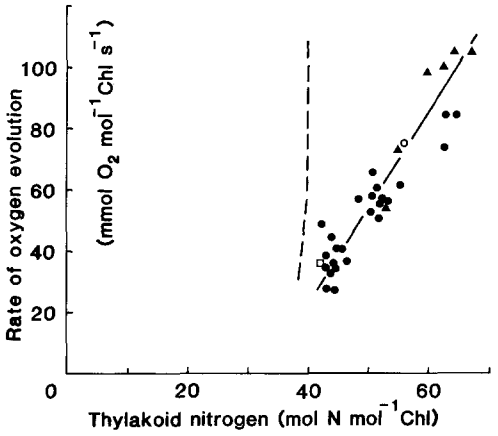

Fig. 3. Rate of oxygen evolution as a function of thylakoid nitrogen. Oxygen evolution was measured near light saturation and ~1% CO_2 in a leaf disc oxygen electrode. Thylakoid nitrogen was determined from Kjeldahl digestion of thylakoid preparations, ● *Pisum sativum* Evans (1987), ▲ *Spinacia oleracea* Terashima and Evans (1988), ○ *Triticum aestivum* and □ *Alocasia macrorrhiza* (unpublished data). The regression equation is $y = 3.16\ N - 104.7$, $r^2 = 0.88$, the dashed line is the estimated cost of complexing the pigments (Evans 1987)

None of the y-intercepts were significantly different from the origin in the regression analyses (Table 3) indicating that the proportion of nitrogen associated with the thylakoids remains constant. For spinach, the electron transport capacity per unit of chlorophyll remained constant across the nitrogen treatments (Evans and Terashima 1987).

The result is different if irradiance during growth is the source of variation (Fig. 4B, Table 4). Generally, a greater proportion of nitrogen is partitioned into the thylakoids when plants are grown at lower irradiance, increasing from ~20 to 40% of total leaf nitrogen at low irradiance. Shade-tolerant plants tended to have the ability to partition far more nitrogen into the thylakoids than sun plants. The second general feature of Fig. 3B is that growth at low irradiance was always associated with a reduction in the nitrogen content per unit leaf area. Examples of plants where thylakoid nitrogen was relatively insensitive to growth irradiance include *Pisum* and *Spinacia*, with 27 and 24% of total nitrogen present in the thylakoids, respectively (Evans 1987; Evans and Terashima 1987).

The strong correlation between chlorophyll and leaf nitrogen does not extend directly to a strong correlation between electron transport capacity and leaf nitrogen, if the source of variation includes irradiance during growth. This was clearly demonstrated with *Spinacia* (Fig. 4), where the electron transport capacity varied 2.5-fold for a given leaf nitrogen content. The decline in electron transport capacity was associated with a proportional decrease in the cytochrome f content per unit of chlorophyll such that there was no effect of growth irradiance when the electron transport capacity was expressed per unit of cytochrome f (Terashima and Evans 1988). While growth under low irradiance is generally associated with lower rates of electron transport per unit of chlorophyll (Table 5, Boardman 1977, Björkman 1981), because plants tend to increase the relative amounts of chlorophyll per unit nitrogen, electron transport per unit of nitrogen is less affected by irradiance. The irradiances used in each comparison in Table 5 vary, which will affect the absolute values. However, the trend is apparent. The mean ratio of electron transport on a chlorophyll basis from high and low light plants was 1.9, which declined to 1.3 on a nitrogen basis (Table 5). The means conceal considerable variation between species. Whereas spinach retains a large dependence on the irradiance during growth on either a chlorophyll or nitrogen basis, both *Flindersia* and *Solanum* show a reversal, with electron transport per unit of nitrogen increasing when grown at low irradiance.

The dependence on irradiance is particularly significant in leaf canopies, where leaves lower in the canopy are older, generally have less nitrogen and experience lower irradiance. It has been argued that the lower nitrogen contents of leaves deeper in the canopy reflect an optimum distribution (Field 1983; Hirose and Werger 1987a, b). This is

