

The Nitrogen Use Efficiency of C₃ and C₄ Plants

II. LEAF NITROGEN EFFECTS ON THE GAS EXCHANGE CHARACTERISTICS OF *CHENOPODIUM ALBUM* (L.) AND *AMARANTHUS RETROFLEXUS* (L.)

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ABSTRACT

The effect of leaf nitrogen (N) on the photosynthetic capacity and the light and temperature response of photosynthesis was studied in the ecologically similar annuals *Chenopodium album* (C₃) and *Amaranthus retroflexus* (C₄). Photosynthesis was linearly dependent on leaf N per unit area (N_a) in both species. *A. retroflexus* exhibited a greater dependence of photosynthesis on N_a than *C. album* and at any given N_a, it had a greater light saturated photosynthesis rate than *C. album*. The difference between the species became larger as N_a increased. These results demonstrate a greater photosynthetic N use efficiency in *A. retroflexus* than *C. album*. However, at a given applied N level, *C. album* allocated more N to a unit of leaf area so that photosynthetic rates were similar in the two species. Leaf conductance to water vapor increased linearly with N_a in both species, but at a given photosynthetic rate, leaf conductance was higher in *C. album*. Thus, *A. retroflexus* had a greater water use efficiency than *C. album*. Water use efficiency was independent of leaf N in *C. album*, but declined with decreasing N in *A. retroflexus*.

of new leaf area. Leaf area production is often a better predictor of growth than photosynthetic capacity per unit area or net assimilation rate (20). As N is required for both production of new leaf area and for increasing photosynthetic capacity, the enhancement of one under limiting N could come at the expense of the other.

In this research, we have compared the N response of photosynthetic nitrogen use efficiency of the ecologically similar weeds *C. album* (C₃) and *A. retroflexus* (C₄). Leaf N effects on the light and temperature dependence of photosynthesis, leaf conductance, and water use efficiency of the two species were also compared. In an accompanying report (22), we show that when grown over a range of N nutrition, *A. retroflexus* had a lower maximum and minimum leaf N content per unit area than *C. album*, yet an equivalent or higher growth rate and leaf area partitioning coefficient. The research reported here was designed to examine in more detail the physiological basis of the differences in the response to N.

MATERIALS AND METHODS

Growth Conditions. *C. album* and *A. retroflexus* plants were grown in a growth chamber at 27/23°C day/night temperatures and a PFD of 600 μmol m⁻² s⁻¹. Plants were grown in equal volumes of sand, vermiculite and perlite. Plants with different leaf N contents were obtained by watering the species with a 0.5 or 0.75 mM N Johnson-Hoagland's solution modified to contain 12, 8, 6, 4, 3, 2, 1.5, 0.5, or 0.15 mM N in a 7:1 NO₃⁻:NH₄⁺ ratio. The concentration of K, P, Ca, and Mg, and the micronutrients were identical in all treatment solutions. In the N deficient solutions, SO₄⁻² and Cl⁻ were used to replace NO₃⁻.

Gas Exchange Measurements. A, g, and C_i were determined on fully expanded leaves with no visible signs of senescence on the main shoot of 2 to 4 week old plants.

The gas-exchange apparatus used in these measurements has been previously described (9) and was modified as follows. Air of known water vapor and CO₂ partial pressures was obtained by mixing air containing 4% CO₂ with CO₂-free air using two Wöstoff precision mixing pumps (models M201 and G-27, Bochum, FRG) connected in series. Water vapor pressure entering the leaf chamber was controlled by first humidifying the air and then partially dehumidifying it in a glass condensing column whose temperature was controlled by circulating water from a thermostated water bath. The leaf chamber was based on the design of Pearcy and Calkin (19), but enlarged to 10 cm by 20 cm. Air within the chamber was circulated by two Micronel fans (Micronel, Vista, CA). Chamber temperature was controlled by circulating water from a second thermostated bath through a heat exchange block mounted on the chamber.

