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Oxygen Inhibition of Photosynthesis

I. TEMPERATURE DEPENDENCE AND RELATION TO O_2/CO_2 SOLUBILITY RATIO[1]

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ABSTRACT

The magnitude of the percentage inhibition of photosynthesis by atmospheric levels of O_2 in the C_3 species *Solanum tuberosum* L., *Medicago sativa* L., *Phaseolus vulgaris* L., *Glycine max* L., and *Triticum aestivum* L. increases in a similar manner with an increase in the apparent solubility ratio of O_2/CO_2 in the leaf over a range of solubility ratios from 25 to 45. The solubility ratio is based on calculated levels of O_2 and CO_2 in the intercellular spaces of leaves as derived from whole leaf measurements of photosynthesis and transpiration. The solubility ratio of O_2/CO_2 can be increased by increased leaf temperature under constant atmospheric levels of O_2 and CO_2 (since O_2 is relatively more soluble than CO_2 with increasing temperature); by increasing the relative levels of O_2/CO_2 in the atmosphere at a given leaf temperature, or by increased stomatal resistance. If the solubility ratio of O_2/CO_2 is kept constant, as leaf temperature is increased, by varying the levels of O_2 or CO_2 in the atmosphere, then the percentage inhibition of photosynthesis by O_2 is similar. The decreased solubility of CO_2 relative to O_2 (decreased CO_2/O_2 ratio) may be partly responsible for the increased percentage inhibition of photosynthesis by O_2 under atmospheric conditions with increasing temperature.

O_2 inhibition of apparent photosynthesis occurs in higher plants which fix CO_2 directly via the Calvin-Benson pathway (C_3 plants). Gas exchange studies with leaves of C_3 plants showed that the percentage inhibition of apparent photosynthesis by O_2 is reduced by increasing the CO_2 concentration, by decreasing the O_2 levels, or by decreasing the temperature (1, 5, 11, 12, 14, 15, 18, 22). One suggestion is that O_2 inhibition of photosynthesis is related to the kinetic properties of RuDP[2] carboxylase-oxygenase. Bowes *et al.* (6) showed that RuDP carboxylase, the enzyme for CO_2 fixation, also catalyzes the oxidation of RuDP by O_2 to form phosphoglycolate, a suggested substrate for photorespiration, and that CO_2 and O_2 show competitive interactions for the substrate RuDP. Thus, O_2 competitively inhibits carboxylase activity with respect to CO_2, and CO_2 competitively inhibits oxygenase activity with respect to O_2. The effect of temperature on O_2 inhibition of photosynthesis recently has been attributed to the differential alteration of the kinetic properties of RuDP carboxylase-oxygenase such that the ratio of RuDP oxygenase activity to carboxylase activity increased with increased temperature (4, 20). Over a temperature range of 5 to 40 C, the percentage inhibition of photosynthesis by O_2 (rate of photosynthesis at 1.5% O_2 − rate of photosynthesis at 21% O_2/rate of photosynthesis at 1.5% O_2)× 100 in various C_3 species (1, 11, 12, 14, 15, 18, 22) increased with increasing temperature although the absolute rate of O_2 inhibition of photosynthesis (rate of photosynthesis at 1.5% O_2 − rate of photosynthesis at 21% O_2) shows an optimum temperature. Generally only atmospheric levels of CO_2 and O_2 have been considered in comparative studies on O_2 inhibition of photosynthesis in various species and on O_2 inhibition of photosynthesis as affected by temperature. In the present study the percentage inhibition of photosynthesis by O_2 was analyzed with several C_3 species in relation to calculated intercellular levels of CO_2 and O_2 and solubility ratios of O_2/CO_2 in the leaf.