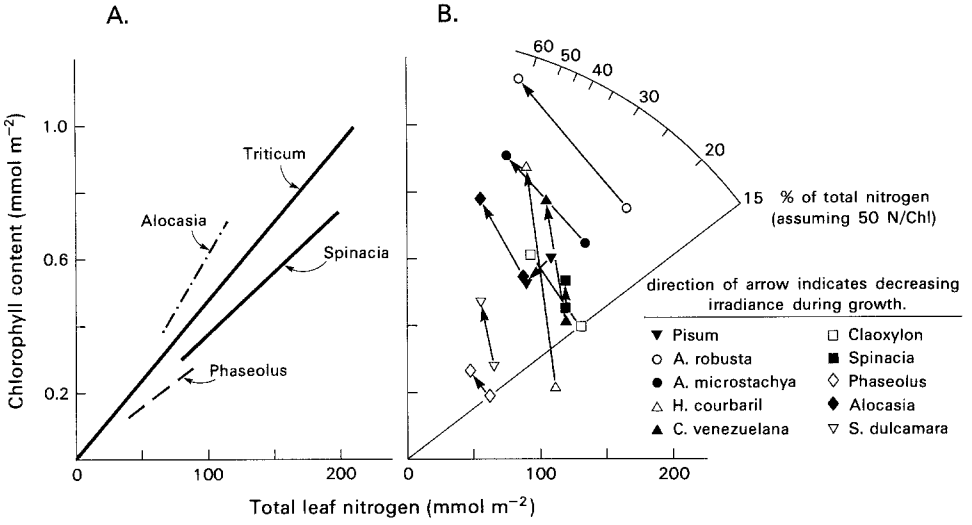

Fig. 4A. Chorophyll content versus total leaf nitrogen when leaf age and nitrogen nutrition are the source of variation. All plants grown at high light (refs as in Fig. 2). **4B** Chlorophyll content versus total leaf nitrogen as influenced by the irradiance during growth. The scale for calculating the percentage of total leaf nitrogen is based on a nitrogen cost of 50 mol N mol^{-1} Chl, which includes the pigment-protein complexes, components of the electron transport chain and the coupling factor (Evans 1987) and is used by joining a straight line from the origin to the curved scale

Table 3. Correlation between leaf chlorophyll content and total leaf nitrogen content for different species grown under high irradiance with variable nitrogen nutrition. Chl (mmol m^{-2}) = $a + b$N (mmol m^{-2})

	a	b	regression coefficient	correlation coefficient	n
Alocasia macrorrhiza[a]	0.031	0.00547***	0.50	0.70**	15
Chenopodium album[b]	0.023	0.00372***	0.54	–	40
Gossypium hirsutum[c]	0.165	0.00226***	0.68	0.83***	18
Phaseolus vulgaris[a]	−0.012	0.00323***	0.84	0.92***	21
Spinacia oleracea[d]	0.022	0.0036***	0.96	0.98***	12
Triticum aestivum[e]	0.024	0.0043***	0.89	0.94***	51

[a] Seemann et al. (1987)
[b] Sage et al. (1987)
[c] Wong (1979b)
[d] Evans and Terashima (1987)
[e] Evans (1983) winter grown plants

Table 4. The ratio of chlorophyll to total leaf nitrogen for leaves from plants grown under high and low irradiance

	High (mmol Chl mol^{-1} N)	Low	Reference
Agathis microstachya	4.7	12.2	Langenheim et al. 1984
A. robusta	4.5	13.3	Langenheim et al. 1984
Alocasia macrorrhiza	5.1	12.0	Seemann et al. 1987
Argyrodendron peralatum	3.8	9.0	Pearcy 1987
Citrus paradisi	2.4	5.2	Syversten & Smith 1984
C. sinensis	2.3	6.2	Syversten & Smith 1984
Claoxylon sandwicense	3.0	6.6	Pearcy & Franceschi 1986
Copaifera venezuelana	3.0	6.6	Langenheim et al. 1984
Flindersia brayleyana	4.4	9.4	Thompson et al. 1988
Hymenaea courbaril	1.7	8.8	Langenheim et al. 1984
Oryza sativa	4.0	4.3	Uchida et al. 1980
Phaseolus vulgaris	2.8	4.7	Seemann et al. 1987
Picea sitchensis	5.3	5.5	Leverenz & Jarvis 1980
Pisum sativum	5.4	6.0	Evans 1987
Solanum dulcamara	4.4	8.6	Ferrar & Osmond 1986
Solidago virgaurea	3.2	5.3	Björkman & Holmgren 1963
Spinacia oleracea	3.8	4.4	Terashima & Evans 1988
Triticum aestivum	3.7	–	Evans 1983
means	3.8 ± 0.3	7.7 ± 0.7	

Table 5. The rate of electron transport on either a chlorophyll or total leaf nitrogen basis, for plants grown under high or low irradiance

	High	Low	High Low	High	Low	High Low
	mmol O_2 mol^{-1} Chl s^{-1}			μmol O_2 mol^{-1} N s^{-1}		
Atriplex patula[a]	28	15	1.9	104	80	1.3
Alocasia macrorrhiza[b]	52	21	2.5	210	155	1.4
Phaseolus vulgaris[c]	103	53	1.9	287	250	1.1
Picea sitchensis[d]	20	8	2.5	104	43	2.4
Pisum sativum[e]	48	30	1.6	259	180	1.4
Spinacia oleracea[f]	132	51	2.6	502	224	2.2
Flindersia brayleana[g]	25	18	1.4	110	169	0.7
Solanum dulcamara[h]	66	38	1.7	290	324	0.9

Data derived from [a] Medina (1971); [b] Chow et al. (1988); [c] Seemann et al. (1987); [d] Lewandowska et al. (1976); [e] Evans (1987); [f] Terashima and Evans (1988); [g] Thompson et al. (1988); [h] Ferrar and Osmond (1986)