In all gas exchange measurements, the leaf to air vapor pressure difference and CO₂ partial pressure were maintained at 5 to 11 mbar and 325 to 345 μbar, respectively. Measurements were

The photosynthetic rate per unit of N² is usually higher in C₄ than C₃ plants (4, 18). This is believed to result from the CO₂ concentrating mechanism of C₄ plants leading to CO₂ saturation of rubisco. Consequently, less of this enzyme is required for high rates of photosynthesis in C₄ than C₃ plants (18, 24). C₄ grasses generally have greater photosynthetic rates per unit of N than C₃ grasses and dicots (3, 5, 24, 29) as well as greater growth and leaf expansion rates per unit N (22, 27, 28). However, exceptions have been noted (5) and the NUE differences of C₃ and C₄ dicots have not been directly compared.

The relationship between PNUE and photosynthetic capacity is unclear. On the one hand, plants with a greater PNUE may have similar N_a and therefore greater photosynthetic capacities than less efficient plants. However, as photosynthetic capacity increases, sink capacity and external environmental constraints may lead to a reduction of carbon fixation per unit of N investment (14, 17). Alternatively, more efficient plants may invest less N per unit area, and proportionally more N to the production

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² Abbreviations: N, nitrogen; A, net CO₂ assimilation rate; C_a, ambient CO₂ partial pressure; C_i, intercellular CO₂ partial pressure; g, leaf conductance to water vapor; N_a, organic nitrogen per unit area; NUE, nitrogen use efficiency; PFD, photon flux density; PNUE, photosynthetic nitrogen use efficiency; rubisco, RuBP carboxylase/oxygenase (EC 4.1.1.39); VPD, leaf-to-air vapor pressure deficit; WUE, water use efficiency.

made of (1) the light saturated CO_2 assimilation rate at 20, 27, and 34°C (any given leaf was measured at only one of these temperatures), (b) the light response of photosynthesis, and (c) the temperature response of photosynthesis. To begin each experiment, single leaves were inserted in the chamber and exposed to about $750 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. After 10 to 15 min, the PFD was increased to a level which saturated photosynthesis (typically 1200 to 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, depending upon N_a) and after a 30 minute equilibration period, light saturated A was recorded. The light response of photosynthesis was determined by decreasing the PFD in steps to darkness. The temperature response was determined by beginning the measurements at 20°C and saturating PFD. Temperatures were first decreased to the lowest values, and then increased in steps to about 40°C.

Following the gas exchange measurements, the leaves were dried at 70°C and weighed. Total N and NO_3^- were then determined using a micro-Kjeldahl procedure and high-pressure liquid chromatography, respectively (22). The difference between total leaf N and leaf NO_3^- was taken as organic N.

All gas exchange parameters were calculated using the equations presented in Von Caemmerer and Farquhar (26).

RESULTS

Assimilation Rate versus Nitrogen Content. Light saturated CO_2 assimilation increased linearly with N_a in both *C. album* and *A. retroflexus* (Fig. 1). Regressions for both species had similar x -intercepts which generally ranged from 46 to 56 mmol m^{-2} , but A increased with increasing N_a more strongly in *A. retroflexus* than *C. album* at all three measurement temperatures (Table I). Consequently, at equal N_a , *A. retroflexus* generally had a greater A than *C. album* (Fig. 2) and this difference increased as A and N_a increased. However, *C. album* achieved a higher N_a at a given applied N and therefore had a similar A as that of *A. retroflexus* at 27°C, the growth temperature.

A/N_a increased curvilinearly with N_a (Fig. 2) since transformation of the linear equation

$$A = dA/dN_a(N_a) + b \quad (1)$$

into the form

$$A/N_a = dA/dN_a + b/N_a \quad (2)$$

gives a curvilinear function when the x -intercept is positive and b , the y -intercept, is negative. At high N_a , the value of A/N_a approaches that of dA/dN_a . In general, A/N_a was greater in *A. retroflexus* than *C. album*, with the differences increasing as temperature increased. However, at 20°C measurement temperature and in leaves with low N_a , there was little difference in A/N_a between the species (Fig. 2).

