

SOME PHOTOSYNTHETIC CHARACTERISTICS OF CITRUS LEAVES

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[Manuscript received March 26, 1968]

Summary

Photosynthesis and respiration were measured in the laboratory with an infrared gas analyser using attached leaves of well-established orange and lemon trees growing in pots. Under optimum conditions the photosynthetic activity of mature leaves reached 10–12 mg CO₂/hr/dm².

At the saturating light intensity of 2500 f.c. photosynthesis was linear with respect to CO₂ concentration up to 300 p.p.m., with an intersection point on the abscissa between 20 and 30 p.p.m. CO₂. The minimum intercellular CO₂ concentration (Γ) was found to be of the same order.

The effect of temperature on net photosynthesis was measured on well-watered plants at a saturating light intensity and normal atmospheric CO₂ concentration. In air dried over calcium chloride a sharp optimum occurred between 15 and 20°C. However, in air with a relative humidity $\geq 80\%$ the sharp optimum was eliminated and net photosynthesis remained unchanged up to 30°C with little reduction at 35°C. Cyclic oscillations in photosynthesis and transpiration occurred when the leaf was exposed to a desiccating environment. This phenomenon is discussed in relation to stomatal control of gas exchange and the mesophyll resistance of the leaf.

I. INTRODUCTION

Although citrus species are widely distributed and used extensively in horticulture, their general photosynthetic characteristics have not been described in detail. The present work was undertaken to provide some information on the effect of light intensity, CO₂ concentration, temperature, and relative humidity on the photosynthetic activity of orange and lemon leaves.

II. MATERIALS AND METHODS

Well-established rooted cuttings of orange, *Citrus sinensis* (L.) cv. Washington Navel and Valencia, and lemon, *Citrus limonum* (L.) cv. Frost Eureka, grown in the glasshouse were used in the experiments.

In some cases comparisons were made with Valencia scion material grafted on to *Poncirus trifoliata* rootstocks and grown out-of-doors. Unless otherwise stated, the experimental data will refer to fully expanded but unhardened leaves (i.e. leaves not extensively suberized and still soft in texture) on glasshouse-grown plants.

Photosynthesis and respiration were measured in the laboratory on single attached leaves with the aid of a Hartmann and Braun infrared gas analyser. Dark respiration was measured in a stream of CO₂-free air, while normal air was used in estimating photosynthesis. The leaves were

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enclosed in a circular cuvette (15 cm internal diameter) with double-walled brass sides and base and double-walled glass lid similar to that described by Hardwick, Lumb, and Woolhouse (1966). The air inside the cuvette was stirred with an electrically driven fan (shaded pole 240 V a.c. motor). Air temperature inside the cuvette could be regulated from 5 to 50 (± 0.1)°C or higher by circulating water between the double walls from a thermostatically controlled water-bath. Air and leaf temperatures were measured with a pair of thermistors (STC type F/23), one of which pressed against the lower surface of the enclosed leaf. Air temperature was recorded on the underside of the leaf.

Light was provided by a combination of mercury vapour (HPLR, 400 W) and incandescent (internal reflector, 300 W) lamps. The light source was mounted above a heat filter (a 2-cm depth of distilled water) which substantially removed the infrared component. The whole assembly could be hydraulically raised or lowered to vary the intensity incident upon the leaf.

The probe from a YSI Kettering radiometer was located inside the cuvette to measure incident radiation (expressed as ergs/sec/cm²). The unmasked sensor occupied a plane slightly below that of the leaf. This type of sensor shows a flat response to incident radiation over the wavelength range 250–3300 nm. Direct calculation from the data provided by Gaastra (1959) and confirmed by comparisons using a selenium photo-cell indicated that 40 ergs/sec/cm² were equivalent to 1 f.c.

Air was drawn from outside the laboratory and passed through two 50-gallon tanks in series to smooth out fluctuations in CO₂ concentration. Humidity sensors (PCRC-11) were placed in the air stream entering and leaving the cuvette and the increase in relative humidity yielded an estimate of leaf transpiration. Needle valves regulated the flow between 100 and 2000 c.c./min (measured on rotameters) and the air stream was dried over calcium chloride before passing into the infrared gas analyser. Flow rate was adjusted so that the total CO₂ depletion of the air passing over the photosynthesizing leaf never exceeded 50 p.p.m. A recorder (50 μ A full-scale deflection) was connected to the infrared gas analyser. In addition, the recorder provided traces of leaf and air temperature and the relative humidity of the air entering and leaving the cuvette.

For the determination of the minimum intercellular CO₂ concentration (Γ), the air stream leaving the cuvette via the infrared gas analyser was piped back to the cuvette through a sealed diaphragm pump. Flow rate in the recirculating system was adjusted to 1500 ml/min.

At the end of each experiment the outline of the leaf was traced and this area determined. Photosynthetic rates are based on the projected area of the lamina and not on the summation of upper and lower leaf surfaces as in some work.

Chlorophyll content was determined by homogenizing leaf disks with 80% acetone and measuring the optical density of a clear extract at 645–663 nm after the method of MacKinney (1941).