MATERIALS AND METHODS

Growth Condition. Plants of potatoes (*Solanum tuberosum* L.) were grown in greenhouse at a day/night temperature range of 20 to 25/15 to 20 C with a light/dark period of 16/8 hr. Plants of wheat (*Triticum aestivum* L.), alfalfa (*Medicago sativa* L.), bean (*Phaseolus vulgaris* L.), and soybean (*Glycine max* L.) were grown in controlled environments at a day/night temperature regime of 20/15 C with a light/dark period of 16/8 hr and 50 to 60% relative humidity. Light was provided by a combination of fluorescent and incandescent lamps giving an irradiance of 40 neinsteins/cm^2·sec between 400 and 700 nm. Plants were watered alternate days with a nutrient solution and water. The nutrient solution contained Ra-pid-Grow (Ra-pid-Gro Corp., Dansville, N.Y.), 2 g/l; and micronutrients according to Johnson *et al.* (13) except iron chelate as Sequestrene 138 Fe (Geigy Agric. Chem., Ardsley, N.Y.), 0.8 g/l. Newly expanded leaves of 2-week-old plants were used for the various experiments.

Gas Exchange Measurements. Rates of photosynthesis and transpiration were measured simultaneously and continuously with a Barnes multispec IR CO_2 and water vapor analyzer in an open circuit system as described previously (18). The attached leaves were enclosed in a 180 cm^3 Plexiglas chamber similar to that designed by Ku and Hunt (19). Eight ports in the sidewalls of the leaf chamber were connected to a closed and independent air-conditioning system which established the leaf temperature. The air recirculates in this system at 13 l/min which minimizes the boundary layer resistance of the leaves to water vapor and CO_2 transfer. Using wet filter paper of similar size and orientation as the leaves, the boundary layer resistance to water vapor transfer was determined for each species under such conditions. Leaf temperature was measured with a 75-μm diameter chromel-constantan thermocouple held against the adaxial surface of the leaf, and was maintained within ±0.3 C of the desired leaf temperature without detectable fluctuation. Using an air conditioner, the temperature around the plant was also kept within ±3 C of the leaf temperature. Irradiance was provided by a 400 w Lucolux lamp (General Electric) in the horizontal position, and was filtered through a 5-cm water tank. Light was measured using a quantum flux sensor (Lambda Instruments, Lincoln, Neb.). Various gas mixtures were provided by mixing gases from

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[2] Abbreviation: RuDP: ribulose 1,5-diphosphate.

N_2, O_2, and 1% CO_2 in N_2 gas cylinders. The gas mixtures were passed into and out of the leaf chamber at a constant rate of 1.5 l/min. Before passing to the leaf chamber and analyzer, the gas stream was saturated with water vapor by bubbling through a water column at a fixed temperature, and then altered by flowing through a series of interconnected condensors at an appropriate temperature (lower than the temperature of water column) to establish the desired moisture. Photosynthesis and transpiration measurements were performed under an incident irradiance of 150 neinsteins/cm^2·sec between 400 and 700 nm at the leaf surface. The leaf-air vapor pressure gradient was maintained in the range of 11 to 15 mbars, and gradients were measured after obtaining steady-state conditions.

The analyzer was calibrated every day with gases of known concentration. The water vapor calibration was made by passing air saturated with water vapor (approximately at 25 C) through a series of interconnected condensors controlled by a constant temperature circulator over a range of 5 to 20 C. A Clark-type O_2 electrode was incorporated into the system for measurement of O_2 concentration. O_2 concentration in the air, taken as 21%, was used along with N_2 for calibration.

The rates of photosynthesis and transpiration were measured after reaching steady-state condition (usually about 20 min). The resistances at the boundary layer (r_a) and stomata (r_s) were determined by the method of Gaastra (8). Stomatal resistance was calculated on one leaf surface area basis. Conversion factors of 1.35 and 1.56 were used to convert r_a, H_2O and r_s, H_2O to r_a, CO_2 and r_s, CO_2, respectively. The level of O_2 inhibition of photosynthesis was determined as the difference between photosynthesis at 1.5% O_2 and photosynthesis at a given higher O_2 concentration. The total percentage inhibition of photosynthesis by O_2 (%I) is given by the equation:

$$\%I = \frac{APS_{1.5\%\ O_2} - APS_{X\%\ O_2}}{APS_{1.5\%\ O_2}}(100)$$

where $APS_{1.5\%}$ O_2 is the apparent rate of photosynthesis at 1.5% O_2, and X is any given O_2 level, generally 21% in the present study.