Light and Temperature Dependence of Photosynthesis. In both species, the light response curves measured at 27°C were essentially identical in leaves with equivalent photosynthetic capacities

(Fig. 3). However, *C. album* required about 40% more N_a in order to accomplish this. The light required for saturation increased with increasing N_a in both species. At a given N_a , *A. retroflexus* had a higher light saturation point than *C. album*.

When measured at $540 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, which was equivalent to the PFD in the growth chamber, A still increased linearly with increasing N_a in both species (Fig. 4). However, the slope was much lower than at light saturation. Linearity of A on N_a was maintained because the decrease in photosynthesis from light saturation to $540 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ was proportional to N_a .

The temperature dependence of photosynthesis in both species was more pronounced in high as compared to low N plants (Fig. 5). The optimum temperature of photosynthesis was higher in *A. retroflexus* than in *C. album* but was little affected by N_a . Because of the differences in the temperature dependence of assimilation in the two species, A/N_a changed only slightly with temperature in *C. album* while it increased substantially with increased temperature in *A. retroflexus* (Fig. 2). The maximum A/N values at the respective temperature optima for each species were $0.21 \mu\text{mol CO}_2 \text{s}^{-1} \text{mmol}^{-1} \text{N}$ in *C. album* and $0.40 \mu\text{mol CO}_2 \text{s}^{-1} \text{mmol}^{-1} \text{N}$ in *A. retroflexus*. However, at measurement temperatures below 20°C, A/N_a was greater in *C. album* than *A. retroflexus*.

Leaf Conductance. Leaf conductance to water vapor (g) was positively correlated with A in both species (Fig. 6). Temperature had little effect on the slope of this relationship, especially in *A. retroflexus*. At the highest N_a , g was 2 to 2.5 times greater in *C. album* than *A. retroflexus* while at the lowest N_a , g was similar in the two species. Because the relationship between A and N_a and g and A were linear, g versus N_a was also linear in both species (data not shown).

The ratio of intracellular to ambient CO_2 partial pressure (C_i/C_a) was independent of N_a in *C. album*, but inversely related to N_a in *A. retroflexus* (Fig. 7). Consequently, at low N_a both species had similar C_i/C_a values. Since at a given VPD, the WUE of a leaf is inversely related to C_i/C_a (13), WUE of *A. retroflexus* was dependent on N_a , ranging from a high of about $12 \mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$ at high N_a to a low of about $3 \mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$ at low N_a (Fig. 8). In contrast, WUE was independent of N_a in *C. album*, averaging $4.3 \mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$.

DISCUSSION

At identical N_a , the photosynthetic capacity of *A. retroflexus* was greater than that of *C. album*. However, for a given applied N level, *C. album* had a greater N_a than *A. retroflexus* so that the actual light saturated assimilation capacities were similar in the two species. A comparison of N_a and photosynthesis of *A. retroflexus* and *C. album* in fields near Davis, California yielded similar results (21). These results show that C_4 photosynthesis does not automatically enable C_4 plants to have a greater photosynthetic capacity than found in C_3 plants, because differences in the amount of N allocated to leaves can offset advantages

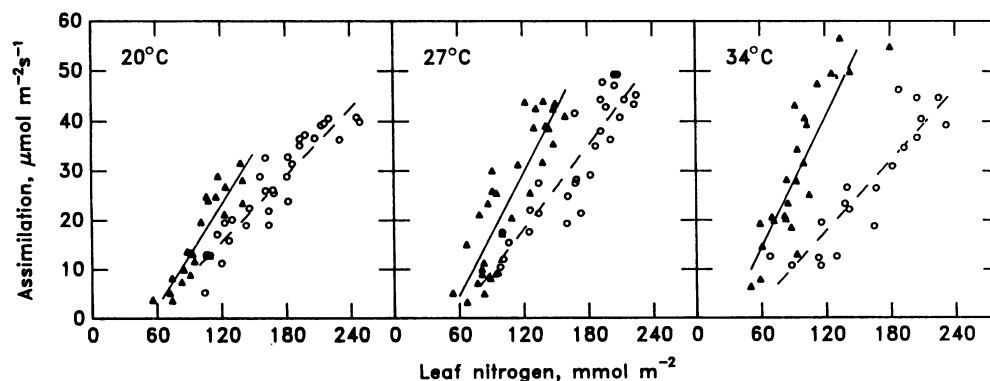


FIG. 1. The relationship between light saturated photosynthetic rate of single leaves and organic leaf nitrogen in *C. album* (dashed line, \circ) and *A. retroflexus* (solid line, \blacktriangle). See Table I for the regression equations. All responses are significant at $P = 0.01$.