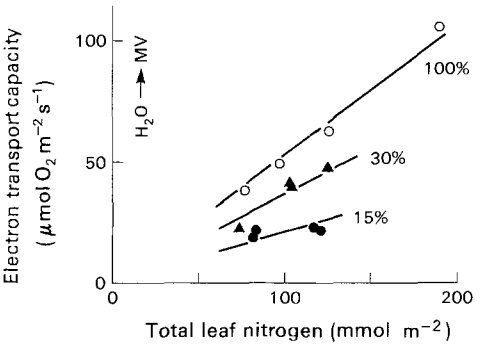

Fig. 5. Light-saturated whole chain electron transport activity in uncoupled thylakoids isolated from spinach leaves versus total leaf nitrogen content. The plants were grown at three different irradiances (% of full sunlight) in combination with four different levels of N-nutrition (Terashima and Evans 1988)

only true if acclimation does not occur such as that seen for spinach (Terashima and Evans 1988, Fig. 5) and can only be assessed if light and nitrogen effects can be manipulated independently. While this is presumably not possible in the field, there are other clues which can be used. Acclimation to low irradiance is generally accompanied by a lowering of both the cytochrome f content and the chlorophyll a/b ratio (see Evans 1988). The latter is due to an increase in the proportion of chlorophyll in the light-harvesting complex and a reduction in the number of photosystem II reaction centres. Thus, if leaves lower in the canopy have lower chlorophyll a/b ratios (which was true for *Solidago altissima*, Hirose pers. comm.) acclimation is to be expected. Consequently, the relationship between the rate of CO_2 assimilation and leaf nitrogen content built up from leaves sampled at different depths within the canopy, is steeper than had leaf nitrogen content been varied for a given irradiance during growth. Optimization calculated by incrementing leaf nitrogen will then inadvertently include changes in irradiance during growth and will probably reduce the decline in nitrogen content expected with depth in the canopy.

Relative balance between soluble and thylakoid nitrogen.

Growth irradiance tends to influence the partitioning of nitrogen into thylakoids and soluble protein in opposite directions. This results in large changes in the ratio of soluble protein or RuBP carboxylase to thylakoid nitrogen or chlorophyll (Goodchild et al. 1972; Björkman et al. 1972; Evans 1988). Leaves grown under high irradiance with sufficient nitrogen, generally have a ratio of 8–11 mmol RuBP carboxylase mol^{-1} Chl or 1 to 1.4 mol RuBP carboxylase N mol^{-1} thylakoid N. The ratio decreases to 0.4 mol RuBP-Case N mol^{-1} thylakoid N for many species when grown under low irradiance, but can drop to 0.06 in the case of *Alocasia* (Seemann et al. 1987). If it is assumed that RuBP carboxylase is never present in great excess, that it is close to co-limiting the rate of CO_2 assimilation at high irradiance, then the nitrogen cost for RuBP carboxylase plus thylakoids ranges from 1.7 mol N mol^{-1} RuBP carboxylase N at high irradiance to 3.5 at low irradiance (or 18 for the extreme case of *Alocasia*). This predicts at least a 2-fold variation in the rate of CO_2 assimilation for a given amount of nitrogen. For example, leaves containing a 100 mmol N m^{-2} had the following rates of oxygen evolution *Spinacia* 42 and 25 μmol m^{-2} s^{-1} for high and low-light grown plants (Terashima and Evans 1988), *Pisum* 35 and 16, respectively (Evans 1987) and *Alocasia* 13 for high-light grown plants (Seemann et al. 1987). For leaves containing ~65 mmol N m^{-2}, *Piper auritum* had a rate of CO_2 assimilation of 12 and 6 for high- and low-light grown leaves (Walters and Field 1987).

Factors introducing curvature to the photosynthesis: nitrogen relationship

While RuBP carboxylase and chlorophyll both tend to increase linearly with leaf nitrogen content, the rate of CO_2 assimilation sometimes shows curvature (*Beta vulgaris* Nevins & Loomis 1970; *Diplacus aurantiacus* Gulmon and Chu 1981; *Glycine maxima* Lugg and Sinclair 1981; *Gossypium hirsutum* Wong 1979a; *Oryza sativa* Takano and Tsunoda 1971; *Spinacia oleracea* Evans and Terashima 1988; *Triticum aestivum* Evans 1983). There are at least two factors contributing to the curvature. Firstly, with increasing leaf nitrogen, the chlorophyll content and electron transport capacity increase. To reach light saturation requires progressively higher irradiances so that if measured at the same irradiance, the rate for the high nitrogen leaf will be underestimated.

The second possible reason is that the rate of CO_2 assimilation is not always linearly related to the RuBP carboxylase content. This is most evident when the slope of the line relating the rate of CO_2 assimilation to intercellular $p(CO_2)$ near the CO_2 compensation point (the mesophyll conductance) is plotted against RuBP carboxylase (Fig. 6). The curvature has been ascribed to a drop in the $p(CO_2)$ between the intercellular space and the sites of carboxylation, due to the resistance to CO_2 transfer imposed by

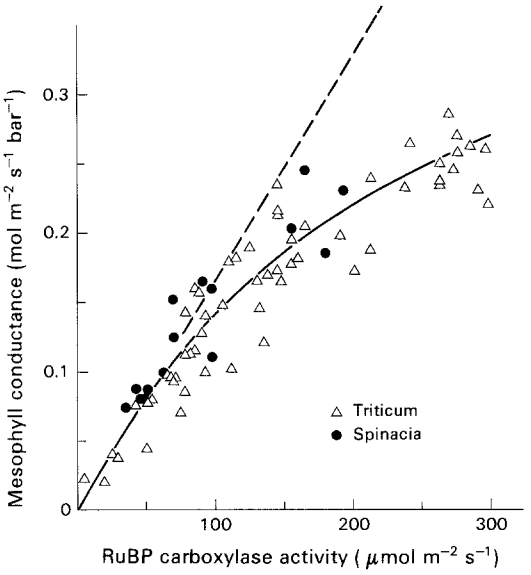

Fig. 6. Mesophyll conductance (the slope of the curve relating the rate of CO_2 assimilation to intercellular p(CO_2) near the CO_2 compensation point, g_m) versus RuBP carboxylase activity, V_c. △ *Triticum aestivum* (Evans 1983), ● *Spinacia oleracea* (Evans & Terashima 1988). The solid curve is $g_m = V_c\ g_w/(V_c + 245)$, where g_w = 0.49 mol m^{-2} s^{-1} bar^{-1} is the CO_2 transfer conductance between the intercellular space and the site of carboxylation

