Effects of Light, Carbon Dioxide, and Temperature on Photosynthesis, Oxygen Inhibition of Photosynthesis, and Transpiration in *Solanum tuberosum*[1]

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ABSTRACT

Individual leaves of potato (*Solanum tuberosum* L. W729R), a C_3 plant, were subjected to various irradiances (400-700 nm), CO_2 levels, and temperatures in a controlled-environment chamber. As irradiance increased, stomatal and mesophyll resistance exerted a strong and somewhat paralleled regulation of photosynthesis as both showed a similar decrease reaching a minimum at about 85 neinsteins·cm^{-2}·sec^{-1} (about $1/2$ of full sunlight). Also, there was a proportional hyperbolic increase in transpiration and photosynthesis with increasing irradiance up to 85 neinsteins·cm^{-2}·sec^{-1}. These results contrast with many C_3 plants that have a near full opening of stomata at much less light than is required for saturation of photosynthesis.

Inhibition of photosynthesis by 21% O_2 was nearly overcome by a 2-fold increase in atmospheric levels of CO_2 (about 1,200 ng·cm^{-3}). Photosynthesis at 25 C, high irradiance, 2.5% O_2 and atmospheric levels of CO_2 was about 80% of the CO_2-saturated rate, suggesting that CO_2 can be rate-limiting even without O_2 inhibition of photosynthesis. With increasing CO_2 concentration, mesophyll resistance decreased slightly while stomatal resistance increased markedly above 550 ng·cm^{-3} which resulted in a significant reduction in transpiration.

Although potato is a very productive C_3 crop, there is substantial O_2 inhibition of photosynthesis. The level of O_2 inhibition was maximum around 25 C but the percentage inhibition of photosynthesis by O_2 increased steadily from 38% at 16 C to 56% at 36 C. Photosynthesis and transpiration showed broad temperature optima (16-25 C). At higher temperatures, both the increased percentage inhibition of photosynthesis by O_2 and the increased stomatal resistance limit photosynthesis, while increased stomatal resistance limits transpiration. Water use efficiency, when considered at a constant vapor pressure gradient, increased with increasing irradiance, CO_2 concentration, and temperature.

In spite of the importance of potato as a staple food crop, only limited studies (9, 24) have been done on its carbon balance and water use efficiency relative to other crops with respect to environmental factors. Potato is a C_3 plant with photorespiration based on its high CO_2 compensation point; yet its productivity is high (average market yield in U.S.: 4.66 metric tons dry weight of tuber/ha[4]) (1) and even comparable to that of some C_4 crops (30). The productivity of a C_3 crop depends on the carbon balance as it effects carbon assimilation processes including photosynthesis, and carbon dissimilation processes including photorespiration and dark respiration. Photorespiration, compared with dark respiration, is a dominant component in carbon dissimilation processes in the light in C_3 plants and is suggested to limit productivity (30). Another gas exchange process, which is important in water use efficiency and productivity, is transpiration. Transpiration regulates the water balance in plants and is influenced indirectly by environmental factors through effects on stomatal opening. It is of interest to determine the magnitude of O_2 inhibition of photosynthesis in potatoes and the effect of irradiance, CO_2 concentration, and temperature on photosynthesis, O_2 inhibition of photosynthesis, and transpiration.

MATERIALS AND METHODS

Growth Condition. Plants of *Solanum tuberosum* L. W729R were grown from eyepieces in plastic pots (22 cm diameter, 25 cm deep) filled with a mixture of sandy loam and peat moss 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^{-1} between 400 and 700 nm. Plants were watered on alternate days with a nutrient solution and water. The nutrient solution contained Rapid Grow (Rapid Gro Corp., Dansville, N.Y.), 2 g/l; and micronutrients according to Johnson *et al.* (19), except iron chelate as Sequestrene 138 Fe (GEIGY Agric. Chem., Ardsley, N.Y.), 0.8 g/l.