Table 1. Regression Coefficients of Response of Light Saturated CO₂ Assimilation Rate to Organic Leaf Nitrogen per Unit Area in *C. album* and *A. retroflexus*

Species	Temperature	Slope	x-Intercept	R ²	N
	°C	($\mu\text{mol s}^{-1}$)/ (mmol)	mmol m ⁻²		
<i>C. album</i>	20	0.23	51	0.87	32
	27	0.28	56	0.81	26
	34	0.24	46	0.82	19
<i>A. retroflexus</i>	20	0.35	53	0.81	22
	27	0.42	49	0.77	31
	34	0.52	37	0.79	23

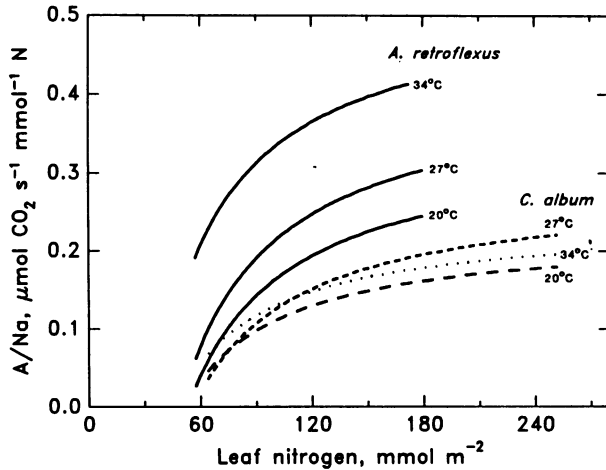


FIG. 2. The relationship between photosynthesis per unit nitrogen and organic leaf nitrogen in *C. album* (dotted, dashed lines) and *A. retroflexus* (solid lines). The relationships were obtained by transforming the linear regression equations of A versus N_a in Table I into the form $A/N = dA/dN_a + b/N_a$.

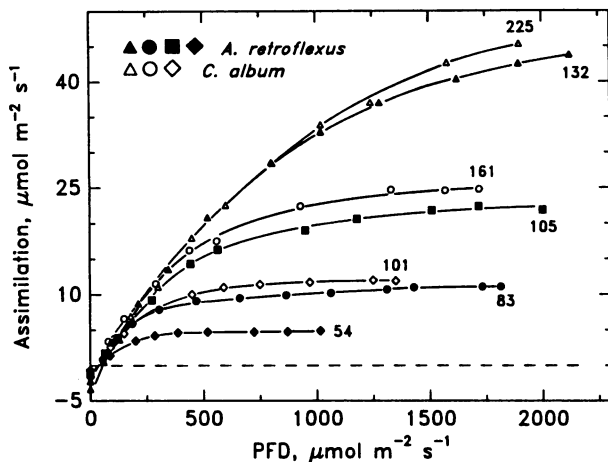


FIG. 3. The light response of photosynthesis in *C. album* (open symbols) and *A. retroflexus* (closed symbols) at 27°C. The values beside each curve represent organic leaf nitrogen contents in mmol m⁻².

resulting from a higher PNUE. However, the greater N cost of photosynthesis in C₃ plants may limit allocation of as much N to other plant processes, such as root or leaf production, as could be possible for C₄ plants. As discussed elsewhere (22), C₄ plants may be able to invest more N into new leaf production than C₃ plants and therefore have a greater whole plant carbon gain and growth rate at high N.

