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COMPARISON OF THE QUANTUM YIELDS FOR CO_2 UPTAKE IN C_3 AND C_4 PLANTS

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It is now well established that the C_4 pathway of photosynthesis enables the plant to photosynthesize more efficiently under conditions where, in the absence of this pathway, the rate would be severely limited by the CO_2 concentration in the intercellular spaces. Thus, the advantages of C_4 photosynthesis are maximal under conditions of high light intensities, high temperatures, and limited water supply. There is, however, no evidence to support the converse supposition that the C_4 pathway would in itself be disadvantageous in other natural environments such as cool coastal habitats. Hatch (1970) discussed the possibility that the higher intrinsic energy requirement of C_4 photosynthesis (two additional ATP molecules per CO_2 fixed) in comparison with conventional C_3 photosynthesis might result in lower efficiency of light utilization at low light intensities by C_4 plants. A lower quantum efficiency for CO_2 fixation would of course be an important disadvantage in shaded habitats. It could also have a significant effect under moderate light intensities and could at least in part be responsible for the unusually high light intensities required for saturation of photosynthesis in many C_4 plants.

To elucidate this question precise measurements of the quantum yield of CO_2 uptake at rate-limiting light intensities were made on intact attached leaves of a number of C_3 and C_4 plants, including our principal study species, *Tidestromia oblongifolia*, *Atriplex glabriuscula*, and *A. sabulosa*. *T. oblongifolia* belongs to a group of C_4 plants utilizing NADP malic enzyme for decarboxylation of C_4 acids in the bundle sheath cells (*Year Book 69*, p. 649), while *A. sabulosa* and the other C_4 *Atriplex* species analyzed appear to belong to a group utilizing NAD malic enzyme. Photosynthetic rates on the basis of absorbed quanta were obtained from CO_2-uptake rates measured as a function of incident quantum flux in the spectral range 400–700 nm (Xenon arc) and from the light absorptance values of the same leaves, determined with an Ulbricht integrating sphere using a Xenon light source with the same spectral distribution used in the photosynthesis measurements. Since photosynthesis is inhibited by the atmospheric O_2 concentration in C_3 plants even at rate-limiting light intensities, quantum yields were determined in both 21% and 2% O_2. The CO_2 partial pressure was that of normal air (310–330 μbar), and leaf temperature was 27°C.

The typical responses of photosynthesis of C_3 and C_4 plants to changes in the quantum flux absorbed by the leaves in the rate-limiting range are shown in Fig. 11. In the C_3 species *Atriplex glabriuscula* the quantum yield (slope of the curve) is 0.051 mole CO_2/absorbed einstein in normal air. A decrease in the O_2 concentration to 2% results in an increase in the quantum yield to 0.073 mole CO_2/absorbed einstein. In the C_4 species *Atriplex argentea* the quantum yield is 0.052 moles CO_2/absorbed einstein, and no enhancement is observed when the O_2 concentration is reduced. These results are very similar to those previously determined for *Atriplex patula* (C_3) and *A. rosea* (C_4) in monochromatic light (*Year Book 68*, p. 630).

Table 4 summarizes the results obtained with a number of C_3 and C_4 species. The quantum yields of the C_3 plants are consistently about one-third higher than in the C_4 plants under a low O_2 concentration. This higher energy requirement of the C_4 plants is consistent with the notion that C_4 photosynthesis requires two more ATP molecules per

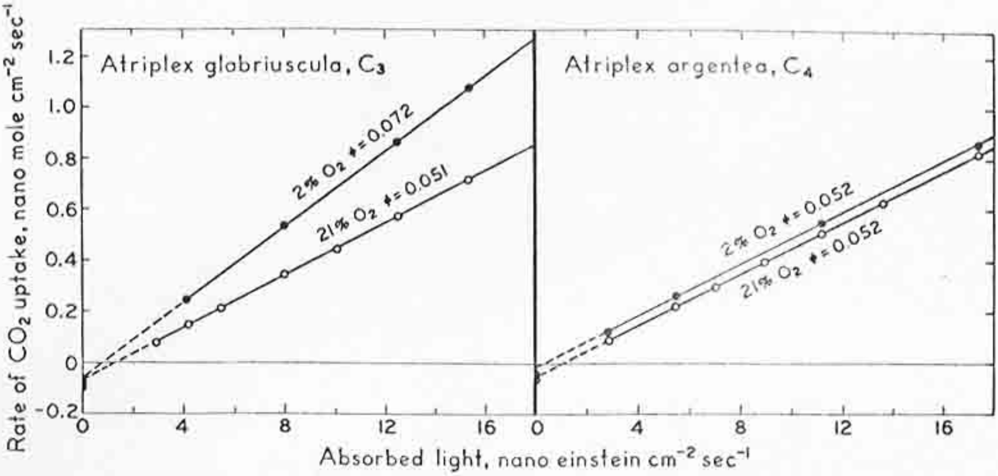

Fig. 11. Initial slopes for the rate of photosynthesis as a function of absorbed quantum flux in *Atriplex glabriuscula* (C_3) and *A. argentea* (C_4).

TABLE 4. Quantum Yields (mole CO_2/absorbed einstein) of Different C_3 and C_4 Species

	Quantum Yield			Quantum Yield	
C_3 Species	2% O_2	21% O_2	C_4 Species	2% O_2	21% O_2
Atriplex glabriuscula	0.072	0.051	*Atriplex argentea*	0.052	0.052
Atriplex heterosperma	0.073	0.053	*Atriplex rosea*	0.054	0.053
Atriplex hortensis	0.073	0.055	*Atriplex sabulosa*	0.054	0.054
Atriplex triangularis	0.073	0.051	*Atriplex serenana*	0.055	0.054
Plantago lanceolata	0.074	0.053	*Tidestromia oblongifolia*	0.054	0.054

CO_2 fixed than does C_3 photosynthesis; the extra ATP molecules are needed for the regeneration of the CO_2 acceptor phospho(enol)pyruvate from pyruvate. However, oxygen causes an inhibition of the quantum yield in the C_3 plants but not in the C_4 plants, and as a result their quantum yields *in normal air* are practically identical (C_3: 0.0526 ± 0.0017; C_4: 0.0534 ± 0.0009 mole/einstein). It certainly seems remarkable that the benefit of the abolishment of O_2 inhibition of photosynthesis conferred by the C_4 pathway is almost exactly offset by the higher intrinsic energy cost of this pathway. One can speculate that it may be more than fortuitous that the quantum yields of C_3 and C_4 plants are so similar in normal air. There very likely exist strong selective pressures against the quantum yields of C_4 plants falling below those of C_3 plants, since photosynthesis in natural canopies is often light limited.

References

Hatch, M. D., in *Prediction and Measurement of Photosynthetic Productivity*, Pudoc, Wageningen, p. 215, 1970.