

The Effect of Temperature on the Occurrence of O₂ and CO₂ Insensitive Photosynthesis in Field Grown Plants¹

Received for publication October 27, 1986 and in revised form February 19, 1987

ROWAN F. SAGE* AND THOMAS D. SHARKEY
Biological Sciences Center, Desert Research Institute, P. O. Box 60220, Reno, Nevada 89506
(R.F.S., T.D.S.), and *Department of Biology, University of Nevada, Reno, Nevada 89557* (T.D.S.)

ABSTRACT

The sensitivity of photosynthesis to O₂ and CO₂ was measured in leaves from field grown plants of six species (*Phaseolus vulgaris*, *Capsicum annuum*, *Lycopersicon esculentum*, *Scrophularia desertorum*, *Cordia draba*, and *Populus fremontii*) from 5°C to 35°C using gas-exchange techniques. In all species but *Phaseolus*, photosynthesis was insensitive to O₂ in normal air below a species dependent temperature. CO₂ insensitivity occurred under the same conditions that resulted in O₂ insensitivity. A complete loss of O₂ sensitivity occurred up to 22°C in *Lycopersicon* but only up to 6°C in *Scrophularia*. In *Lycopersicon* and *Populus*, O₂ and CO₂ insensitivity occurred under conditions regularly encountered during the cooler portions of the day. Because O₂ insensitivity is an indicator of feedback limited photosynthesis, these results indicate that feedback limitations can play a role in determining the diurnal carbon gain in the field. At higher partial pressures of CO₂ the temperature at which O₂ insensitivity occurred was higher, indicating that feedback limitations in the field will become more important as the CO₂ concentration in the atmosphere increases.

increase the rate of photosynthesis because the energy and enzymatic capacity required for photorespiration are in excess supply. In effect, O₂ insensitivity is an indicator of a feedback limitation on photosynthesis. Recent studies document the occurrence of Pi regeneration limitations on photosynthesis and associate them with O₂ insensitivity (8, 12, 19–21).

It is unknown whether Pi regeneration limitations are important under ecologically relevant conditions. Loss of O₂ and CO₂ sensitivity is typically observed at light saturation and elevated CO₂ pressure. Low temperature (5, 9), water stress (17), and long light periods (1) promote the occurrence of CO₂ and O₂ insensitivity. However, with the exception of low temperature, O₂ insensitivity at normal CO₂ pressure has not often been reported, and O₂ insensitivity has never been documented in field plants.

In order to determine the importance of feedback limitations in the field, we have used a field gas exchange system to measure the occurrence of O₂ and CO₂ insensitive photosynthesis over a range of temperatures in a variety of field grown plants.

THEORY

The sensitivity of photosynthesis to O₂ may be predicted for Rubisco or RuBP regeneration limited photosynthesis using the equations of Farquhar and von Caemmerer (6) and Sharkey (18). Oxygen sensitivity will depend upon whether photosynthesis is Rubisco or RuBP regeneration limited (18). Oxygenase activity normally declines with temperature (11), and this affects the predicted O₂ sensitivity under either limitation, though not in exactly the same way. If photosynthesis is 'co-limited' to any degree by the RuBP regeneration and Rubisco capacities, then, in the absence of feedback limitations, the two predictions of O₂ sensitivity represent extremes between which the actual value should fall. The rate of CO₂ fixation under a Rubisco limitation is determined by

$$A = \frac{(1 - 0.5\phi)V_{max}C}{C + K_c(1 + O/K_o)} - R_d \quad (1)$$

where ϕ equals the ratio of oxygenation to carboxylation; V_{max} is the maximum carboxylation rate; C and O are the CO₂ and O₂ concentrations, respectively; R_d is nonphotorespiratory, day respiration; and K_c and K_o are the Michaelis constants for carboxylation and oxygenation, respectively. Assuming the effect of R_d to be negligible, the sensitivity to a reduction of O₂ from 180 to 30 mbar will approximately equal

$$1 - \frac{A_{180}}{A_{30}} \cong 1 - \frac{\frac{1 - 0.5\phi_1}{C + K_c(1 + O1/K_o)}}{\frac{1 - 0.5\phi_2}{C + K_c(1 + O2/K_o)}} \quad (2)$$

A_{180} and A_{30} are the CO₂ assimilation rates at 180 and 30 mbar

Oxygenation of RuBP² by Rubisco and subsequent events in the photorespiratory cycle inhibit photosynthesis by (a) releasing previously fixed CO₂, (b) competitively inhibiting RuBP carboxylation, and (c) consuming RuBP which would otherwise be available for carboxylation (18). Across the physiological range of temperatures, O₂ removal should stimulate photosynthesis from 5 to 60% (14, 18). Numerous studies, however, have described cases where photosynthesis is either unaffected or is inhibited by a 90% reduction of O₂ (5, 9, 13, 16, 17, 25). This insensitivity to O₂ does not result from a reduction in oxygenase activity, since photorespiration occurs under O₂ insensitive conditions (17). Conditions promoting O₂ insensitivity also cause a loss of CO₂ sensitivity, demonstrating that the underlying cause for O₂ insensitivity is not an O₂ specific effect on pseudocyclic photophosphorylation. It has been hypothesized (16, 17) that O₂ insensitivity occurs when the capacity of a leaf to make phosphorylated intermediates exceeds its capacity to use them. Photosynthesis can then be limited by the capacity to regenerate Pi for photophosphorylation. When photosynthesis is limited in this way, suppression of photorespiration by low O₂ does not

¹ Research supported by Department of Energy contract DE-FG08-84ER13234.