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 (21). The third leaf from the top of plants at the six-leaf stage was selected for various studies. The attached leaflets were enclosed in a 180 cm^3 Plexiglas chamber similar to that designed by Ku and Hunt (21). Eight ports in the side walls of the leaf chamber were connected to a closed and independent air-conditioning system which established the leaf temperature. The air is recirculating in this system at 13 l/min which minimizes the boundary layer resistance of the leaves to water vapor and CO_2 transfer. Using filter paper of similar size and orientation as the leaves, the boundary layer resistance to water vapor transfer was determined to be 0.20 sec·cm^{-1} 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 ±1 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-

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[4] Conversion was made on the basis of 18% dry matter for potato tubers.

cm water tank. Differing irradiances were obtained by inserting cheesecloth screens between the chamber and water tank. Light was measured using a quantum flux sensor (Lambda Instruments, Lincoln, Neb.). According to our measurements, the potato leaves absorbed 83%, reflected 9%, and transmitted 8% of the total incident radiation. Various gas mixtures were provided by mixing gases from N_2, O_2 and 1% CO_2 in N_2 gas cylinders. The gas mixtures 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 controlled temperature and then altered by flowing through a series of interconnected condensers at an appropriate temperature (lower than the temperature of water column) to establish the desired moisture. Unless otherwise specified, photosynthesis and transpiration measurements were performed at a leaf temperature of 25 C, 570 ng·cm^{-3} CO_2 concentration with either 21% or 2.5% O_2 under an incident irradiance of 150 neinsteins·cm^{-2}·sec^{-1} 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 in the varying light and varying CO_2 studies and 10 to 25 mbars in the varying temperature study, and gradients were measured after obtaining steady-state conditions. For comparison on the same basis, transpiration rates were weighted for constant vapor pressure gradient (10 mbars).

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 condensers 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. Oxygen concentration in the air, taken as 21%, was used along with N_2 for calibration.

The rates of photosynthesis and transpiration were taken after reaching steady-state condition (usually about 20 min). The resistances at the boundary layer (r_a), stomata (r_s) and mesophyll (r_m)[5] were determined by the method of Gaastra (12) except the CO_2 concentration at the chloroplast was assumed to be the CO_2 compensation point since potato is a C_3 species with photorespiration. Stomatal resistance was calculated on one leaf surface area basis. Carbon dioxide compensation point, extrapolated from the plot of photosynthetic rate in normal air *versus* external CO_2 concentration, changed slightly with irradiance at a given temperature but increased linearly with temperature, being 85, 95, 120, 152, 205 ng·cm^{-3} at 16, 20, 25, 30, 36 C, respectively. The changes in CO_2 compensation point with temperature were taken into account in the calculation of mesophyll resistance. Conversion factors of 1.35 and 1.56 were used to calculate r_a,CO_2 and r_s,CO_2, respectively. The level of O_2 inhibition of photosynthesis was determined as the difference between true (photosynthesis at 2.5% O_2) and net photosynthesis (photosynthesis at 21% O_2). Percentage inhibition of photosynthesis by 21% O_2 was defined as (O_2 inhibition of photosynthesis/true photosynthesis)·100. Water use efficiency was indicated by the ratio of total conductance (the reciprocal of resistance) of CO_2 to stomatal conductance of water vapor (r_s,H_2O/[r_s,CO_2 + r_m]). The greater the ratio, the higher the water use efficiency.

RESULTS AND DISCUSSION

Net photosynthesis of potato leaves responded to light hyperbolically and saturated at an irradiance of 85 neinsteins·cm^{-3}·sec^{-1}, which is equivalent to about half of full sun-

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[5] In this paper, r_m is taken as a total measure of the residual resistance which includes a carboxylase-oxygenase component, photochemical component, and diffusive resistance in the aqueous phase. The relative magnitude of the components would vary depending upon light, CO_2 and O_2 levels.

light (Fig. 1). The effect of light on transpiration was similar to the effect of light on photosynthesis and is essentially a function of stomatal opening when the leaf temperature and vapor pressure gradient were held constant (Fig. 1). Water use efficiency, as indicated by the ratio of total conductance of CO_2 to stomatal conductance of water vapor, increased with an increase in irradiance (Table I). Downes (11) reported that water use efficiency of wheat was improved by increasing irradiance.