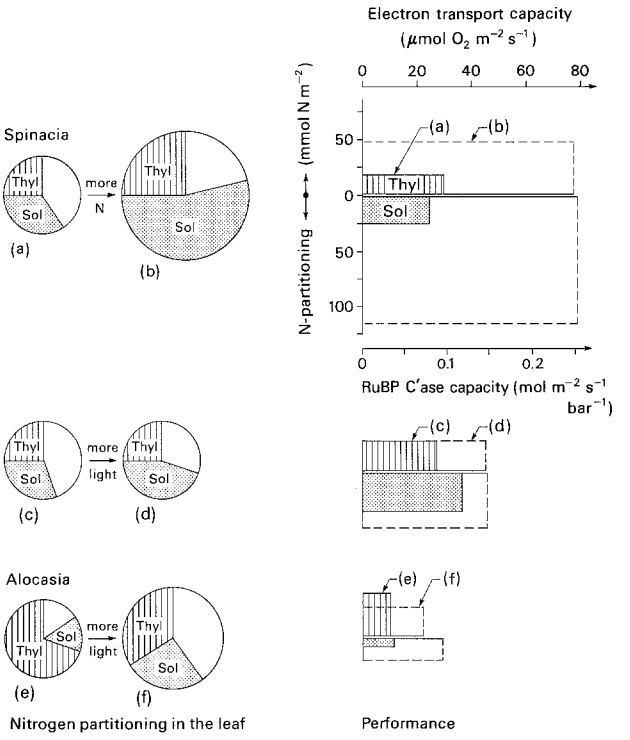

Fig. 7. Nitrogen partitioning (left-hand side) and performance (right-hand side) of leaves supplied with different amounts of nitrogen, or grown at different irradiances. The relative area of each pair of circles is proportional to the nitrogen content of the leaves, being 75 (*a*) and 200 mmol N m^{-2} (*b*) for spinach receiving different levels of N, 115 mmol N m^{-2} for spinach grown at 15% (*c*) and 100% (*d*) sunlight and 57 (*e*) and 95 mmol N m^{-2} (*f*) for *Alocasia* grown at 20 mmol quanta m^{-2} s^{-1} and full sunlight (Terashima and Evans 1988; Seemann et al. 1987). Nitrogen determinations were not made for the soluble and thylakoid fractions in *Alocasia* and were calculated assuming that there were 50 mol thylakoid N mol^{-1} Chl and that RuBP carboxylase represented 50% of the soluble protein. On the right hand side, the amounts (y-axis) and performance (x-axis) of thylakoid and soluble protein are represented. The larger boxes (dashed lines) represent the state when the leaf has a higher nitrogen content or was grown under higher irradiance, i.e. the right-hand pie diagram

the cell wall and liquid phase (Evans 1983). It may also partly reflect the drop in p(CO_2) across the leaf (Parkhurst 1986). The curvature does not appear to be due to enzyme inactivation (Evans and Terashima 1988). The curvature is less noticeable in the photosynthesis: leaf nitrogen content relationship because the proportion of nitrogen in RuBP caboxylase generally increases with increasing leaf nitrogen due to the nonzero intercept (see Fig. 2). It is evident that in some species, notably *Raphanus* (Kuppers et al. 1988) *Chenopodium* (Sage and Pearcy 1987), see also *Oryza* and *Triticum* (Makino et al. 1988), neither of these two mechanisms result in noticeable curvature.

Nitrogen partitioning and performance

The changes in nitrogen partitioning that occur in response to changing nitrogen content or growth irradiance, as well as the net effect in terms of performance are illustrated in Fig. 7. A nearly three-fold increase in the nitrogen content of a spinach leaf was accompanied by an equivalent increase in thylakoid nitrogen such that it remained at 24%. Soluble protein increased from 33 to 58% at the expense of the 'other' fraction which includes ~15% for nucleic acids (Chapin and Kedrowski 1983). While the proportion of the 'other' fraction declined from 43 to 18%, the absolute amount remained relatively constant (32 and 36 mmol N m^{-2}, respectively). If the cell number per unit leaf area is unaltered by the nitrogen content of the leaf, then the amount of total leaf nitrogen in the nuclear and cytoplasmic components should also remain relatively unchanged. That is, the amount of nitrogen per unit leaf area in the 'other' fraction is constant. Higher leaf nitrogen contents will then be due to more thylakoids and Calvin cycle enzymes so that the proportion of nitrogen in the 'other' fraction will tend to decrease with increasing nitrogen content per unit leaf area.

The situation is similar when spinach leaves grown under different irradiances are compared at the same nitrogen content. The proportion of nitrogen in the thylakoids remained at 24% while the soluble protein pool increased from 31 to 44%. The shade plant *Alocasia* behaves differently with increasing irradiance. The proportion of nitrogen in the thylakoids declines from a massive 71% to 29%, while soluble protein increases from 14 to 21% (Fig. 7). The changes in the 'other' fraction with irradiance are difficult to assess because of associated changes in leaf structure such as cell size, number of cell layers, specific leaf weight and the, as yet, unspecified nature of the 'other' fraction.