² Abbreviations: RuBP, ribulose 1,5-bisphosphate; C_a , ambient partial pressure of CO₂; C_i , intercellular partial pressure of CO₂; operational C_i , the C_i at a C_a of 320 μ bar; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase (EC 4.1.1.39); T_L , leaf temperature.

O₂, respectively; ϕ_1 and ϕ_2 are the oxygenation to carboxylation ratios at 180 and 30 mbar O₂, respectively; and O_1 and O_2 are the O₂ concentrations in the chloroplast at 180 and 30 mbar (gas phase), respectively. In this treatment, the kinetic constants given by Jordan and Ogren (11) were used. Because their values for K_c and K_o are given in terms of concentration, we have used concentration values for C and O , converting from partial pressure to aqueous concentration using Henry's constants for CO₂ and O₂ (10). No salt effects were assumed in the calculation of Henry's constant since in a ratio, this effect would be small.

Under an RuBP regeneration limitation, photosynthesis is described by

$$A = \frac{(1 - 0.5\phi) J}{9.36 + 10.38\phi} - R_d \quad (3)$$

where J is the rate of photon absorption. The sensitivity to an O₂ reduction from 180 to 30 mbar O₂ is approximately

$$1 - \frac{A_{180}}{A_{30}} \cong 1 - \frac{\frac{1 - 0.5\phi_1}{9.36 + 10.38\phi_1}}{\frac{1 - 0.5\phi_2}{9.36 + 10.38\phi_2}} \quad (4)$$

The value of ϕ equals $2\Gamma^*/C$ where Γ^* is the CO₂ compensation point when R_d equals zero. Γ^* has been measured in a number of species and changes little between them (4). Using equations 2 and 4, and the respective values for C , O , K_c , K_o , and Γ^* , we have modeled the predicted O₂ sensitivities over a range of temperatures and compared them to sensitivities measured in the field. In order to approximate the behavior of C₃ plants in the field, particularly at lower temperatures, we used a constant C_i at 220 μ bars for our calculations. At this C_i , the model predicted a greater O₂ sensitivity for RuBP regeneration limited than Rubisco limited photosynthesis. This is the opposite of what has been previously predicted (18) because of variation in the published values of K_o . Differences in the sensitivity to O₂ between the two limitations are to be expected, because under a Rubisco limitation, photorespiratory CO₂ release and O₂ competition are important, while under an RuBP regeneration limitation, photorespiratory CO₂ release and the use of RuBP during oxygenation are important (18).

MATERIALS AND METHODS

Plant Material. Three cultivated and three native species were studied. The cultivated species were kidney bean (*Phaseolus vulgaris* L. var Linden), bell pepper (*Capsicum annuum* L.), and tomato (*Lycopersicon esculentum* L.). These species were grown in an outdoor garden and were watered three times weekly. The native species were *Scrophularia desertorum* (Munz) R. Shaw, a desert perennial of rock outcrops; hoary-cress (*Cardaria draba* Desv.), a cosmopolitan weed; and cottonwood (*Populus fremontii* Wats.). These species grew wild within 100 m of the Desert Research Institute and received no care during the growing season.

All measurements were made between May 20 and September 2, 1986. During this period, temperature in the Reno area ranged from 4°C to 37°C. The mean maximum temperature during this period was 32°C; the mean minimum was 10°C. Reno is situated at 1500 m elevation on the western edge of the Great Basin Desert. Ambient CO₂ is 310 μ bar. Ambient O₂ is 180 mbar. Summer humidity averages 7 mbar. From May to September 1986, 1.7 cm of rain fell on Reno. Most days during this period were cloud free, with about 80% of the possible sunshine reaching the plants (U.S. Weather Service data).

Field Gas-Exchange. All gas exchange measurements were carried out at light saturation using a null balance gas-exchange

system previously described (17) and modified for field use. Briefly, air ranging from 80 to 2000 μ bar CO₂ and 20 to 200 mbar O₂ was prepared from compressed N₂, O₂, and 3% CO₂ in air using Tylan mass flow controllers (Tylan Corp., Carson, CA). Leaves were enclosed in a 20 × 10 × 5 cm aluminum chamber. Chamber temperature was maintained by peltier blocks, which were cooled by water flowing from an 80 L ice chest. CO₂ and H₂O exchange were measured with a Binos IR gas analyzer (Leybold-Heraeus, Köln, West Germany). CO₂ was bled into the chamber with a Tylan flow controller to compensate for CO₂ removal by the leaf. Thus, the CO₂ analyzer was primarily used as a null point detector. Water vapor was only supplied by transpiration. It was not possible to maintain a constant vapor pressure deficit at the higher temperatures.

The response of photosynthesis to T_L was measured on all six species at 180 and 30 mbar O₂. Leaves were first equilibrated with the chamber environment at 180 mbar and 20 to 30°C. Then, T_L was either increased to the maximum (*Phaseolus*, *Lycopersicon*, *Cardaria*, and *Populus*) and measurements made as T_L was decreased in steps, or T_L was decreased to a minimum (*Capsicum*, *Scrophularia*) and measurements made as it was increased in steps. At each temperature, the photosynthesis rate at 180 mbar O₂ was first obtained. Then the leaf was exposed to 30 mbar O₂, and allowed to reequilibrate before the measurements were repeated. Following 30% of the low O₂ measurements, the rate at 180 mbar was rechecked before T_L was changed. At 180 mbar O₂, C_a was 310 to 330 μ bar. It was increased to 370 μ bar at 30 mbar O₂ so that the C_i would be the same as or higher than the C_i at 180 mbar O₂.