Under low light, the rate of net photosynthesis is apparently limited by the closing of stomata and by decreased photochemical activity as indicated by the high stomatal and mesophyll resistance, respectively (Fig. 1). The effect of irradiance on stomatal resistance in potatoes seems to be somewhat intermediate between a number of C_3 and C_4 species examined. Stomata of many C_3 species, such as tobacco (29), *Vicia faba* (18), and wheat (3), opened at intensities less than 5% of full sunlight which is considerably lower than the intensity necessary to achieve maximal rate of photosynthesis. On the other hand, stomata of C_4 species, such as corn (3) and sorghum (11), tended to remain closed in low light and continued to open with irradiance above half of sunlight. In our study, mesophyll resistance behaved similarly to stomatal resistance with respect to irradi-
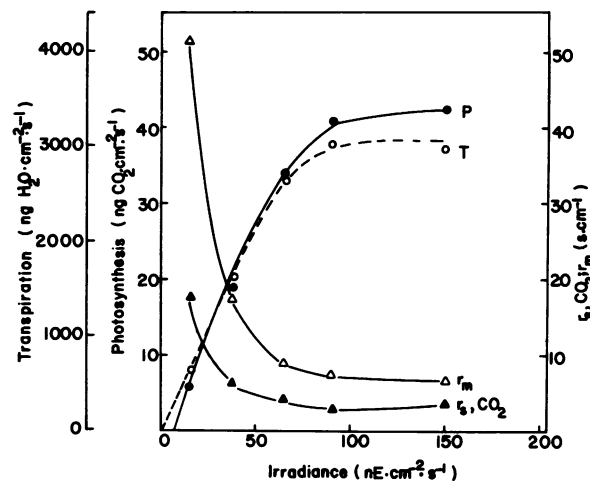

FIG. 1. Net photosynthesis (P), transpiration (T), stomatal resistance to CO_2 diffusion (r_s,CO_2), and mesophyll resistance (r_m) as a function of irradiance for potato leaves at 25 C in air containing 21% O_2 and 570 ng·cm^{-3} CO_2.

Table I. Water use efficiency at various irradiances, CO_2 concentrations, and temperatures.

Water use efficiency was determined from the ratio of total conductance (the reciprocal of resistance) of CO_2 to stomatal conductance of water vapor (r_s,H_2O/r_s,CO_2 + r_m).

Factor	Level	Water use efficiency (r_s,H_2O/r_s,CO_2 + r_m)
Light (nE·cm^{-2}·sec^{-1})	15	0.115
	39	0.134
	65	0.154
	90	0.153
	150	0.171
CO_2 (ng·cm^{-3})	343	0.131
	488	0.151
	686	0.186
	848	0.223
	1115	0.303
Temperature (C)	17	0.093
	20	0.113
	24	0.142
	31	0.139
	36	0.207

ance. However, mesophyll resistance decreased more rapidly than stomatal resistance with increasing irradiance, as indicated by the ratio of $r_m/r_s,CO_2$ which ranged from 3.3 at 15 nein-steins·cm^{-2}·sec^{-1} to 1.9 at 150 neinsteins·cm^{-2}·sec^{-1}. This would indicate that mesophyll resistance has relatively more control over CO_2 fixation at low light.

Oxygen inhibition of photosynthesis increased with irradiance from 15 to 65 neinsteins·cm^{-2}·sec^{-1} and remained constant thereafter (Fig. 2). The response of O_2 inhibition of photosynthesis to irradiance conforms with results obtained with *Rumex acetosa* L. (17) and with *Medicago sativa* L. (22). By contrast, percentage inhibition of photosynthesis by 21% O_2 decreased throughout the entire range of irradiance studied, being 50% at 15 neinsteins·cm^{-2}·sec^{-1} and 37% at 150 neinsteins·cm^{-2}·sec^{-1} (Fig. 2). A similar trend has been reported in alfalfa (22).

At 21% O_2, leaf temperature of 25 C, and an irradiance of 150 neinsteins·cm^{-2}·sec^{-1}, photosynthesis increased with external CO_2 concentration up to 1,115 ng·cm^{-3} (Fig. 3). At 1,115 ng·cm^{-3} of CO_2, photosynthetic rate was about two times higher than that at 600 ng·cm^{-3} (near atmospheric levels). Carbon dioxide compensation point, extrapolated from the plot of photosynthesis rate in normal air *versus* external CO_2 concentration, was estimated to be 120 ng·cm^{-3} under such conditions. On the other hand, photosynthesis at 2.5% O_2 was enhanced with increasing CO_2 and saturated at a CO_2 concentration of 900 ng·cm^{-3}. In wheat, similar curves for CO_2 assimilation with varying CO_2 levels at 21% or 3% O_2 has been recorded by Jolliffe and Tregunna (20). Bjorkman (7) also observed somewhat similar results with *Atriplex patula*: at 1.5% O_2 there was no significant difference between the rates of CO_2 uptake at 550 ng·cm^{-3} and 1280 ng·cm^{-3} CO_2 and the rates of CO_2 uptake were also quite similar at 1.5% and 21% O_2 when CO_2 concentration was kept at 1280 ng·cm^{-3}. With potatoes at 25 C, saturating light, and near atmospheric levels of CO_2 (550 ng·cm^{-3}), net photosynthesis would be increased 41% by elimination of O_2. However, under these conditions without O_2 inhibition, true photosynthesis is still limited by CO_2. There was a 22% increase in photosynthesis under 2.5% O_2 by increasing CO_2 from atmospheric levels to saturating levels.