Solubility of CO_2 and O_2. Solubility of CO_2 (0.03%) and O_2 (21%) in pure water as a function of temperature was calculated according to their Bunsen coefficients (26) (Fig. 1). Both solubilities of CO_2 and O_2 decrease curvilinearly with increasing temperature from 0 to 45 C. However, the solubility of O_2 decreases with increasing temperature relatively less than that of CO_2 so that the solubility ratio of O_2/CO_2 increases with increasing temperature, being 20 at 0 C and 32 at 45 C.

Calculation and Manipulation of Solubility Ratio of O_2/CO_2 in Photosynthetic Cells. The intercellular concentration of CO_2 in the leaf cannot be at complete equilibrium with ambient concentration because of boundary layer and stomatal resistances to free gas exchange. According to Gaastra (8), the CO_2 concentration in the intercellular spaces or around the photosynthetic cells (CO_{2int}) during photosynthesis is estimated as:

$$CO_{2int} = CO_{2ext} - APS\cdot(r_{a,CO_2} + r_{s,CO_2})$$

where CO_{2ext} is the CO_2 concentration in the ambient air, APS is the rate of apparent photosynthesis, r_{a,CO_2} and r_{s,CO_2} are the boundary layer and stomatal resistance to CO_2 transfer, respectively.

By using similar analog of resistance to CO_2 transfer during photosynthesis and the diffusivity of CO_2 and O_2, Samish (25) showed that the build up of O_2 evolved during photosynthesis within normal leaves is smaller than that of the ambient concentration of 0.03% CO_2 and thus is negligible. Therefore, the ambient O_2 concentration was used as the O_2 concentration in the intercellular spaces around the photosynthetic cells.

From the levels of CO_2 and O_2 in the intercellular spaces in a photosynthesizing leaf at a particular leaf temperature, the solubilities of the gases in water are calculated from the Bunsen coefficients and the solubility ratio of O_2/CO_2 determined. This ratio calculated from water is assumed to be close to the solubility of O_2 and CO_2 in the aqueous phase around the mesophyll cells in the leaf since salt concentrations found in plant saps (about 0.1 M) only depressed the solubilities of the gases by an order of 5 to 10% (23). Also, pH of the aqueous phase around the cells is not considered as a factor in the solubility ratio since only the solubility of free CO_2 is determined and not HCO_3^-. The basis for using only CO_2 is due to it serving as an activator and substrate for RuDP carboxylase in carbon assimilation (21). The solubility ratio of O_2/CO_2 in leaves can be manipulated by changing the leaf temperature, ambient CO_2 and O_2 concentrations.

RESULTS

Table I shows the effect of leaf temperature on the percentage inhibition of photosynthesis by O_2 with potatoes. In experiment 1 of Table I, a constant O_2 level (21%) and near constant CO_2 level (in μl/l) similar to atmospheric conditions resulted in an increased solubility ratio of O_2/CO_2 in the leaf at higher temperatures. This increased solubility ratio with increased temperature is due to: (*a*) an increased stomatal resistance with increased

Table I. Effect of solubility ratio of O_2:CO_2 in the leaf on percentage inhibition of photosynthesis by O_2 in potatoes at three temperatures.

Measurements were made progressively from low to high temperature and from high O_2 to 1.5% O_2 at each temperature. Data presented are averages of two replications. Calculations of various parameters are described in the text.