The CO₂ response of photosynthesis at 10, 20, and 30°C was determined for *Capsicum*, *Lycopersicon*, *Scrophularia*, and *Populus*. Leaves were first equilibrated at 320 μ bar CO₂, and 180 mbar O₂. The C_a was first decreased to the lowest value and then measurements were made as C_a was increased stepwise to the highest value.

All gas-exchange parameters were calculated according to von Caemmerer and Farquhar (22).

RESULTS

The Temperature Response of O₂ Sensitivity. Photosynthesis rapidly increased with increasing temperature from 10 to 20°C in all species (Fig. 1). From 10 to 20°C and at 180 mbar O₂, photosynthesis doubled in *Lycopersicon* and *Populus*, but increased somewhat less in the remaining species. All species but *Capsicum* exhibited their temperature optimum at 20 to 30°C. In these five species, the temperature optimum for photosynthesis was similar at 180 and 30 mbar O₂.

At a lower T_L , photosynthesis at 180 mbar O₂ was equal to or greater than the rate at 30 mbar in all species but *Phaseolus* (Figs. 1, 2). This total loss of O₂ sensitivity was most pronounced in *Lycopersicon*, where it occurred as high as 20°C. *Populus* totally lost sensitivity at 16°C, *Capsicum* at 12°C, and *Scrophularia* and *Cardaria* below 10°C. Replicate measurements made on *Lycopersicon* (Fig. 2) and *Populus* (not shown) indicated that the temperature of total O₂ insensitivity varied among leaves over a 2 to 3°C range within a species. On April 10, 1986, *Scrophularia* exhibited total O₂ insensitivity at the same T_L as it did in late May (data not shown), indicating that there was little acclimation of O₂ insensitivity to growth temperature in this species.

Our modeled values of O₂ sensitivity at a C_i of 220 μ bars were similar to observed values in most species above the point where a feedback limitation became apparent. At no temperature did the predicted sensitivity reach zero. Dramatic deviation from the modeled response occurred above 20°C in *Lycopersicon* and *Populus*. This indicates that a feedback limitation may be playing an important role in these species at temperatures over 20°C. In

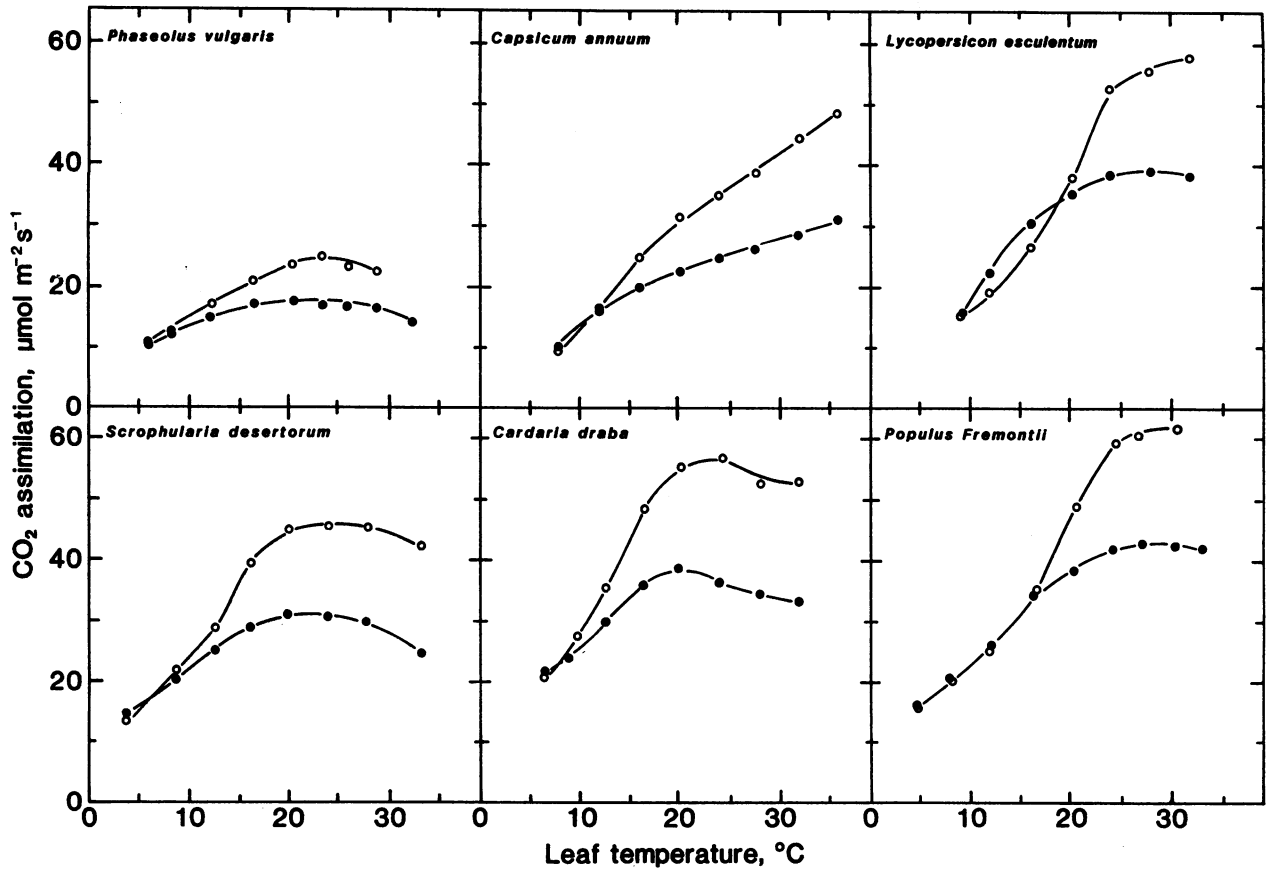


FIG. 1. Temperature response of net photosynthesis at 180 mbar O_2 (●) and 30 mbar O_2 (○).