Since the performance of thylakoid nitrogen depends on the irradiance during growth (Fig. 4), it is important to consider partitioning in conjunction with performance. The right hand side of Fig. 7 represents the amount of nitrogen in the thylakoids or soluble protein along the y-axis and the performance of that nitrogen along the x-axis. With a greater nitrogen content, the amount of thylakoid nitrogen per unit leaf area increases (although not as a proportion). The electron transport capacity increases by the same

proportion because it is unaffected by nitrogen treatment. There is a relatively greater increase in the amount of soluble protein. However due to the CO_2 transfer resistance (Fig. 6) the increase in RuBP carboxylase activity in vivo is slightly less, maintaining the balance between electron transport and RuBP carboxylation capacities (Evans & Terashima 1988). By contrast, higher irradiance during growth increases the electron transport capacity of the leaf without additional thylakoid nitrogen. This requires an increase in the amount of soluble protein, to balance the increase in electron transport capacity. The third response, which is perhaps more general, that of *Alocasia*, shows that higher irradiance during growth actually reduces the thylakoid nitrogen while at the same time results in an increase in the electron transport capacity. This is matched by a similar increase in soluble protein such that the balance between electron transport and RuBP carboxylase activity is maintained.

As noted by Seemann et al. (1987), the photosynthetic capacity of *Alocasia* was only one third to one half that of *Phaseolus* for a given leaf nitrogen content. The ability to proliferate thylakoid membranes when grown in the shade is a feature of many species (Fig. 3) and occurs at the expense of both soluble protein and the 'other' fraction, since the total nitrogen contents are also reduced. Acclimation to shade at the thylakoid level is consistent with reducing the nitrogen cost of light capture (Evans 1987). Without taking account of the costs of leaf synthesis and maintenance, acclimation to shade appears to increase the nitrogen cost of light saturated photosynthesis. However, if leaves are compared at low irradiances, acclimation can be seen to be beneficial due to the reduced rate of respiration for a given leaf nitrogen content (Terashima and Evans 1988). The ability to succeed in particular environments may be evident in the photosynthesis: nitrogen relationship. In a comparison of *Piper auritum* and *P. hispidum*, the former being restricted to open sites had both a greater rate of CO_2 assimilation for a given nitrogen content and a greater rate of dark respiration for a given rate of CO_2 assimilation (Walters and Field 1987; Field 1988). The former would benefit *P. auritum* in open sites and the latter would benefit *P. hispidum* in shady sites. In a comparison of dune grasses, the introduced *Ammophila arenaria* has outcompeted the native *Elymus mollis* in a habitat that is severely nutrient limited (Pavlik 1983). Laboratory grown material demonstrated that for a given leaf nitrogen content, *Ammophila* had a greater rate of CO_2 assimilation. In the field, *Ammophila* still had higher nitrogen use efficiency which meant that despite having lower rates of CO_2 assimilation per unit leaf area, it was able to produce more leaf area for a given nitrogen input.

Apart from the variation which can be ascribed to partitioning into RuBP carboxylase, thylakoids and their performance per unit of protein, variation also arises due to environmental stress and defense. In the analysis by Field and Mooney (1986), the data were collected from plants in their natural high-light habitats. Although the plants were probably not under stress when measured, large variations are evident in the photosynthesis: nitrogen relationship for sclerophylls such as *Eucalyptus*. For example, the rate of CO_2 assimilation for leaves with 125 mmol N m^{-2} was ~ 8 μmol m^{-2} s^{-1} (Mooney et al. 1978) and 24 μmol m^{-2} s^{-1} for glasshouse-grown *E. pauciflora* seedlings (Wong unpublished data, see 1979a). *E. maculata* had a rate of 250 nmol g^{-1} s^{-1} with a leaf nitrogen content of 1.8 mmol g^{-1} (Cromer 1984) and *E. grandis* a rate of 680 nmol g^{-1} s^{-1} at 3.5 mmol N g^{-1} (P. Jarvis and R. Cromer, pers. comm.). It is apparent that under favourable growing conditions, the sclerophyll *Eucalyptus* can achieve both high nitrogen contents and high rates of CO_2 assimilation.

Many species are known to possess nitrogen-based antiherbivore compounds, such as the cyanogenic glucosides in *Prunus ilicifolia* (Field and Mooney 1986). The nitrogen incorporated is not lost to the plant because the plant can remobilise it for use in subsequent protein synthesis (Selmar et al. 1988) and may allow the plant to sequester and store more nitrogen than it requires for photosynthesis, particularly in the low light environment in which seedlings begin. The poor performance of rainforest trees, Californian evergreens and most sclerophylls in the field, in terms of their photosynthetic capacity for a given nitrogen content, suggests that a constraint other than nitrogen is limiting.

Photosynthesis: Nitrogen – a general or variable relationship?