Expt.	Temperature C	r_{s,CO_2} sec/cm	CO_{2ext} µl/l (ng/cm^3)	CO_{2int} µl/l (ng/cm^3)	O_2 %	Solubility ratio µM O_2:µM CO_2	Apparent photosynthesis 1.5% O_2	Apparent photosynthesis 21% O_2	O_2 inhibition	Inhibition %
							ng CO_2/cm^2/sec			
1	22.5	1.39	288 (524)	250 (453)	21	30.3	60.5	42.8	17.7	29.3
	28.8	1.47	288 (513)	241 (429)	21	34.1	73.0	48.3	24.7	33.8
	36.0	3.26	283 (492)	203 (353)	21	43.2	63.5	39.4	24.1	38.0
2	24.0	1.91	290 (525)	239 (433)	21	34.1	62.0	42.2	19.8	31.9
	30.5	2.53	315 (558)	244 (433)	21	34.6	64.9	44.7	20.2	31.1
	36.0	8.11	427 (742)	242 (420)	21	36.4	55.5	38.4	17.1	30.8
3	25.0	2.70	285 (514)	216 (390)	21	36.8	61.2	41.7	19.5	31.9
	30.0	2.99	290 (516)	221 (396)	19.2	34.2	55.8	37.4	18.4	33.0
	34.8	7.32	281 (489)	163 (284)	13.3	35.3	39.5	26.6	12.9	32.7

temperature reducing the internal CO_2 concentration; and (*b*) a greater solubility of O_2 relative to CO_2 with increasing temperature (Fig. 1). The percentage inhibition of photosynthesis by 21% O_2 increased from 29.3% to 38.0% when the ratio increased from 30.3 at 22.5 C to 43.2 at 36.0 C.

Another approach to demonstrate the relation between the solubility ratio of O_2/CO_2 in the leaf and the percentage inhibition of photosynthesis by O_2 is to maintain a near constant solubility ratio with increasing temperature and determine the percentage inhibition of photosynthesis by O_2. Manipulation of solubility ratio in the leaf can be accomplished by changing either external CO_2 or O_2 concentration in addition to increasing temperature. In experiment 2 of Table I a constant solubility ratio (35.3 ± 1.1) was obtained by increasing the external CO_2 concentration with increasing temperature while the atmospheric level of O_2 was kept constant (21%). The elevated external CO_2 concentration overcame the increased stomatal resistance at higher temperatures and gave comparable internal CO_2 concentration at the three temperatures. In spite of increasing temperature, the constant solubility ratio gave a constant percentage of inhibition of photosynthesis (31.3% ± 0.5%) over a range of temperatures from 24 to 36 C. In experiment 3 (Table I), a constant solubility ratio (35.5 ± 1.3) was obtained by decreasing O_2 concentration with increasing temperature when the external CO_2 concentration was held relatively constant. In spite of increasing temperature, the constant solubility ratio also gave similar percentage inhibition of photosynthesis (32.5% ± 0.5%) over a range of temperatures from 25 to 34.8 C. The levels of O_2 inhibition of photosynthesis at the higher temperatures in both experiments 2 and 3 were lower than those in experiment 1. This is attributed to an elevated internal CO_2 concentration in experiment 2 and a decreased O_2 level in experiment 3. Although the percentage inhibition of photosynthesis is apparently related to the solubility ratio of O_2/CO_2 in potatoes, it is clear from Table I that percentage inhibition of photosynthesis is not correlated with the rate of apparent photosynthesis or with the level of O_2 inhibition.