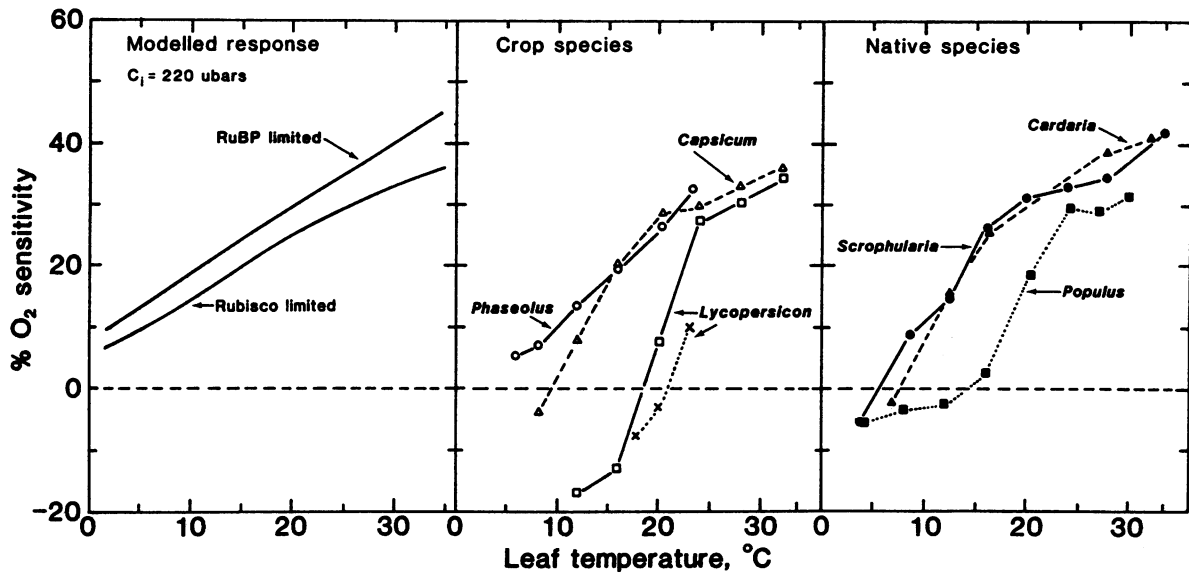


FIG. 2. Response of O_2 sensitivity of photosynthesis to temperature. O_2 sensitivity = $1 - A_{180}/A_{30}$, where A_{180} and A_{30} are the photosynthesis rates at 180 and 30 mbar O_2 , respectively. The modeled responses were calculated as described in the "Theory" section and assume a C_i of 220 μ bars.

Capsicum, *Scrophularia*, and *Cardaria*, substantial deviation from the modeled response occurred at 10 to 12°C.

The CO_2 Response of Photosynthesis. Leaf temperature had little effect on the initial slope of the CO_2 response curve in each species (Fig. 3). This is because (a) Rubisco generally controls the initial slope of photosynthesis, and (b) Rubisco activity at low CO_2 pressures is insensitive to temperature since the K_m and V_{max} have identical Q_{10} values (3). The CO_2 saturated rate of photosynthesis increased dramatically with T_L in each species as

did the CO_2 saturation point. The increase in the CO_2 saturated rate allows the initial slope to extend to higher C_i at the warmer temperatures. Thus, the C_i corresponding to a C_a of 320 μ bar (the operational C_i) occurred well within the initial slope at 30°C in each species, whereas at 10°C it was at or near the CO_2 saturation point. Since the initial slope is believed to be determined by the Rubisco activity (22) this indicates that the leaves of each species were Rubisco limited at 30°C but not at 10°C.

