Fig. 30. Light dependence of net CO_2 uptake by single attached leaves of *Encelia farinosa* differing in their degree of pubescence. Rates were determined at a leaf temperature of 30°C, a CO_2 partial pressure of 325 μbar, an O_2 concentration of 21% by volume, and a water vapor pressure deficit of less than 10 μbar. α = absorption coefficient.

quantum absorbed). Net photosynthesis is so dramatically affected by pubescence that at a leaf absorptance of 53% the net photosynthetic rate is nearly linear with light intensity up to full sunlight. Stomatal conductances to water and CO_2 exchange were similar for the leaves at any given light intensity, suggesting that CO_2 diffusion limitations were not responsible for differences among the curves. When photosynthetic data from these three curves are plotted against absorbed rather than incident quanta, all data lie on a single curve, indicating that the principal differences among the curves were due primarily to decreases in light absorption due to pubescence and not to physiological differences.

Studies on the ecophysiology of the genus *Encelia* will continue in the oncoming year. Having documented the extraordinary capability of the pubes-

cence layer to reflect light and also to affect physiological processes, this coming year's work will focus on three main questions that have arisen during the past year: (1) What are the causes of the extremely high photosynthetic rates observed in leaves of *Encelia* species? (2) What other heat transfer or energy balance functions does the pubescence layer have? In particular, does the pubescence serve as an insulating layer between the metabolically active tissues and the hot, arid external environment? (3) What are the ecological relationships in the tradeoff between carbon gain and reduced heat load on the leaf in pubescent leaves along aridity gradients?

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CARBON DIOXIDE AND TEMPERATURE DEPENDENCE OF THE QUANTUM YIELD FOR CO_2 UPTAKE IN C_3 AND C_4 PLANTS

James Ehleringer and Olle Björkman

Last year we reported that at a leaf temperature of about 30°C and in nor-

mal air the quantum yield for CO_2 uptake in plants possessing the C_3 path-

way was equivalent to that of plants possessing the C_4 pathway (*Year Book 74*, pp. 760–761). This seemed remarkable since it means that the decrease in the quantum yield of C_4 plants by its inherent higher energy requirement (2 additional ATP molecules per CO_2 fixed) offsets the decrease in the quantum yield of C_3 plants caused by oxygen inhibition under normal atmospheric conditions. This year we have extended this study to include the effects of changing CO_2 partial pressure and leaf temperature on the quantum yield of leaves to determine how these factors interact with the inhibitory effect of O_2 and if the quantum yields of C_3 and C_4 plants are indeed equivalent over a range of temperatures. All measurements were made at strictly rate-limiting light intensities on intact leaves attached to the plants. All plants were potted and grown under conditions of sufficient water and nutrients in growth cabinets.

The quantum yield for CO_2 uptake at normal atmospheric CO_2 concentration is markedly inhibited by 21% O_2 in C_3 plants, but it is unaffected by oxygen in C_4 plants (Björkman, 1966; *Year Book 68*, pp. 629–631; *Year Book 70*, pp. 522–524; *Year Book 71*, pp. 141–148; *Year Book 74*, pp. 760–761). Similarly, at normal atmospheric O_2 concentration the quantum yield is markedly CO_2 dependent in C_3 but not in C_4 plants (*Year Book 70*, pp. 522–524; *Year Book 71*, pp. 141–148). Figure 31 shows the quantum yield of the C_3 plant *Encelia californica* as a function of CO_2 concentration in low and normal O_2 concentration and 30°C leaf temperature. Over the range of intercellular CO_2 concentrations normally encountered by leaves (8–14 μM, equivalent to a partial pressure of 200–350 μbar) the quantum yield in 21% oxygen is markedly dependent on CO_2 concentration, ranging from 0.042 to 0.059 mol CO_2/absorbed einstein over this span. Even at intercellular CO_2 pressures as high as 1500 μbar, the quantum yield is still measurably lowered by 21% oxygen. At low CO_2 intercellular pressures (less than 200 μbar) the oxy-
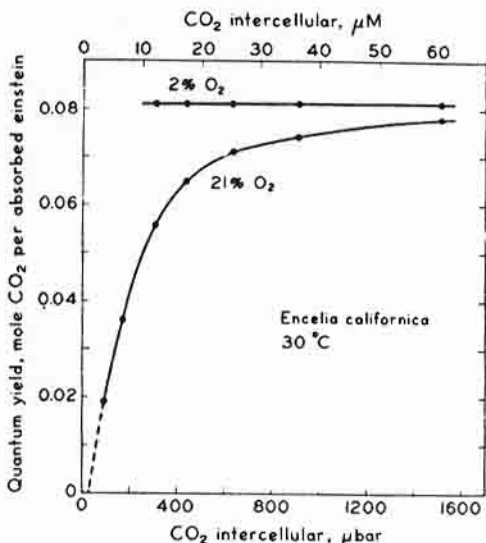