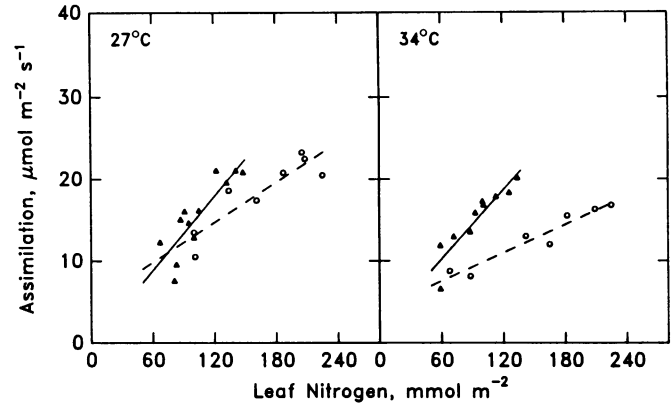


FIG. 4. The relationship between single leaf photosynthesis at a PFD of 540 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and organic leaf nitrogen in *C. album* (○) and *A. retroflexus* (▲) at 27°C and 34°C. The regression equations are: $y = 0.082x + 4.9$ ($R^2 = 0.81$) for *C. album* at 27°C, $y = 0.058x + 4.1$ ($R^2 = 0.92$) for *C. album* at 34°C, $y = 0.151x - 0.23$ ($R^2 = 0.74$) for *A. retroflexus* at 27°C, and $y = 0.141x + 1.73$ ($R^2 = 0.84$) for *A. retroflexus* at 34°C.

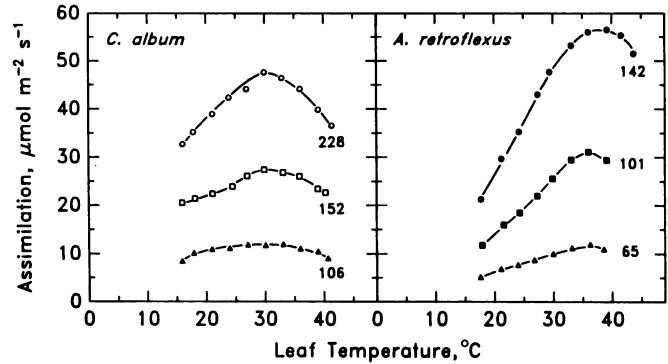


FIG. 5. The temperature of photosynthesis in *C. album* and *A. retroflexus* at light saturation. The values beside each curve represent organic leaf nitrogen content in mmol m⁻².

Most workers have used A/N as an index of PNUE (1, 4, 12). With this index, most C₄ plants, including *A. retroflexus*, generally have a greater PNUE than similar C₃ plants (3–5, 12, 24, 29). However, comparisons of PNUE based on A/N may be difficult to interpret if the x -intercept of A versus N_a is unknown. As shown by Eq. 2, A/N is dependent on N_a , so that comparisons between species with different N_a may lead to erroneous assessments of PNUE. This problem can be seen if *A. retroflexus* leaves with low N_a are compared with *C. album* leaves with high N_a . In addition, A/N at equivalent N_a will vary if the x -intercept of A versus N_a differs significantly. This intercept can range from near 0 to 60 mmol m⁻² for different species (8, 10, 15, 16, 30). A different measure of PNUE is the slope of A versus N_a , dA/dN_a , which gives the increase in assimilation capacity per unit increase in N investment. Because dA/dN_a is independent of N_a when A versus N_a is linear, PNUE comparisons between species with different N_a can be facilitated. However, species with different x -intercepts can have identical slopes, in which case the plant with the lower x -intercept has a greater A/N . Because of these problems, it is probably best to utilize both A/N_a and dA/dN_a in studies of PNUE differences.

As with A/N , the value of dA/dN_a tends to be larger in C₄ plants than similar C₃ plants. Values of dA/dN_a as large as 0.68 $\mu\text{mol s}^{-1} \text{mmol}^{-1}$ have been measured in C₄ plants (21). In C₃ annuals, dA/dN_a typically ranges from 0.2 to 0.3 $\mu\text{mol s}^{-1} \text{mmol}^{-1}$ (8, 10, 16, 30). High growth rate annuals show the