Where O_2 sensitivity was lost, CO_2 sensitivity was also lost. In

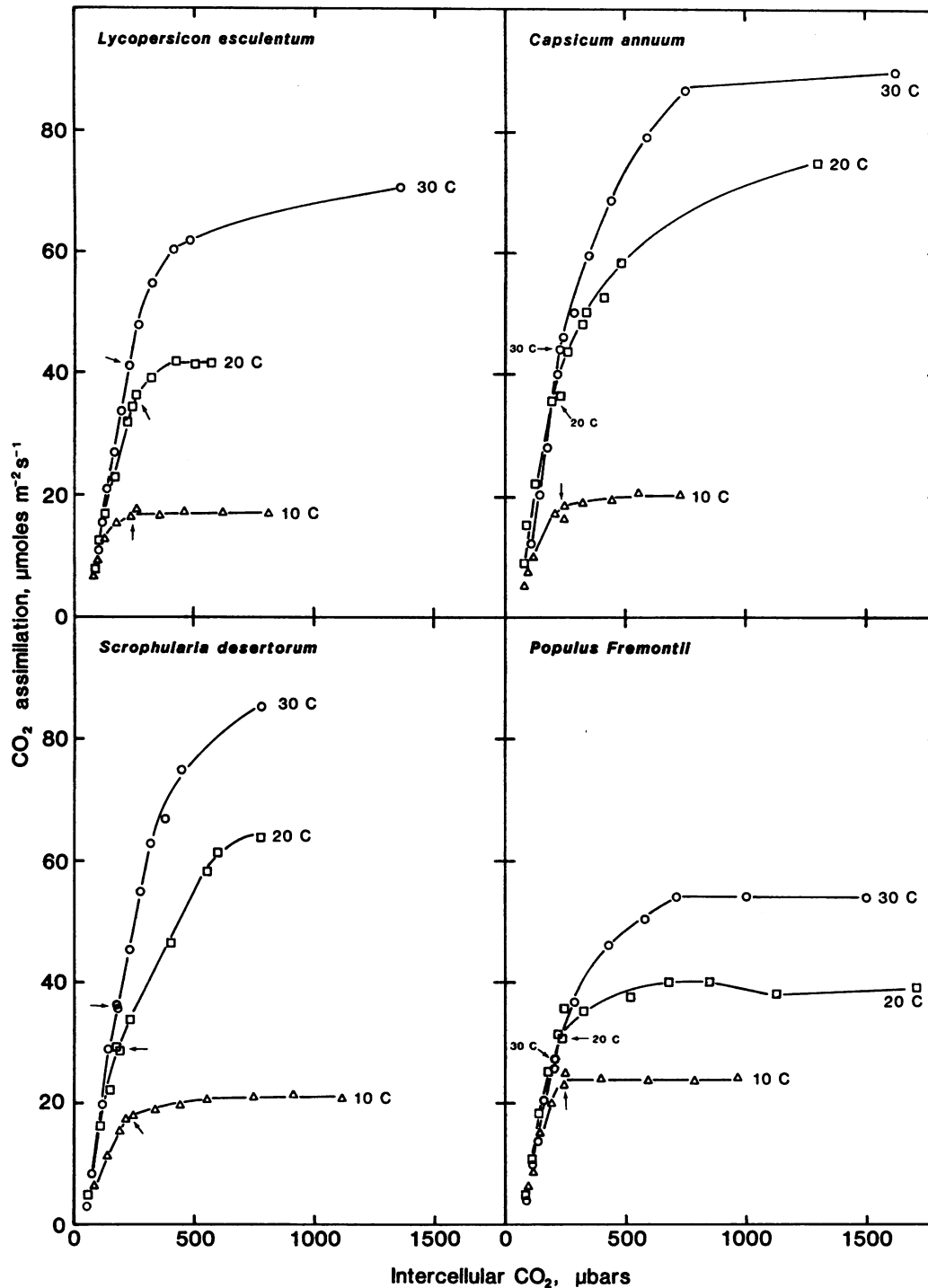


FIG. 3. CO₂ response of photosynthesis at 10, 20, and 30°C. The arrows indicate the C_i at a C_a of 320 µbar.

Lycopersicon and *Populus*, the CO₂ saturation point approached the operational C_i at 20°C. In *Capsicum* and *Scrophularia*, by contrast, the CO₂ saturation point was well above the operational C_i at 20°C (Fig. 3). The operational C_i and the CO₂ saturation point were nearly identical when the temperature was below that where total O₂ insensitivity was first observed. At 10°C, *Capsicum*, *Lycopersicon*, and *Populus*, show total CO₂ insensitivity at the operational C_i, while in *Scrophularia*, some CO₂ sensitivity was apparent above the operational C_i.

As T_L increased, the partial pressure of CO₂ at which CO₂ or O₂ insensitivity appeared increased (Fig. 4). Similar observations have been previously made (5, 13). Stated differently, at higher

CO₂ partial pressures, CO₂ or O₂ insensitivity occurred at higher T_L. This indicates that at elevated atmospheric CO₂ concentrations, feedback limitations will occur at increasingly warmer temperatures and, in the absence of acclimation, the dramatic rise in CO₂ forecast for the next century will be accompanied by an increase in the frequency of feedback limitations in the field.

Leaf Temperatures. On days when the gas-exchange measurements were made, T_L of fully illuminated leaves was followed using copper-constantan thermocouples connected to a Campbell Scientific data logger (Logan, UT). In *Capsicum* and *Scrophularia*, T_L from May to September did not approach those where O₂ insensitivity was observed. Minimum T_L ranged from

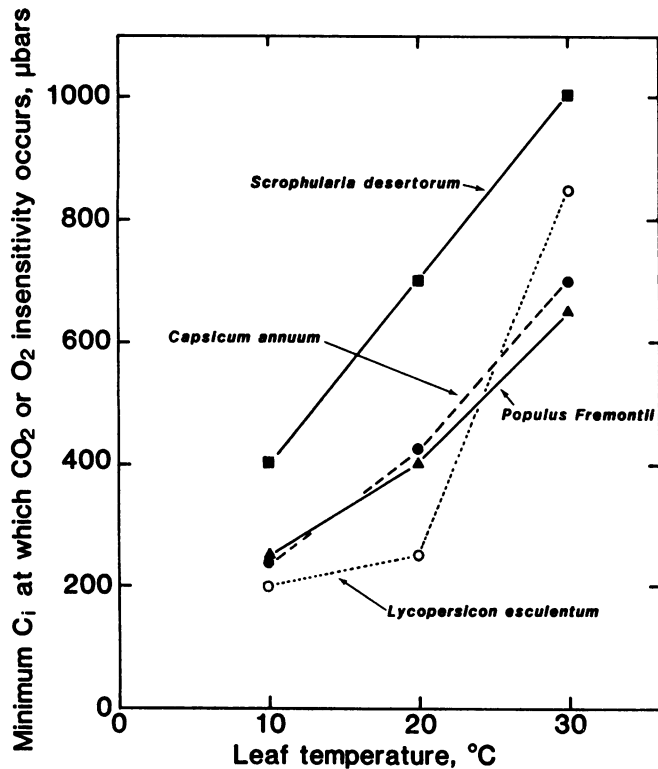


FIG. 4. Effect of temperature on the minimum partial pressure of CO_2 at which photosynthesis is O_2 or CO_2 insensitive.

