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 absorbance 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 upcoming year. Having documented the extraordinary capability of the pubes-

ence 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

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Last year we reported that at a leaf temperature of about 30°C and in normal air the quantum yield for CO$_2$ up-
take 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 \( C_4 \) 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 \( C_4 \) 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 \( \mu M \), equivalent to a partial pressure of 200–350 \( \mu \text{bar} \)) 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 \( \mu \text{bar} \), the quantum yield is still measurably lowered by 21\% oxygen. At low \( CO_2 \) intercellular pressures (less than 200 \( \mu \text{bar} \)) the oxygen 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 \( C_4 \) 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-oxidase in vivo is saturated by 300 \( \mu \text{bar} \) \( CO_2 \) 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
carboxylation sites effectively makes light-limited photosynthesis of C₄ plants independent of intercellular CO₂ pressure over a very wide range. However, in a primitive atmosphere of high CO₂, or low O₂ concentrations, or both, selective pressures would strongly favor the C₃ pathway because of its lower intrinsic quantum requirement for CO₂ fixation.

Figure 32 compares the temperature dependence of the quantum yield for CO₂ uptake in the C₃ species *E. californica* with that of the C₄ species *Atriplex rosea* in normal air of 325 μbar CO₂ and 21% O₂ (Fig. 32). These results show clearly that in normal air the quantum yield of the C₃ plant is superior to that of the C₄ plant at leaf temperatures below approximately 30°C, but at higher temperatures the quantum yield of the C₄ plant is superior to that of the C₃ plant. This change in the quantum yield in the C₃ species with temperature cannot be accounted for by changes in the liquid phase solubilities of CO₂ and O₂ 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 C₃ 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°C 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% O₂ 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 O₂ 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 C₃ and C₄ species in nature correlates generally with daylight temperature, i.e., C₄ 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 C₃ and C₄ species as a function of leaf temperature may be an important factor in determining their distribution. Under conditions of sufficient soil moisture, a C₃ plant will have greater potential for carbon gain at low temperatures. Conversely, a C₄ 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 C₄ plants at low temperatures would imply that C₄ 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,
the C₄ 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. C₄ photosynthesis would of course be particularly advantageous in hot, sunbaked desert habitats where little mutual shading of the leaves occurs within the plant stands. However, under these conditions the advantage of C₄ 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 expected 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 C₄ pathway to increase the concentration of CO₂ at the site of fixation by RuDP carboxylase.

References

HYBRIDIZATIONS IN Atriplex
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In 1968 the first hybrid between a species having the C₄ photosynthetic pathway and one with the C₃ pathway was successfully obtained. This F₁ 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 C₄ vs. the C₃ 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 C₃ and C₄ species which would remain diploid and be sufficiently fertile for genetic analysis. The second was to obtain hybrid combinations between different C₄ species to determine whether in later generations there would be segregation within the C₄ 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