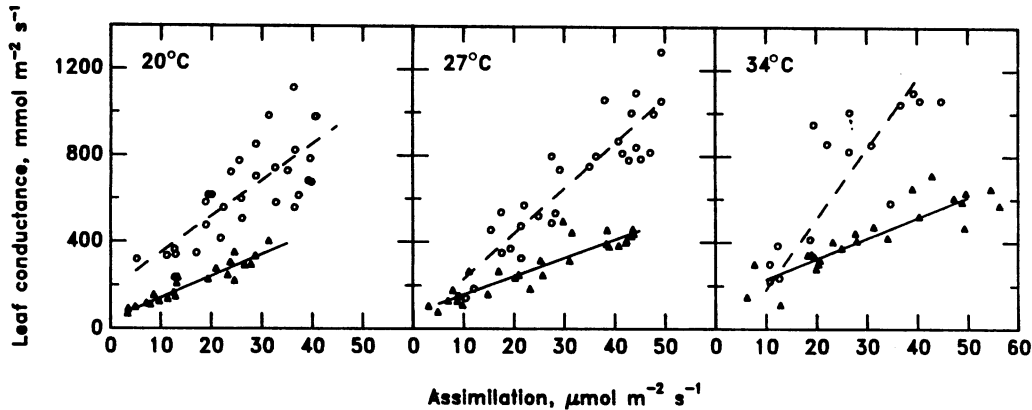


FIG. 6. The relationship between leaf conductance to water vapor and photosynthesis in single leaves of *C. album* (dashed lines, ○) and *A. retroflexus* (solid lines, ▲). All trends are significant at $P = 0.01$.

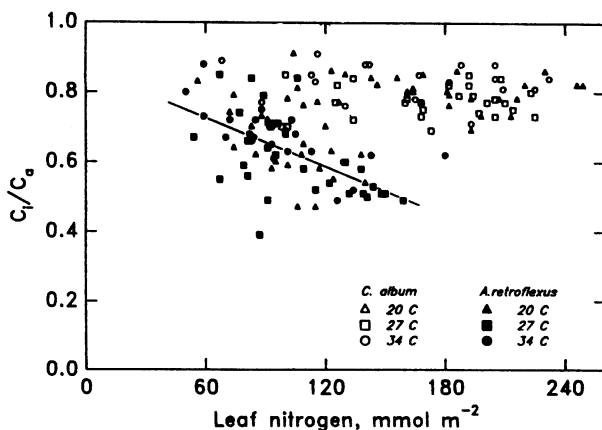


FIG. 7. The ratio of intercellular to ambient CO_2 partial pressure (C_i/C_a) versus organic leaf nitrogen in *C. album* and *A. retroflexus*. The regression equation for the significant trend ($P = 0.01$) in *A. retroflexus* was $y = -0.00233x + 0.872$ ($R^2 = 0.39$).

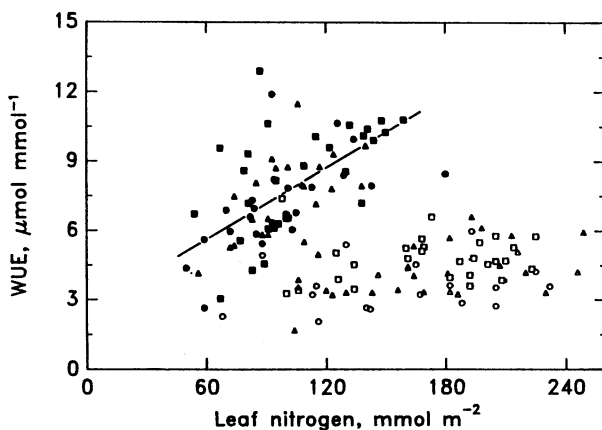


FIG. 8. The relationship between water use efficiency and leaf nitrogen per unit area in *C. album* (open symbols) and *A. retroflexus* (closed symbols), assuming a VPD of 10 mbar. Symbol legends are the same as in Figure 7. The regression equation for the response in *A. retroflexus* was $y = 0.0505x + 2.61$ ($R^2 = 0.38$; significant at $P = 0.01$).

greatest response of A to N_a , deciduous trees and shrubs have an intermediate response, and evergreen species have a low response (12). Similarly, in plants adapted to high nutrient availability, A responds strongly to increasing N while in plants adapted to low nutrient availability, A does not respond strongly to increasing N (21). Because of this, it is important that comparisons of C_3 and C_4 plants be made using species with similar growth forms

and ecological requirements. Low growth capacity C_4 plants may have a lower PNUE than high growth capacity C_3 plants. However, low growth capacity C_4 plants probably have a greater PNUE than similar, low growth capacity C_3 plants.