15 to 19°C in the morning prior to direct illumination by the sun. Following direct illumination, T_L rapidly rose 5 to 10°C and ranged from 24 to 34°C during the course of the day. In *Lycopersicon* and *Populus*, morning T_L was in the range that O_2 insensitivity occurred. T_L ranged from 19 to 26°C in both species from 8 to 11 AM. Leaves perpendicular to the sun's rays were 24 to 26°C during this period; leaves parallel to the sun were 19 to 20°C. After 11 AM T_L ranged from 25 to 33°C in these species.

At 10 AM on September 9, 1986, a cool, windy day, air temperature was 15°C, and T_L of leaves generally perpendicular to the sun's rays were 18 to 20°C in *Capsicum*, 16 to 26°C in *Lycopersicon*, and 16 to 19°C in *Populus*. In *Lycopersicon* and *Populus*, these leaf temperatures were within the range at which photosynthesis was observed to be O_2 insensitive.

Stomatal Limitation. The stomatal limitation on photosynthesis was calculated as $1 - A_{320}/A_{C_i}$ where A_{320} is the assimilation rate at a C_i of 320 μbar and A_{C_i} is the assimilation rate at the operational C_i (7). A_{320} was extrapolated from the CO_2 response curves in Figure 3.

Stomatal limitations increased with T_L in all species (Fig. 5). This increase was not always associated with a drop in C_i . In *Capsicum* and *Lycopersicon*, stomatal limitations increased even though conductance increased and C_i remained constant. In these instances, stomatal conductance increased proportionally with assimilation, and the increase in stomatal limitation resulted from a change in the properties of the photosynthetic apparatus in the mesophyll, rather than a change in the properties of the stomata. Stomatal limitation fell to near zero in *Capsicum*, *Lycopersicon*, and *Populus* at 10°C, a result of the total loss of CO_2 sensitivity at these temperatures.

DISCUSSION

O_2 Insensitivity versus Temperature. Complete photosynthetic O_2 insensitivity was observed in leaves of five of six field grown species at leaf temperatures ranging from 6 to 20°C. The one

exception, *Phaseolus*, readily exhibits O_2 insensitivity up to 20°C when grown in pots and a controlled environment (RF Sage, TD Sharkey, unpublished data). In some leaves of two of the species, *Lycopersicon* and *Populus*, CO_2 and O_2 insensitivity occurred at a temperature and C_i regularly encountered in the field, indicating that feedback limitations on photosynthesis occur over the course of the day in field grown plants. In the remaining species, feedback limitations were important only at temperatures well below those encountered in the May to September study period. However, *Scrophularia* is active from February to October, and in the early months fully illuminated leaves frequently experience the cold temperatures at which feedback effects can occur.

In *Lycopersicon* and *Populus*, feedback limitations do not appear to play a major role in limiting the diurnal carbon gain, since O_2 insensitivity occurred at the lower range of temperatures encountered by these plants in the field. However, in cooler habitats, under water stress, or following CO_2 enrichment, feedback limitations will be increasingly important in sensitive species such as *Lycopersicon* and *Populus*, unless substantial acclimation occurs. Feedback limitations may presently limit the range of many native and crop species. As the atmospheric CO_2 concentration rises, increased restrictions in the distribution of species sensitive to feedback limitations may result because of increased competition from species less likely to be feedback limited.

Acclimation of O_2 insensitivity in response to decreasing temperature or increasing growth CO_2 levels does occur (2, 18, 23). For example, Cornic and Louason (5) observed a 7°C shift in the temperature of total O_2 insensitivity between mustard plants grown at 12 and 27°C. Acclimation to high CO_2 can involve a readjustment of resources within the photosynthetic apparatus so that plants are Rubisco limited to much higher C_i values (24).

Acclimation of O_2 insensitivity to low temperatures or high CO_2 does not always occur. *Scrophularia* plants in early April lost all sensitivity to O_2 at the same T_L as they did in late May, despite a substantial increase in daily temperatures. T. D. Sharkey (unpublished data) found no difference in the CO_2 response of *Xanthium* and *Phaseolus* plants grown at high and low CO_2 .

No clear relationship existed between habitat of origin and the occurrence of O_2 insensitivity. Similar conclusions can be drawn from a survey of the studies using potted plants (5, 9, 16, 17). In this study, of three crop species derived from tropical or subtropical stock, only *Lycopersicon* lost O_2 sensitivity at relatively warm temperatures. Among the temperate species, only *Populus* lost sensitivity at temperatures well above 10°C. However, while *Scrophularia* and *Cardaria* are active prior to May, when cold temperatures regularly occur, *Populus* is dormant, and does not break bud until warmer temperatures return in May.