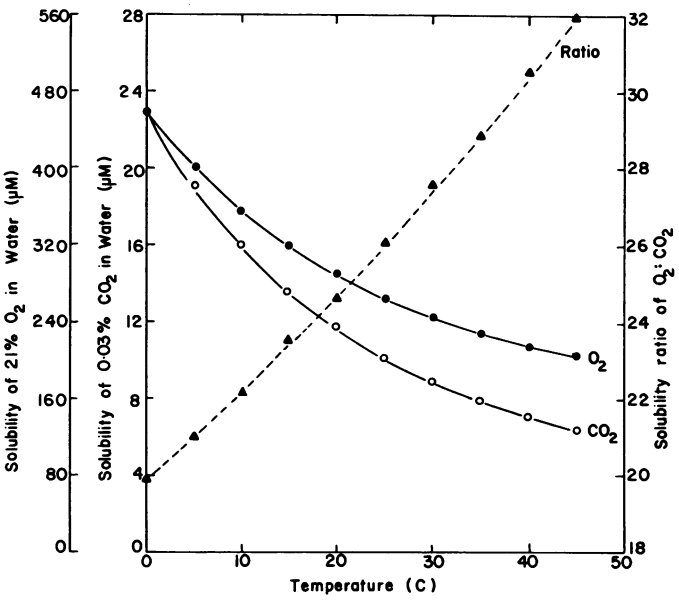

FIG. 1. Solubility of atmospheric O_2 and CO_2, and solubility ratio of O_2/CO_2 in pure water as a function of temperature.

The effect of solubility ratio of O_2/CO_2 on the percentage inhibition of photosynthesis by 21% O_2 in wheat is shown in Table II. At 22 C decreasing external CO_2 concentration from 300 to 239 to 164 μl/l (stomatal resistance remained constant) resulted in increasing the solubility ratio in the leaf from 26.8 to 33.8 to 47.5, respectively. Again, these solubility ratios were highly correlated with percentage inhibition of photosynthesis by O_2, being 23.3%, 32.4% and 45.1%, respectively. Thus, at a relatively low temperature the percentage inhibition of photosynthesis is high when the solubility ratio of O_2/CO_2 is high. At 32 C, similar results were obtained when higher external levels of CO_2 were used to maintain solubility ratios comparable to those of 22 C. A solubility ratio of 26.8 at 22 C gave 23.3% inhibition of photosynthesis and a solubility ratio of 25.8 at 32 C also gave 23% inhibition. Similarly, a solubility ratio of 33.8 at 22 C gave 32.4% inhibition of photosynthesis and a solubility ratio of 33.8 at 32 C gave 31.9% inhibition.

Several other C_3 species were examined to see if there was a consistent relationship between solubility ratio and percentage inhibition of photosynthesis by O_2 (Table III). Photosynthetic activities were measured at low (around 20 C) and high (around 33 C) leaf temperatures. At the high temperature, an increased solubility ratio of O_2/CO_2 in the leaf was obtained without changing the external CO_2 concentration. A similar solubility ratio was obtained at the two temperatures by increasing the external CO_2 concentration at the higher temperature (O_2 constant at 21%). In all species examined, an increase in solubility ratio of O_2/CO_2 in the leaf with temperature also caused an increase in percentage inhibition of photosynthesis while maintaining a near constant solubility ratio at the two temperatures gave rise to a similar percentage inhibition of photosynthesis by O_2 at both temperatures. However, the percentage inhibition of photosynthesis by O_2 in bean and soybean at high temperatures

Table II. Effect of solubility ratio of O_2:CO_2 in the leaf on percentage inhibition of photosynthesis by 21% O_2 in wheat at two temperatures.

Measurements were made progressively from 22 to 32 C and from 21% to 1.5% O_2 for each solubility ratio at a given temperature. Various solubility ratios were obtained by changing external CO_2 concentration when O_2 concentration was kept constant (21%). Data presented are averages of four replications. Calculations of various parameters are described in the text.

Temperature	r_{s,CO_2}	CO_{2ext}	CO_{2int}	Solubility ratio	Apparent photosynthesis		O_2 inhibition	Inhibition
C	sec/cm	μl/l (ng/cm³)	μl/l (ng/cm³)	μM O_2:μM CO_2	1.5% O_2	21% O_2		
					ng CO_2/cm²/sec			%
22.0	0.45	300 (546)	272 (495)	26.8	122.1	93.7	28.4	23.3
22.0	0.48	239 (435)	215 (392)	33.8	109.2	73.8	35.4	32.4
22.0	0.48	164 (298)	150 (272)	47.5	81.8	44.9	36.9	45.1
32.0	0.66	388 (683)	326 (573)	25.8	187.5	144.4	43.1	23.0
32.0	0.70	302 (532)	249 (438)	33.8	173.3	118.0	55.3	31.9

Table III. Effect of solubility ratio of O_2:CO_2 in the leaf on percentage inhibition of photosynthesis by 21% O_2 in four C_3 species at two temperatures.