Field and Mooney (1986) compiled a comprehensive survey of their photosynthesis: nitrogen data collected in natural environments and cogently argue that there is an underlying causal relationship. Given that nitrogen is a valuable resource, it can be expected that the plant will optimise the partitioning of that nitrogen such that photosynthesis is maximised. However, the optimum will depend on factors such as the irradiance and temperature and hence vary with habitat. The most obvious example of this is the acclimation to low irradiance where proportionately more protein is associated with complexing pigments and at the same time, the electron transport capacity declines per unit of chlorophyll. Thus, for a given leaf nitrogen content, plants acclimated to low irradiance have lower rates of CO_2 assimilation.

In general, across many species, a strong causal correlation exists between leaf nitrogen content and photosynthesis. Also, given the positive $\times$ intercept, the photosynthesis per unit of nitrogen increases with increasing nitrogen contents. To distinguish variation in the photosynthetic capacity per unit of nitrogen, it is therefore necessary to compare plants with similar nitrogen contents. Examples have been presented of variation between species in the partitioning of nitrogen into RuBP carboxylase (Fig. 2), or the specific activity of the enzyme (Table 1) and of partitioning into the thylakoids as judged by the chlorophyll content (Fig. 4). Variation due to acclimation to irradiance is also clear (Fig. 3, Tables 4, 5). When comparing different species with similar growth form from the same habitat, variation is sometimes small, for example desert annuals (Mooney et al. 1981, Seemann et al. 1981) or may be significant (dune grasses, Pavlik 1983, trees, Jia & Ingestad 1984). Similarly, when comparing between habitats, variation may be absent (*Solanum dulcamara*, Osmond 1983, Ferrar and Osmond 1986) or present (*Silene*, Wilmot and Moore 1973).

Despite good correlation coefficients between photosynthesis and nitrogen contents across diverse species, I have argued that there is significant variation in photosynthetic capacity per unit of nitrogen. Selective advantages would flow from even small relative differences, but many other characteristics come into play which may mask this. For example, leaf longevity affects the carbon gain for a given

nitrogen content (Berendse and Aerts 1987). The difficulty in analysing the partitioning of leaf nitrogen in many species poses unanswered questions. However, the examples which can be provided from more tractable herbaceous leaves point to the ways in which the variation can arise.

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References

Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? Functional Ecology 1:293–296

Berzborn RJ, Muller D, Roos P, Anderson B (1981) Significance of different quantitative determinations of photosynthetic ATP synthetase, CF_1, for heterogeneous CF_2 distribution and grana formation. In: Akoyunoglou G (ed) Proceedings V international photosynthesis congress. Balaban International Science Services, Philadelphia Vol. 3: pp 107–120

Besford RT, Withers AC, Ludwig LJ (1985) Ribulose bisphosphate carboxylase activity and photosynthesis during leaf development in the tomato. J Exp Bot 36:1530–1541

Björkman O (1968) Further studies on differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virgaurea*. Physiol Plant 21:84–99

Björkman O (1981) Responses to different quantum flux densities. In Lange OL, Nobel PS, Osmond CB, Ziegler H (eds). Physiological plant ecology 1. Responses to the physical environment. Springer, Berlin, Heidelberg, New York, pp. 57–107

Björkman O, Holmgren P (1963) Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol Plant 16:889–914

Björkman O, Boardman NK, Anderson JM, Thorne SW, Goodchild DJ, Pyliotis NA (1972) Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. Carnegie Institute Washington Yrbk 71:115–135

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Annu Rev Plant Physiol 28:355–377

Brooks A (1986) Effects of phosphorus nutrition on ribulose 1,5-bisphosphate carboxylase activation, photosynthetic quantum yield and amounts of some Cavin-cycle metabolites in spinach leaves. Aust J Plant Physiol 13:221–237

Brown RH, Wilson JR (1983) Nitrogen response of *Panicum* species differing in CO_2 fixation pathways. II. CO_2 exchange characteristics. Crop Sci 23:1154–1159

Caemmerer S von, Edmondson DL (1986) Relationship between steady-state gas exchange, in vivo ribulose bisphosphate carboxylase activity and some carbon reduction cycle intermediates in *Raphanus sativum*. Aust J Plant Physiol 13:669–688

Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387

Caemmerer S von, Farquhar GD (1984) Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta 160:320–329

Chapin FS III, Kedrowski RA (1983) Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64:376–391

Chow WS, Qian L, Goodchild DJ, Anderson JM (1988) Photosynthetic acclimation of *Alocasia macrorrhiza* L. to growth irradiance: structure, function and composition of chloroplasts. In: Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 107–122

Cook MG, Evans LT (1983a) Nutrient responses of seedlings of wild and cultivated *Oryza* species. Field Crops Res 6:205–218

Cook MG, Evans LT (1983b) Some physiological aspects of the demestication and improvement of rice (*Oryza spp.*). Field Crops Res 6:219–238

Cromer RN (1984) The influence of nutrition on growth and photosynthesis in *Eucalyptus*. In: Grey DC, Schönan APG, Schutz CJ, Laar A van (eds) IUFRO symposium on site and productivity of fast growing plantations. Rep. of Sth. Africa. Vol. 2 pp 669–678

Davies EC, Jordan BR, Partis MD, Chow WS (1987) Immunochemical investigation of thylakoid coupling factor protein during photosynthetic acclimation to irradiance. J Exp Bot 38:1517–1527

Evans JR (1983) Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). Plant Physiol 72:297–302