The Temperature Response of Photosynthesis. Recent advances in our understanding of photosynthetic limitations allow us to interpret the temperature response of photosynthesis in terms of a Rubisco limitation, an RuBP regeneration limitation, or a feedback limitation. Where photosynthesis is totally O_2 insensitive, the capacity for starch and sucrose synthesis is limiting and the temperature response of photosynthesis is a rough profile of the temperature response of Pi regeneration. In *Lycopersicon* and *Populus*, the Q_{10} for O_2 insensitive photosynthesis is 2.2 and 2.0, respectively. The Q_{10} for electron transport and other photosynthetic processes is also near 2 (3). However, Rubisco-limited photosynthesis is largely insensitive to temperature because both the K_m and V_{max} of Rubisco have a Q_{10} of 2 and C_i is normally near the K_m (3). Therefore, in leaves at constant C_i , photosynthesis becomes relatively temperature insensitive when it is Rubisco limited. Under a RuBP or Pi regeneration limitation, the temperature optimum will be relatively sharp, while under a Rubisco limitation, it will be broad. Based on the CO_2 response curves (Fig. 3), all species studied

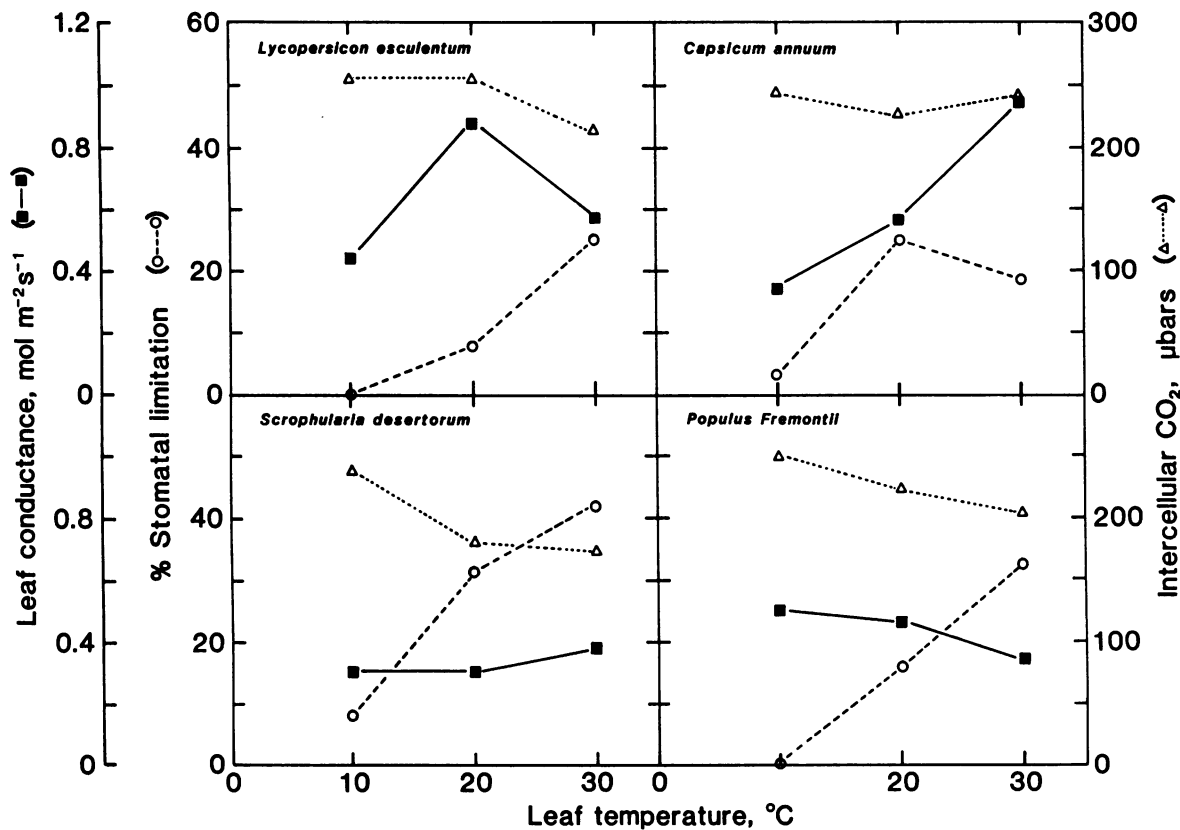


FIG. 5. Response of leaf conductance, stomatal limitation, and C_i to leaf temperature. Data were compiled from the CO₂ response curves in Figure 3.

were Rubisco limited at the temperature optimum.

At constant C_i , the upper limit on a Rubisco limited temperature optimum is determined by the day respiration rate and the increase in photorespiration with temperature. In the field, particularly in arid environments, increasing temperature is accompanied by a sharp reduction in relative humidity. This often causes a drop in C_i (15). In this study, we could not control humidity so the leaves were allowed to respond as they would outside the leaf chamber. In all species but *Capsicum*, C_i declined at the warmer temperatures. This decline in C_i appears to determine the upper limit of the temperature optimum in these five species. In *Capsicum*, the lack of a temperature optimum was due to a rise in C_i which occurred from 20 to 35°C (Fig. 5; data not shown). At the operational C_i , photosynthesis at 25 to 35°C had such a high CO₂ sensitivity, that increases in C_i stimulated photosynthesis enough to overcome increasing O₂ inhibition and day respiration.

Stomatal Limitations. According to Farquhar and Sharkey (7), the stomatal limitation reflects the increase in the CO₂ assimilation rate which would occur if the stomatal and boundary layer resistances were removed. Therefore, the magnitude of the stomatal limitation is dependent upon both the stomatal apparatus and the sensitivity of the photosynthetic apparatus to CO₂ between the C_a and the operational C_i . As is further demonstrated in this study, it is incorrect to assume that an increase in the stomatal limitation must be accompanied by a decrease in C_i . Our data indicate that in the field, stomatal limitations will generally increase with temperature because (a) the photosynthetic apparatus will become Rubisco limited, and therefore more sensitive to CO₂, and (b) the vapor pressure deficit will typically increase, promoting stomatal closure. At lower temperatures, feedback effects can remove all sensitivity to CO₂ above the

operational C_i , and the stomatal limitation may fall to zero even though C_i remains unchanged.

