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

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SUN-BEN KU,2 GERARD E. EDWARDS,2 AND CHAMP B. TANNER3
Departments of Horticulture and Soil Science, University of Wisconsin, Madison, Wisconsin 53706

ABSTRACT

Individual leaves of potato (*Solanum tuberosum* L. W729R), a C3 plant, were subjected to various irradiances (400-700 nm), CO2 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 neinstein·cm⁻²·sec⁻¹ (about ½ of full sunlight). Also, there was a proportional hyperbolic increase in transpiration and photosynthesis with increasing irradiance up to 85 neinstein·cm⁻²·sec⁻¹. These results contrast with many C4 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% O₂ was nearly overcome by a 2-fold increase in atmospheric levels of CO₂ (about 1,200 ng·cm⁻³). Photosynthesis at 25 C, high irradiance, 2.5% O₂, and atmospheric levels of CO₂ was about 80% of the CO₂-saturated rate, suggesting that CO₂ can be rate-limiting even without O₂ inhibition of photosynthesis. With increasing CO₂ concentration, mesophyll resistance increased 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 C3 crop, there is substantial O₂ inhibition of photosynthesis. The level of O₂ inhibition was maximum around 25 C but the percentage inhibition of photosynthesis by O₂ 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 O₂ 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, CO₂ 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 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 C3 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 O₂ inhibition of photosynthesis in potatoes and the effect of irradiance, CO₂ concentration, and temperature on photosynthesis, O₂ 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 neinstein·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 CO₂ 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 cm³ 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 CO₂ 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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2 Department of Horticulture.
3 Department of soil Science.
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 N₂, O₂ and 1% CO₂ in N₂ 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·CO₂ concentration with either 21% or 2.5% O₂ under an incident irradiance of 150 neinstems·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 CO₂ 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 O₂ electrode was incorporated into the system for measurement of O₂ concentration. Oxygen concentration in the air, taken as 21%, was used along with N₂ 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 (rₛ), stomata (rₛ) and mesophyll (rₘ)⁴ were determined by the method of Gastra (12) except the CO₂ concentration at the chloroplast was assumed to be the CO₂ compensation point since potato is a C₃ species with photosynthesis. 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 CO₂ 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 CO₂ 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 rₛ, CO₂ and rₘ, CO₂, respectively. The level of O₂ inhibition was determined as the difference between true (photosynthesis at 2.5% O₂) and net photosynthesis (photosynthesis at 21% O₂). Percentage inhibition of photosynthesis by 21% O₂ was defined as (O₂ inhibition of photosynthesis/true photosynthesis)·100. Water use efficiency was indicated by the ratio of total conductance (the reciprocal of resistance) of CO₂ to stomatal conductance of water vapor (rₛ, H₂O/rₛ, CO₂ + rₘ). 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 neinstems·cm⁻²·sec⁻¹, which is equivalent to about half of full sun-

⁴ In this paper, rₘ 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, CO₂ and O₂ levels.
ance. However, mesophyll resistance decreased more rapidly than stomatal resistance with increasing irradiance, as indicated by the ratio of \( r_n/r_s \), which ranged from 3.3 at 15 neinsteins·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 twice 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 \( \mu l \cdot l^{-1} \) of CO\(_2\), but increasing the CO\(_2\) level to 1,500 \( \mu l \cdot l^{-1} \) increased stomatal resistance from 2.5 to 5 sec·cm\(^{-2}\).

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 1). 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 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 CO₂ assimilation. Other temperate species with photosynthesis such as sugar beet, soybean, wheat, barley, and orchard grass 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 1). 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% O₂ relative to 21% O₂. These results agree with those 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 O₂ 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 O₂ inhibition occurred about 10 to 15 °C higher than that for maximal net photosynthesis. Based on available data, it is difficult to conclude that O₂ 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, CO₂ compensation point, or O₂ inhibition of net photosynthesis with increasing temperature may be due in part to a change in the kinetic properties of RuDP carboxylase-oxygenase. However, O₂ 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 O₂ inhibition of photosynthesis (Fig. 6).

Unlike the level of O₂ inhibition of photosynthesis, percentage inhibition of photosynthesis by O₂ 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 O₂ 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 CO₂ level ranged from 30 to 45 ng CO₂ 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 C₄ 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 shown that after tuberization, ¹⁴CO₂ assimilation in potato leaves increased two to three times and this was accompanied by an increase in the amount of ¹⁴C 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 CO₂ concentration or decreasing O₂ level down to 2.5% (Fig. 3). These results therefore fit a current theory on the mechanism of O₂ inhibition of photosynthesis that O₂ competes for ribulose 1,5-diphosphate carboxylase at the same site as CO₂ (5, 26). However, photosynthesis was still increased by further increasing CO₂ above atmospheric levels even under conditions where O₂ inhibition was suppressed (Fig. 3). Potatoes are very productive but we have found that there is a large
inhibition of photosynthesis by O₂ over a wide temperature range and a low rate of photosynthesis at high temperatures. It might be possible to increase production further by repressing O₂ inhibition. In 1918 Cummings and Jones (10) found a 2-fold increase in vegetative and tuber growth in potatoes with CO₂ enrichment above atmospheric levels.

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LITERATURE CITED

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