Mesophyll resistance decreased slightly with increasing CO_2 concentration. Stomatal resistance remained relatively constant at low CO_2 concentration but increased considerably above 600 ng·cm^{-3}, the usual atmospheric CO_2 concentration. This is consistent with Gaastra's earlier observations (12) that there was no change in stomatal resistance at high irradiance in turnip leaves between 0 and 300 μl·l^{-1} of CO_2, but increasing the CO_2 level to 1,500 μl·l^{-1} increased stomatal resistance from 2.5 to 5 sec·cm^{-1}.

Transpiration remained fairly constant below a CO_2 concentration of 600 ng·cm^{-3} and then dropped considerably at higher CO_2 levels which was associated with an elevated stomatal resistance (Fig. 3). At a leaf temperature of 25 C, water use efficiency increased rapidly with increasing CO_2 concentration (Table I). Similar results have been reported by Akita and Tanaka (4) in a number of C_3 and C_4 species. This resulted from an increase of net photosynthesis but a decrease of transpiration with increasing external CO_2 concentration.

Oxygen inhibition of photosynthesis increased slightly with increased CO_2 concentration from 350 up to 700 ng·cm^{-3} and then decreased sharply (Fig. 4). By contrast, percentage inhibition of photosynthesis by O_2 decreased steeply with increasing CO_2 concentration, from 53% at 350 ng·cm^{-3} to 10% at 1,115 ng·cm^{-3}. Similar results have been reported with wheat by Jolliffe and Tregunna (20) in which they found that percentage inhibition at 25 C decreased from 55% at 190 ng·cm^{-3} to 11% at 920 ng·cm^{-3} CO_2.

The relationship between net photosynthesis, transpiration, and leaf temperature is shown in Figure 5. With saturating light
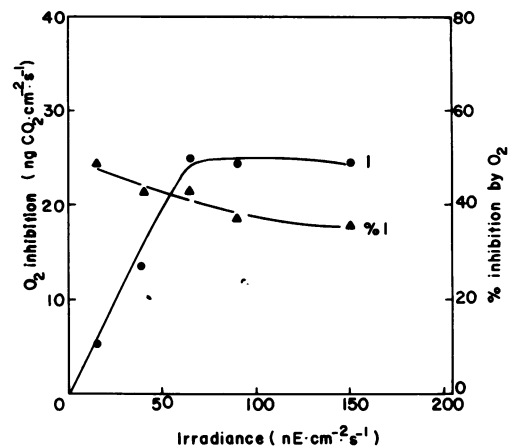

FIG. 2. Oxygen inhibition of photosynthesis (I) and percentage inhibition of photosynthesis by 21% O_2 (% I) as a function of irradiance for potato leaves at 25 C in air containing 570 ng·cm^{-3} CO_2.
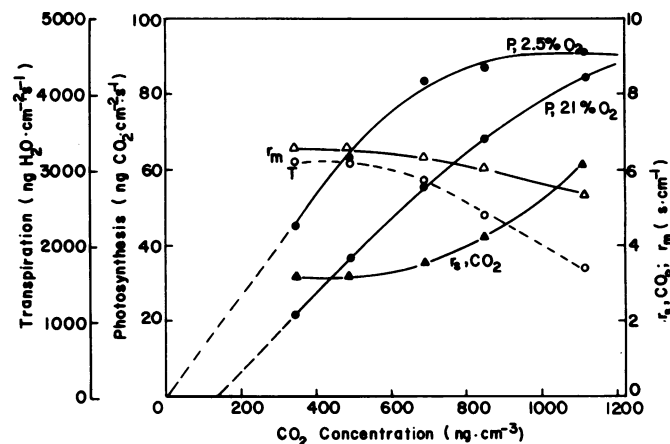