Fig. 31. Quantum yield for CO_2 uptake in *Encelia californica* (C_3) determined as a function of intercellular pressure in 21% and in 2% oxygen. Leaf temperature was 30°C.

gen inhibition is much greater than at normal CO_2 pressures and the quantum yield extrapolates to zero at the CO_2 compensation point. In contrast, under low oxygen the quantum yield of the C_3 plant *E. californica* is independent of CO_2 pressure. The absence of a CO_2 dependence of the quantum yield in low oxygen suggests that the carboxylase activity of RuDP carboxylase-oxygenase in vivo is saturated by 300 μbar CO_2 at rate-limiting light intensities. The presence of a strong CO_2 dependence of the quantum yield in C_3 plants at higher O_2 concentrations is consistent with the view that the O_2 inhibition of net CO_2 uptake is primarily caused by the oxygenase activity of RuDP carboxylase.

The steep dependence of the quantum yield in C_3 plants such as *E. californica* (and other C_3 species) on CO_2 concentration at normal atmospheric O_2 concentration and the independence of the quantum yield on CO_2 in C_4 plants such as *Atriplex rosea* point out one of the selective pressures favoring the evolution of the C_4 pathway. The ability of the C_4 pathway to concentrate CO_2 at the Calvin cycle

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carboxylation sites effectively makes light-limited photosynthesis of C_4 plants independent of intercellular CO_2 pressure over a very wide range. However, in a primitive atmosphere of high CO_2, or low O_2 concentrations, or both, selective pressures would strongly favor the C_3 pathway because of its lower intrinsic quantum requirement for CO_2 fixation.

Figure 32 compares the temperature dependence of the quantum yield for CO_2 uptake in the C_3 species *E. californica* with that of the C_4 species *Atriplex rosea* in normal air of 325 μbar CO_2 and 21% O_2 (Fig. 32). These results show clearly that in normal air the quantum yield of the C_3 plant is superior to that of the C_4 plant at leaf temperatures below approximately 30°C, but at higher temperatures the quantum yield of the C_4 plant is superior to that of the C_3 plant. This change in the quantum yield in the C_3 species with temperature cannot be accounted for by changes in the liquid phase solubilities of CO_2 and O_2 over the temperature span, since corrections for changes in the solubilities of these gases fail to alter the observed quantum yields significantly. The change in
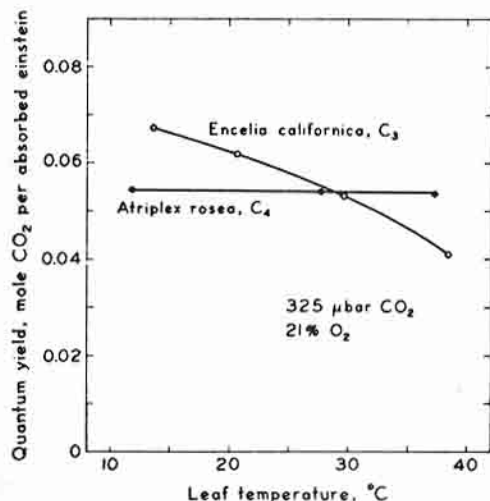
the quantum yield in C_3 plants such as *E. californica* with leaf temperature must therefore be due to a change in the degree of oxygen inhibition with temperature. Oxygen inhibition of the quantum yield increases exponentially as the temperature is increased from 10° to 40°C. In normal air the oxygen inhibition is only 14% at 14°C but increases to 47% at 38°C. Over this same temperature span there is no change in the absolute value of the quantum yield of *E. californica* when measured in low oxygen. The change in quantum yield due to inhibition by 21% O_2 in *E. californica* follows the Arrhenius equation, giving an activation energy approximately equivalent to -8 Kcal mol^{-1}. If the view is correct that the O_2 inhibition of the quantum yield is caused by the oxygenase activity of RuDP carboxylase, then the present results imply that oxygenase activity increases more steeply with temperature than does carboxylase activity. Experiments designed to determine if this is the case are being conducted with the purified enzyme by Dr. Murray Badger in this laboratory.