Measurements were made progressively from low to high temperature and from 21% to 1.5% O_2 at each temperature. Various solubility ratios were obtained by changing external CO_2 concentration when O_2 concentration was kept constant (21%). Data presented are averages of two replications. Calculations of various parameters are described in the text.

Species	Temperature	r_{s,CO_2}	CO_{2ext}	CO_{2int}	Solubility ratio	Apparent photosynthesis		O_2 inhibition	Inhibition
	C	sec/cm	µl/l (ng/cm^3)	µl/l (ng/cm^3)	µM O_2:µm CO_2	1.5% O_2	21% O_2	ng CO_2/cm^2/sec	%
Wheat	20.4	0.25	296 (542)	281 (515)	26.5	126.7	93.1	33.6	26.5
	32.5	0.84	283 (498)	234 (411)	36.0	147.8	92.7	55.1	37.3
	32.8	0.83	380 (667)	314 (552)	28.6	169.8	123.1	46.7	27.5
Alfalfa	19.8	0.35	288 (528)	266 (487)	27.7	105.3	82.6	22.7	21.6
	31.6	0.70	289 (510)	239 (422)	35.1	148.9	103.1	45.8	30.8
	32.1	0.86	343 (603)	281 (494)	30.0	152.0	113.2	38.8	25.5
Bean	19.9	0.80	298 (547)	265 (485)	27.9	70.9	58.2	12.7	17.9
	31.8	0.95	297 (524)	240 (422)	35.0	122.6	83.8	38.8	31.7
	32.1	1.19	377 (663)	294 (517)	28.0	127.1	99.9	27.2	21.4
Soybean	22.2	1.07	295 (537)	261 (476)	28.9	55.7	45.4	10.3	18.5
	33.6	1.01	294 (515)	248 (434)	34.4	89.5	63.3	26.2	29.3
	33.6	1.02	370 (649)	311 (544)	27.5	102.0	81.6	20.4	20.0

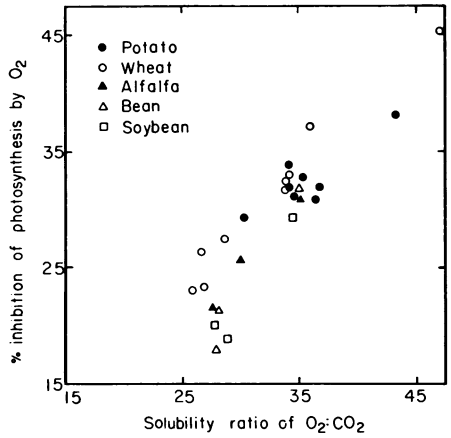

FIG. 2. Relationship between solubility ratio of O_2/CO_2, calculated from O_2 and CO_2 concentrations in the intercellular air spaces in the leaf, and percentage inhibition of photosynthesis by O_2 for five C_3 species. Data from Tables I, II, and III.

was slightly higher than that at low temperatures when the solubility ratio in the leaf was kept relatively constant at both temperatures. For a given solubility ratio in the leaf, the percentage inhibition of photosynthesis by O_2 varied with the species. For example, a solubility ratio of 26.5 in wheat gave 26.5% inhibition whereas a solubility ratio of 28.9 in soybean gave only 18.5% inhibition. Based on the data collected with the various species, the general relationship between the solubility ratio of O_2/CO_2 in the leaf and percentage inhibition of photosynthesis by O_2 for five C_3 species is shown in Figure 2 (data plotted from Tables I-III). These data show a general correlation between the solubility ratio and percentage inhibition of photosynthesis by O_2 when the O_2/CO_2 ratio varies from about 25 to 45.