In this study, we have shown that feedback limitations occur under natural conditions in the field and have characterized the temperature response of O₂ insensitive photosynthesis. We believe that the measurement of O₂ sensitivity is an important tool for analyzing the temperature response of photosynthesis and for studying mechanisms which may be important in temperature adaptation in native and cultivated species.

LITERATURE CITED

1. AZCON-BIETO J 1983 Inhibition of photosynthesis by carbohydrates in wheat leaves. *Plant Physiol* 173: 681-686
2. BERRY JA, O BJÖRKMAN 1980 Photosynthetic response and adaptation to temperature in higher plants. *Annu Rev Plant Physiol* 31: 491-543
3. BERRY JA, JK RAISON 1981 Responses of macrophytes to temperature. In OL Lange, PS Nobel, CB Osmond, H Zeigler, eds, *Encyclopedia of Plant Physiology*, New Series, Vol 12A. Springer-Verlag, Heidelberg, pp 277-338
4. BROOKS A, GD FARQUHAR 1985 Effect of temperature on the CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas-exchange measurements on spinach. *Planta* 165: 397-406
5. CORNIC G, G LOUASON 1980 The effects of O₂ on net photosynthesis at low temperatures (5°C). *Plant Cell Environ* 3: 149-157
6. FARQUHAR GD, S VON CAEMMERER 1982 Modelling of photosynthetic response to environmental conditions. In OL Lange, PS Nobel, CB Osmond, H Zeigler, eds, *Encyclopedia of Plant Physiology*, New Series, Vol 12B. Springer-Verlag, Heidelberg, pp 549-588
7. FARQUHAR GD, TD SHARKEY 1982 Stomatal conductance and photosynthesis. *Annu Rev Plant Physiol* 33: 317-345
8. HARRIS GC, JK CHEESBROUGH, DA WALKER 1983 Effects of mannose on photosynthetic gas exchange in spinach leaf discs. *Plant Physiol* 71: 108-111
9. JOLLIFFE PA, EB TREGUNNA 1973 Environmental regulation of the oxygen effect on apparent photosynthesis in wheat. *Can J Bot* 51: 841-853
10. JONES HB 1958 Solubility of various gases in water. In CD Hodgeman, RC West and SM Selby, eds, *Handbook of Chemistry and Physics*, Ed 41. Chemical Rubber Publishing, Cleveland, pp 1708-1709

11. JORDAN DB, WL OGREN 1984 The CO₂/O₂ specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose bisphosphate concentration, pH, and temperature. *Planta* 161: 308-313
12. LEEGOOD RC, RT FURBANK 1986 Stimulation of photosynthesis by 2% oxygen at low temperatures is restored by phosphate. *Planta* 168: 84-93
13. MCVETTY PBE, DT CANVIN 1981 Inhibition of photosynthesis by low oxygen concentrations. *Can J Bot* 59: 721-725
14. MONSON RK, MA STIDHAM, GJ WILLIAMS, GE EDWARDS, EG URIBE 1982 Temperature dependence of photosynthesis in *Agropyron smithii* Rydb. I. Factors affecting net CO₂ uptake in intact leaves and contributions from ribulose-1,5-bisphosphate carboxylase measured *in vivo* and *in vitro*. *Plant Physiol* 69: 921-928
15. SCHULZE ED 1986 Carbon dioxide and water vapor exchange in response to drought in the atmosphere and the soil. *Annu Rev Plant Physiol* 37: 247-274
16. SHARKEY TD 1985 Photosynthesis in intact leaves of C₃ plants: physics, physiology and rate limitations. *Bot Rev* 51: 53-105
17. SHARKEY TD 1985 O₂ insensitivity in C₃ plants. Its occurrence and a possible explanation. *Plant Physiol* 78: 71-75
18. SHARKEY TD 1986 Theoretical and experimental observations on O₂ sensitivity of C₃ photosynthesis. *In* R Marcelle, H Clijsters, M van Poucke, eds, *Biological Control of Photosynthesis*, Martinus Nijhoff/Dr W Junk, The Hague, pp 115-125
19. SHARKEY TD, M STITT, D HEINEKE, R GERHARDT, K RASCHKE, HW HELDT 1986 Limitation of photosynthesis by carbon metabolism. II. O₂ insensitive CO₂ assimilation results from triose phosphate utilization limitations. *Plant Physiol* 81: 1123-1129
20. SIVAK MN, DA WALKER 1986 Photosynthesis *in vivo* can be limited by phosphate supply. *New Phytol* 102: 499-512
21. STITT M 1986 Limitation of photosynthesis by carbon metabolism. I. Evidence for excess electron transport capacity in leaves carrying out photosynthesis in saturating light and CO₂. *Plant Physiol* 81: 1115-1122
22. VON CAEMMERER S, GD FARQUHAR 1981 Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376-387
23. VON CAEMMERER S, GD FARQUHAR 1984 Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO₂) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* 160: 320-329
24. WONG SC 1979 Elevated atmospheric partial pressure of CO₂ and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C₃ and C₄ plants. *Oecologia* 44: 68-74
25. WOO KC, WONG SC 1983 Inhibition of CO₂ assimilation by supraoptimal CO₂: Effect of light and temperature. *Aust J Plant Physiol* 10: 75-85