The distribution of C_3 and C_4 species in nature correlates generally with daylight temperature, i.e., C_4 species are more common in hot climates than in cool or cold climates. Since the rate of photosynthesis and primary production in many plant canopies is strongly light limited, the observed difference in quantum yield between C_3 and C_4 species as a function of leaf temperature may be an important factor in determining their distribution. Under conditions of sufficient soil moisture, a C_3 plant will have greater potential for carbon gain at low temperatures. Conversely, a C_4 plant will have greater potential for carbon gain at high temperatures with a crossover point at approximately 25°–30°C. This greater potential for carbon gain in C_3 plants at low temperatures would imply that C_4 photosynthesis would be at a disadvantage in cool, *low*-light habitats such as the floor of cool temperate forests and the arctic tundra. On the other hand,

Fig. 32. Quantum yield for CO_2 uptake in *Encelia californica* (C_3) and *Atriplex rosea* (C_4) as a function of leaf temperature. The CO_2 pressure was held constant at 325 μbar and the oxygen concentration was 21% by volume.

the C_4 pathway would be selectively more advantageous in shaded habitats of high temperature and in dense stands in high-light, high-temperature habitats such as tropical grasslands. C_4 photosynthesis would of course be particularly advantageous in hot, sun-baked desert habitats where little mutual shading of the leaves occurs within the plant stands. However, under these conditions the advantage of C_4 photosynthesis is largely due to the increased capacity for photosynthesis at high light intensities. Nevertheless, the higher quantum yield at high temperatures would also be ex-pected to confer a significant advantage. It is apparent that both the increased capacity for photosynthesis at high light intensities and the higher quantum yield at high temperatures are the results of the same mechanism, namely the ability of the C_4 pathway to increase the concentration of CO_2 at the site of fixation by RuDP carboxylase.

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HYBRIDIZATIONS IN *Atriplex*

Malcolm A. Nobs

In 1968 the first hybrid between a species having the C_4 photosynthetic pathway and one with the C_3 pathway was successfully obtained. This F_1 hybrid, *Atriplex rosea* L. × *A. triangularis* Wildenoo (*A. patula* ssp. *hastata*, Hall and Clements), was a diploid with $2n = 18$. During the reduction division in this hybrid, only four pairs of chromosomes formed, resulting in less than 10% fertility. The progeny obtained in the second generation formed a series of polyploids ranging from triploid to above pentaploid, making a critical genetic analysis of the inheritance of the C_4 vs. the C_3 pathways impossible.

During the ensuing years, 22 additional intraspecific hybridizations have been attempted. These attempts were made for three basic reasons. The first was to obtain a hybrid combination between C_3 and C_4 species which would remain diploid and be sufficiently fertile for genetic analysis. The second was to obtain hybrid combinations between different C_4 species to determine whether in later generations there would be segregation within the C_4 characteristics. The third was to obtain data on the genetic relationships within the genus *Atriplex* which could supplement the studies by Thompson on DNA hybridization.

The crossing diagram (Fig. 33) summarizes these accumulated data. It is apparent that during the evolution of *Atriplex* the *Obione* subgenus diverged profoundly from the subgenus *Euatriplex*. Only one hybrid combination out of eight attempts, *A. rosea* × *argentea* ssp. *expansa*, has yielded hybrids; within *Euatriplex*, by contrast, six of the eight attempts have yielded hybrid progeny, and within *Obione* two out of five have been successful.

Within *Euatriplex* the species studied have become highly differentiated genetically. Table 16 summarizes the cytological data. In three of the combinations the hybrids were so weak that they never reached maturity. The remaining three form a progressive series from nearly sterile to partially fertile. The low fertility in the *rosea* × *sabulosa* combination, both in the *rosea* group and believed by Hall and Clements (1923) to be very closely related, is in part due to chromosomal rearrangements. Bridges and fragments are commonly seen during the first anaphase of reduction division.

The one fertile hybrid, as judged by regular reduction division resulting in 98% normal pollen, is *A. fruticulosa* × *A. serenana*. Both species are diploids in the pentandra group of *Obione*. It is