DISCUSSION

In the present study, stomatal resistance varies with species, with temperature within a species, and even with CO_2 concentration at a given temperature (Tables I-III). The expression of CO_2 and O_2 level in the leaf on a solubility basis can eliminate differences in comparing some photosynthetic parameters due to change in stomatal resistance in the cases where external CO_2 concentration is used, and change in temperature (since increased temperature decreases both CO_2 and O_2 solubilities) in the cases where either atmospheric or intercellular CO_2 concentration is used.

There are several alternative mechanisms for O_2 inhibition of photosynthesis (9, 16, 20, 24, 27) although the degree of inhibition by O_2 is known to be dependent on relative levels of O_2 and CO_2 in the atmosphere. Regardless of the mechanism of O_2 inhibition, the change in the percentage inhibition of photosynthesis by O_2 by changing the solubility ratio of O_2/CO_2 in the leaf appears to be similar whether the ratio changes due to external CO_2, O_2 levels or to temperature.

At high temperatures, C_3 plants show a limited capacity for increased photosynthesis and an associated increased percentage inhibition of photosynthesis by atmospheric levels of O_2 (1, 11, 12, 14, 15, 18, 22). The basis for the higher sensitivity of photosynthesis to O_2 with increasing temperature has not been clarified although recent suggestions of apparent changes in the biochemical characteristics of RuDP carboxylase-oxygenase have been given. Badger and Andrews (4) suggested that the activation energy of RuDP oxygenase is substantially higher than the activation energy of RuDP carboxylase which could result in relatively greater increase in V_{max} of the oxygenase reaction than the carboxylase reaction with increased temperature. However, Laing *et al.* (20) observed that the activation energies of the two reactions were nearly identical and suggested that V_{max} carboxylase/V_{max} oxygenase would be constant with varying temperature but that K*m* oxygenase/K*m* carboxylase would decrease with increase in temperature primarily due to an increased K*m* for CO_2. Either of the above reasons, based on *in vitro* studies, could account for the increased percentage inhibition of photosynthesis by O_2 by increasing temperature with whole leaves, although the results of the present study do not favor these interpretations. By maintaining a relatively constant solubility ratio of O_2/CO_2 in the five C_3 species studied, the percentage inhibition of photosynthesis within a species remained relatively constant at varying temperatures. Limitations on photosynthesis in C_3 species with increased temperature might be explained by the solubility properties of O_2 and CO_2 as shown in Figure 1.

First, decreased solubility of CO_2 with increasing temperature would limit the rate of photosynthesis since this substrate at atmospheric levels is rate-limiting in C_3 plants (1-3, 15, 18). Second, the relative solubility ratio of O_2/CO_2 increases with temperature which would naturally favor an increased percentage inhibition of photosynthesis by O_2. In addition, an increased leaf temperature up to 35 C may increase stomatal resistance to CO_2 transfer in some species and further increase O_2/CO_2 ratios (Tables I-III, 18). In contrast to these negative effects of increasing temperature on photosynthesis in C_3 species, one positive factor with increased temperature may be an increased V_{max} for carbon assimilation (17).

In C_4 plants, a proposed CO_2 concentrating mechanism through C_4 acid decarboxylation may increase the CO_2/O_2 ratio in the leaf (7, 10) and effectively overcome the limitations apparently imposed by CO_2 and O_2 solubility characteristics (Fig. 1) of decreasing CO_2 concentration and increasing O_2/CO_2 ratio with increasing temperature.

When the solubility ratio is maintained constant, the percentage inhibition of photosynthesis by O_2 is similar within a species although the relative rate of apparent photosynthesis varies noticeably with temperature (Tables I-III). This suggests that the percentage inhibition is dependent on the solubility ratio but is not affected by variations in the relative velocity of CO_2 exchange at least around atmospheric levels of CO_2. It appears that the percentage inhibition of photosynthesis by O_2 can be a useful measure of the relative effect of O_2 at the cellular level on a given rate of true photosynthesis if comparisons are made on a solubility basis.

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