It has been reported that A versus N_a is curvilinear when a sufficiently broad range of N_a is examined (10). While studies have reported curvilinearity between A and N_a (10, 16), when the measurements are conducted on plants of similar age, growth conditions, and variety, and N storage forms such as NO_3^- and asparagine are accounted for, A versus N_a is usually linear across the entire range of N_a (8, 15, 21, 30). In *C. album* and *A. retroflexus*, failure to account for stored NO_3^- would have resulted in a curvilinear relationship between A and N_a . Ultimately, however, at very high N levels, the A to N_a relationship should become curvilinear because of other limitations imposed on photosynthesis (11). Evans (10), presents evidence that a 'wall resistance' to CO_2 diffusion may become significant at high N , resulting in curvilinearity between A and N_a . In this study, the linear response may result from our accounting for NO_3^- accumulation as well as a regulation of the maximum N_a below levels where A versus N_a becomes curvilinear.

According to Mooney and Gulmon (17), an optimal N allocation exists when leaf N is modulated so that the resulting photosynthetic rate corresponds to the maximum rate which the most limiting environmental resource can support. By this argument, the leaf N of *C. album* and *A. retroflexus* should be allocated so that the corresponding light saturation point occurs at about the growth PFD of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$. In *C. album* this would mean an A of 18 to $24 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a maximum N_a of 120 to 150mmol m^{-2} . That A is double this suggests that leaf N and photosynthesis capacity is determined by factors other than simply instantaneous or average PFD. Data of Chabot (7) and Bunce (6), indicate leaf development responds more to daily integrated PFD, rather than a high instantaneous PFD. The daily PFD in our chamber was $34 \text{mol m}^{-2} \text{d}^{-1}$, which is about 70% of the typical daily PFD on a sunny day (2). This level may be high enough to stimulate leaf development in *C. album* and *A. retroflexus* similar to that found in natural, high light environments.

While dg/dN_a is an index to PNUE, the slope of g versus A is inversely related to leaf water use efficiency (25). In C_4 as compared to C_3 plants dg/dA is smaller while dg/dN_a is greater. In plants which are not photosynthetically CO_2 saturated, PNUE is inversely related to WUE (13). This is because a change in dg/dA can change C_i and therefore A without any change in N_a . However, WUE is not necessarily inversely related to PNUE. If g adjusts proportionally to A , an increase in dg/dN_a can raise photosynthetic capacity, but C_i and WUE may be unchanged. This was evident in *A. retroflexus*, where dg/dN_a increased substantially with temperature while dg/dA remained constant.

Thus, leaf temperature at a constant VPD had little effect on WUE in *A. retroflexus* (Fig. 8).

In both *C. album* and *A. retroflexus*, biochemical rather than stomatal limitations account for the decline in photosynthesis with leaf N, since C₃/C₄ either increased or was unaffected by N_a. A similar conclusion regarding the importance of biochemical limitations was reached with studies of other C₃ and C₄ species where A was changed by limiting nitrogen, leaf age, phosphorus, or growth light level (25).

Few studies have addressed the question of how the environment influences dA/dN_a . In the short term, it is clear that changes in the environment which reduce photosynthetic rate also reduce dA/dN_a . However, in the long term, where changes in photosynthetic capacity are involved, it is unclear whether changes in the environment can cause a change in dA/dN_a , or simply alter the N_a while keeping dA/dN_a constant. Some evidence indicates the latter possibility (23). Acclimation responses to light, temperature and water stress may involve a repartitioning of leaf N among photosynthetic components such that the component most limited by the environment will be proportionally increased relative to less limited components. How these changes in N partitioning with leaf N will affect the A versus N response is unknown.

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