Evans JR (1985) A comparison of the photosynthetic properties of flag leaves from *Triticum aestivum* and *T. monococcum*. In: Jeffcoat B, Hawkins AF, Stead AD (eds) Regulation of sources and sinks in crop plants. British Plant Growth Regulator Group, Bristol, pp 111–125

Evans JR (1986) The relationship between CO_2-limited photosynthetic rate and RuBP carboxylase content in two nuclear cytoplasm substitution lines of wheat and the coordination of RuBP carboxylation and electron transport capacities. Planta 167:351–358

Evans JR (1987) The relationship between electron transport components and photosynthetic capacity in pea leaves grown at different irradiances. Aust J Plant Physiol 14:157–170

Evans JR (1988) Acclimation by the thylakoid membranes to growth irradiance and the partitioning of nitrogen between soluble and thylakoid proteins. In: Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 93–106

Evans JR, Anderson JM (1987) Absolute absorption spectra for the five major chlorophyll-protein complexes and their 77K fluorescence excitation spectra. Biochim Biophys Acta 892:759–765

Evans JR, Austin RB (1986) Ribulose 1,5-bisphosphate carboxylase specific activity in relation to wheat genotype. Planta 167:344–350

Evans JR, Seemann JR (1984) Differences between wheat genotypes in specific activity of ribulose 1,5-bisphosphate carboxylase and the relationship to photosynthesis. Plant Physiol 74:759–765

Evans JR, Terashima I (1987) Effects of nitrogen nutrition on electron transport components and photosynthesis in spinach. Aust J Plant Physiol 14:59–68

Evans JR, Terashima I (1988) Photosynthetic characteristics of spinach leaves grown with different nitrogen treatments. Plant Cell Physiol 29:157–165

Farquhar GD, Caemmerer S von (1982) Modelling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physical plant ecology II. Water relations and carbon assimilation. Springer Verlag, Berlin, pp 550–587

Ferrar PJ, Osmond CB (1986) Nitrogen supply as a factor influencing photoinhibition and photosynthetic acclimation after transfer of shade-grown *Solanum dulcamara* to bright light. Planta 168:563–570

Field C (1983) Allocating leaf nitrogen for the maximisation of carbon gain: leaf age as a control on the allocation program. Oecologia 56:341–347

Field C (1988) On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. In: Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 343–358

Field C, Mooney HA (1983) Leaf age and seasonal effects on light, water and nitrogen use efficiency in a California shrub. Oecologia 56:348–355

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givinsh TJ (ed) On the economy of form and function. Cambridge University Press, Cambridge, pp 25–55

Field C, Merino J, Mooney HA (1983) Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60:384–389

Goodchild DJ, Björkman O, Pyliotis NA (1972) Chloroplast ultrastructure, leaf anatomy and content of chlorophyll and soluble protein in rainforest species. Carnegie Institute Washington Yrbk 71:102–107

Gulmon SL, Chu CC (1981) The effects of light and nitrogen on photosynthesis, leaf characteristics and dry matter allocation in the Chaparral shrub *Diplacus aurantiacus*. Oecologia 49:207–212

Hirose T, Werger MJA (1987a) Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. Physiol Plant 709:215–222

Hirose T, Werger MJA (1987b) Maximising daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72:520–526

Jia HJ, Ingestad T (1984) Nutrient requirements and stress response of *Populus simonii* and *Paulownia tomentosa*. Physiol Plant 62:117–124

Körner Ch, Bannister P, Mark AF (1986) Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. Oecologia 69:577–588

Körner Ch, Scheel JA, Bauer H. (1979) Maximum leaf diffusive conductance in vascular plants. Photosynthetica 13:45–82

Küppers M, Koch G, Mooney HA (1988) The effect of photoperiod, light level and nitrogen nutrition on photosynthetic characteristics, dry weight partitioning and growth of wild radish. In Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 287–298

Langenheim JH, Osmond CB, Brooks A, Ferrar PJ (1984) Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest trees species. Oecologia 63:215–224

Leverenz JW, Jarvis PG (1980) Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.) X. Acclimation to quantum flux density within and between trees. J Appl Ecol 17:697–708

Lewandowska M, Hart JW, Jarvis PG (1976) Photosynthetic electron transport in plants of Sitka spruce subjected to differing light environments during growth. Physiol Plant 37:269–274

Lugg DG, Sinclair TR (1981) Seasonal changes in photosynthesis of field grown soybean leaflets. 2. Relation to nitrogen content. Photosynthetica 15:138–144

Makino A, Mae T, Ohira K (1984) Relation between nitrogen and ribulose 1,5-bisphosphate carboxylase in rice leaves from emergence through senescence. Plant Cell Physiol 25:429–437

Makino A, Mae T, Ohira K (1985) Photosynthesis and ribulose 1,5-bisphosphate carboxylase/oxygenase in rice leaves from emergence through senescence. Quantitative analysis of carboxylation/oxygenation and regeneration of ribulose 1,5-bisphosphate. Planta 166:414–420

Makino A, Mae T, Ohira K (1988) Differences between wheat and rice in the enzymic properties of ribulose 1,5-bisphosphate carboxylase/oxygenase and the relationship to photosynthetic gas exchange. Planta 174:30–38

Medina E (1971) Effect of nitrogen supply and light intensity during grown on the photosynthetic capacity and carboxy- dismutase activity of leaves of *Atriplex patula* ssp *hastata*. Carnegie Institute Washington Yrbk 70:551–559