FIG. 3. Effects of external CO_2 concentration on photosynthesis (P), transpiration (T), stomatal resistance to CO_2 diffusion (r_s,CO_2), and mesophyll resistance (r_m) of potato leaves at 25 C in air containing either 2.5 or 21% O_2 under a saturating irradiance of 150 neinsteins·cm^{-2}·sec^{-1}.
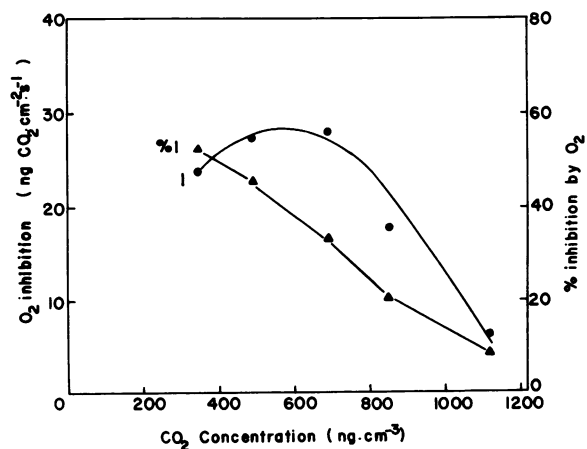

FIG. 4. Effects of external CO_2 concentration on O_2 inhibition of photosynthesis (I) and percentage inhibition of photosynthesis by 21% O_2 (% I) of potato leaves at 25 C under a saturating irradiance of 150 neinsteins·cm^{-2}·sec^{-1}.

and in normal air, both photosynthesis and transpiration showed broad temperature optima ranging from 16 to 25 C, but decreased rapidly above 25 C. Potato originated from regions with

relatively cool climate (8) and the results here confirm that plants of temperate latitudes perform best over a wide range of low to moderate temperatures for their CO_2 assimilation. Other temperate species with photorespiration such as sugar beet, soybean, wheat, barley, and orchardgrass also show broad low temperature optima at high light intensity in air measured between 10 and 35 C (16, 25).

Stomatal and mesophyll resistance remained relatively low and constant at leaf temperatures below 25 C but increased markedly above 25 C, especially the stomatal resistance. Temperature affects transpiration directly via a minor change in diffusive processes at the leaf surfaces and indirectly due to the effect of temperature on stomatal opening. The high stomatal resistance at leaf temperature above 25 C is primarily responsible for the big reduction in transpiration while increased stomatal and mesophyll resistance contribute to reduced photosynthesis. For many species, when leaves were well hydrated, the stomata were progressively more open as the temperature increased from 10 to 35 C (15, 28). In contrast, stomatal resistance of potato leaves increased slightly with leaf temperature from 16 to 25 C, but increased sharply above 25 C under conditions where the vapor pressure gradient from the leaf to air was kept relatively constant. The closure of potato stomata with increasing temperature may be a reflection of its adaptation to a cooler environment. Water use efficiency, on a constant vapor pressure gradient basis, increased steadily with increasing temperature (Table I). Contrary observations have been reported by Downes (11) with various species, in which he suggested that water use efficiency was independent of leaf temperature, although comparisons were not made at a constant vapor pressure gradient.

Oxygen inhibition of photosynthesis also showed an optimal temperature around 25 C (Fig. 6). Apparently, there was no marked upward displacement of the optimum temperature for photosynthesis at 2.5% O_2 relative to 21% O_2. These results agree with those studies reported for individual leaves of soybean, sugar beet, and *Atriplex hastata* by Hofstra and Hesketh (16), and individual leaves of alfalfa by Ku and Hunt (22), in which maximum rates of O_2 inhibition occurred at the temperature where rates of net photosynthesis were maximum. The present results do not agree with those recorded for individual leaves of sunflower (14), and whole plants of wheat (20) and alfalfa (27) and wheat and rice (4), in which maximal O_2 inhibition occurred about 10 to 15 C higher than that for maximal net photosynthesis. Based on available data, it is difficult to conclude that O_2 inhibition of photosynthesis is closely associated with net photosynthesis. Badger and Andrews (6) and Laing *et al*. (23) have suggested that the increase in photorespiration, CO_2 compensation point, or O_2 inhibition of net photosynthesis
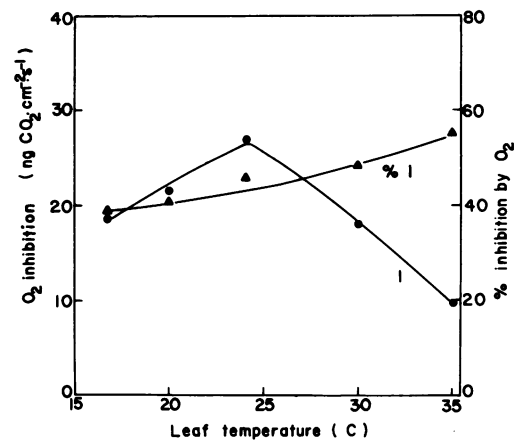