Mooney HA, Ferrar PJ, Slatyer RO (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. Oecologia 36:103–111

Mooney HA, Field C, Gulmon SL, Bazzaz FA (1981) Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. Oecologia 50:109–112

Mooney HA, Field C, Gulmon SL, Rundel P, Krüger FJ (1983) Photosynthetic characteristics of South African sclerophylls. Oecologia 58:398–401

Nevins DJ, Loomis RS (1970) Nitrogen nutrition and photosynthesis in sugar beet (*Beta vulgaris* L.). Crop Sci 10:21–25

Osmond CB (1983) Interactions between irradiance, nitrogen nutrition and water stress in the sun-shade responses of *Solanum dulcamara*. Oecologia 57:316–321

Park RB, Pon NG (1963) Chemical composition and substructure of lamellae isolated from *Spinacia oleracea* chloroplasts. J Mol Biol 6:105–114

Parkhurst DF (1986) Internal leaf structure: a three dimensional perspective. In Givnish TJ (ed) On the economy of form and function. Cambridge University Press, Cambridge. pp 215–249

Pavlik BM (1983) Nutrient and productivity relations of the dune grasses *Ammophila arenaria* and *Elymus mollis*. I. Blade photosynthesis and nitrogen use efficiency in the laboratory and field. Oecologia 57:227–232

Pearcy RW (1987) Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understorey micro-environments. Functional Ecology 1:169–178

Pearcy RW (1988) Photosynthetic utilization of sunflecks by understorey plants. In Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 223–238

Pearcy RW, Franceschi VR (1986) Photosynthetic characteristics and chloroplast ultrastructure of C_3 and C_4 tree species grown in high- and low-light environments. Photosynth Res 9:317–331

Picaud A, Acker S, Duranton J (1982) A single step separation of PSI, PS2 and chlorophyll antenna particles from spinach chloroplasts. Photosynth Res 3:203–213

Sage RF, Pearcy RW (1987) The nitrogen use efficiency of C_3 and C_4 plants. II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). Plant Physiol 84:959–963

Sage RF, Pearcy RW, Seemann JR (1987) The nitrogen-use efficiency of C_3 and C_4 plants. III. Leaf nitrogen effects on the activity of carboxylating enzymes in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). Plant Physiol 85:355–359

Seemann JR, Berry JA (1982) Interspecific differences in the kinetic properties of RuBP carboxylase protein. Carnegie Institute Washington Yearbook 81:78–83

Seemann JR, Critchley C (1985) Effects of salt stress on the growth, ion content, stomatal behaviour and photosynthetic capacity of a salt-sensitive species, *Phaseolus vulgaris* L. Planta 164:151–162

Seemann JR, Badger MR, Berry JA (1984) Variation in the specific activity of ribulose 1,5-bisphosphate carboxylase between species utilising differing photosynthetic pathways. Plant Physiol. 74:791–794

Seemann JR, Sharkey TD, Wang JL, Osmond CB (1987) Environmental effects on photosynthesis, nitrogen-use efficiency and metabolite pools in leaves of sun and shade plants. Plant Physiol 84:796–802

Seemann JR, Tepperman JM, Berry JA (1981) The relationship between photosynthetic performance and the levels and kinetic properties of RuBP carboxylase-oxygenase from desert winter annuals. Carnegie Inst Wash Yearbook 80:67–72

Selmar D, Lieberei R, Biehl B (1988) Mobilisation and utilisation of cyanogenic glucosides. The linustatin pathway. Plant Physiol 86:711–716

Sharkey TD (1985) Photosynthesis in intact leaves of C_3 plants: Physics, physiology and limitations. Bot Rev 51:53–105

Syvertsen JP, Smith ML (1984) Light acclimation in citrus leaves. I. Changes in physical characteristics, chlorophyll and nitrogen content. J Am Soc Hort Sci 109:807–812

Takano Y, Tsunoda S (1971) Curvilinear regression of the leaf photosynthetic rate on leaf nitrogen content among strains of *Oryza* species. Jpn J Breeding 21:69–76

Terashima I, Evans JR (1988) Effects of light and nitrogen nutrition on the organization of the photosynthetic apparatus in spinach. Plant Cell Physiol 29:143–155

Thompson WA, Stocker GC, Kriedemann PE (1988) Photosynthetic attributes of *Flindersia brayleyana* F. Muell.: a tree species with broad tolerance to sunlight supply in rainforest distur-

bance gaps. In: Evans JR, Caemmerer S von, Adams WW II (eds) Ecology of photosynthesis in sun and shade. CSIRO, Melbourne pp 299–316

Uchida N, Itoh R, Murata Y (1980) Studies on the changes in the photosynthetic activity of a crop leaf during its development and senescence. I. Changes in the developmental stage of a rice leaf. Jpn J Crop Sci 49:127–134

Walters MB, Field CB (1987) Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. Oecologia 72:449–456

Wild A, Ke B, Shaw ER (1973) The effects of light intensity during growth of *Sinapis alba* on the electron transport components. Z Pflanzenphysiol 69:344–350

Wilmot A, Moore PD (1973) Adaptation to light intensity in *Silene alba* and *S. dioica*. Oikos 24:458–464

Wong SC (1979a) Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44:68–74

Wong SC (1979b) Stomatal behaviour in relation to photosynthesis. Ph.D. thesis, Australian National University, Canberra

Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. Nature 282:424–426

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