FIG. 6. Temperature dependence of O_2 inhibition of photosynthesis (I) and percentage inhibition of photosynthesis by 21% O_2 (% I) in potato leaves in air containing 570 ng·cm^{-3} CO_2 under a saturating irradiance of 150 neinsteins·cm^{-2}·sec^{-1}.

with increasing temperature may be due in part to a change in the kinetic properties of RuDP carboxylase-oxygenase. However, O_2 inhibition of net photosynthesis in potatoes increased with temperature from 16 to 25 C but decreased drastically thereafter (Fig. 6). The large decrease in net photosynthesis above 25 C would appear to be due primarily to increased stomatal and mesophyll resistances (Fig. 5) rather than increased O_2 inhibition of photosynthesis (Fig. 6).

Unlike the level of O_2 inhibition of photosynthesis, percentage inhibition of photosynthesis by O_2 increased steadily from 38% at 16 C to 56% at 36 C. Such a trend conforms to those calculated from data presented by Hew *et al*. (14), Akita and Miyasaka (2), and Hofstra and Hesketh (16), and to that by Pearson and Hunt (27) showing an increased O_2 inhibition of photosynthesis from 20% at 10 to 20 C to 35 to 60% at 40 C.

CONCLUSION

Based on the present study, potatoes have a range of maximum carbon assimilation efficiency and water use efficiency from 16 to 25 C. Under optimal conditions, the rate of net photosynthesis in potatoes at atmospheric CO_2 level ranged from 30 to 45 ng CO_2·cm^{-2}·sec^{-1} (Figs. 1, 3, and 5). These rates are comparable to or even higher than those previously reported for potatoes (9). It appears that the reported rates of net photosynthesis in potato are lower than for most C_3 crops, such as sunflower, tobacco and wheat (13), and sugar beet (12). However, the rate of net photosynthesis in potatoes may be influenced by source-sink relationship. Moorby (24) has showed that after tuberization, $^{14}CO_2$ assimilation in potato leaves increased two to three times and this was accompanied by an increase in the amount of ^{14}C moving into the tuber from the leaves. Plants employed in this study had not formed tubers. Net photosynthetic rates of outdoor-grown potato with tubers were also about two times higher than values reported here (Ku and Edwards, unpublished). An increase in photosynthetic capacity of potatoes with tuberization might contribute to its high productivity and deserves further investigation.

Oxygen inhibition of photosynthesis in potatoes was repressed by either increasing external CO_2 concentration or decreasing O_2 level down to 2.5% (Fig. 3). These results therefore fit a current theory on the mechanism of O_2 inhibition of photosynthesis that O_2 competes for ribulose 1,5-diP carboxylase at the same site as CO_2 (5, 26). However, photosynthesis was still increased by further increasing CO_2 above atmospheric levels even under conditions where O_2 inhibition was suppressed (Fig. 3). Potatoes are very productive but we have found that there is a large
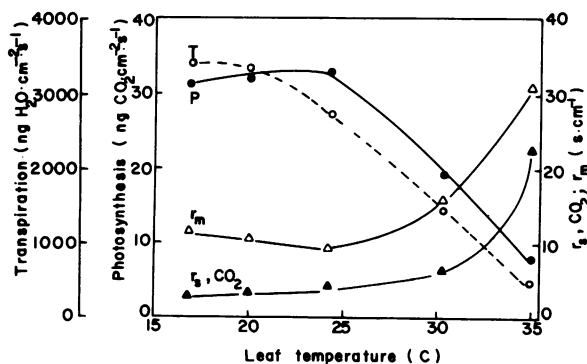

FIG. 5. Temperature dependence of net photosynthesis (P), transpiration (T), stomatal resistance to CO_2 diffusion (r_s,CO_2), and mesophyll resistance (r_m) in potato leaves in air containing 21% O_2 and 570 ng·cm^{-3} CO_2 under a saturating irradiance of 150 neinsteins·cm^{-2}·sec^{-1}.

inhibition of photosynthesis by O_2 over a wide temperature range and a low rate of photosynthesis at high temperatures. It might be possible to increase production further by repressing O_2 inhibition. In 1918 Cummings and Jones (10) found a 2-fold increase in vegetative and tuber growth in potatoes with CO_2 enrichment above atmospheric levels.

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