III. RESULTS

(a) *Effect of Light Intensity on Net Photosynthesis*

Figures 1(a) and 1(b) show the effect of light intensity on net photosynthesis for orange and lemon leaves respectively. Assimilation was measured at 20°C in air of normal atmospheric CO₂ concentration (c. 300 p.p.m.) with a relative humidity between 50 and 60%. Each trace represents a single experiment using a given leaf at the age indicated. The effect of light intensity on citrus leaf photosynthesis was studied on 16 occasions and the data of Figures 1(a) and 1(b) are completely typical.

Light intensity at which photosynthesis reached saturation was approximately 1.0×10^5 ergs/sec/cm² (2500 f.c.) which would be equivalent to between one-quarter and one-fifth the intensity of full sunlight. The light compensation point was between 100 and 200 f.c. The photosynthetic rates achieved in these particular experiments

compare with the average light-saturated rates of 10.14 ± 1.3 mg CO₂/hr/dm² for orange and 8.7 ± 0.7 mg CO₂/hr/dm² for lemon (16 determinations).

The dark respiration rate [indicated below the abscissa in Figs. 1(a) and 1(b)] was of the order of 1.0 mg CO₂/hr/dm² for both orange and lemon leaves with mean values of 0.89 ± 0.08 and 0.92 ± 0.05 mg CO₂/hr/dm² respectively for a total of 14 observations.

The above data were gained from fully expanded leaves on plants grown in the glasshouse, and, comparing them with hardened leaves on plants grown out-of-doors (Valencia orange on *P. trifoliata* stock), the light intensity required to saturate photosynthesis was the same but the assimilation rate for outdoor plants was commonly lower.

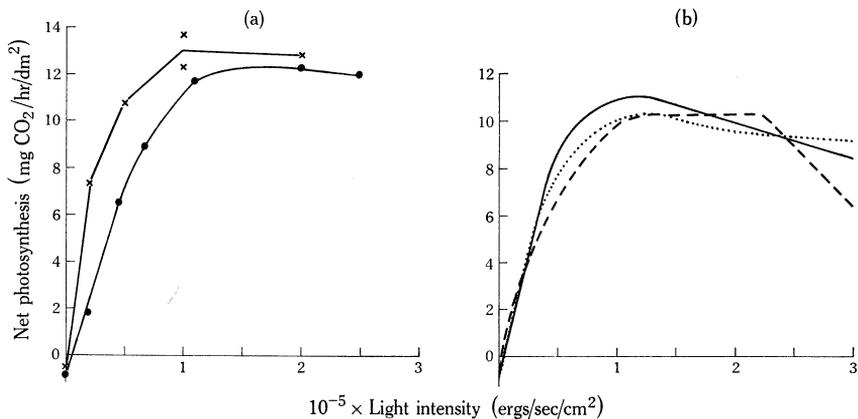


Fig. 1.—Orange leaf (a) and lemon leaf (b) photosynthesis in relation to light intensity. Light was provided from a combination of mercury vapour and incandescent lamps. Intensity incident upon the leaf was measured with a radiometer. 1.0×10^5 ergs/sec/cm² approximates to 2500 f.c. Leaf ages: (a) 2 months (×), 4 months (●); (b) 1 month (....), 4 months (—), 6 months (---).

For the glasshouse-grown lemons high light intensity was usually found to be inhibitory as indicated in Figure 1(b). This particular effect was examined further, and was found to be more pronounced if mercury vapour lamps were used in the absence of incandescent light. The reduction at high light intensity did not occur if incandescent lamps alone were used.

(b) Effect of CO₂ Concentration on Net Photosynthesis

The effect of atmospheric CO₂ concentration on citrus leaf photosynthesis was studied at a light intensity of 1.0×10^5 ergs/sec/cm² and at a leaf temperature of 20°C. The relative humidity of the incoming air stream varied between 50 and 60%. Figure 2 is based on data obtained from single leaves of orange and lemon and demonstrates a linear response of net photosynthesis to increasing CO₂ concentration up to 300 p.p.m. The point of intersection on the abscissa occurred at 24 and 22 p.p.m. for orange and lemon leaves respectively.

(c) *CO₂ Compensation Point*

Immediately upon completion of the measurements described in Section III(b), the CO₂ compensation point Γ (minimum intercellular CO₂ concentration) of the same leaves was measured in a recirculating gas stream. The leaves were undisturbed and only minor alterations were required in the circuit. Under the same conditions of light intensity and temperature, Γ for orange and lemon leaves was 60 and 65 p.p.m. respectively. The effect of temperature on Γ was measured for some other lemon leaves; in one set of experiments measurements were conducted in a gas stream

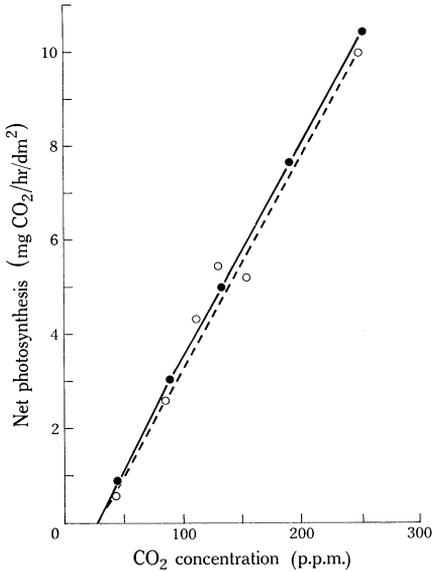


Fig. 2.—Effect of CO₂ concentration on photosynthesis in orange (●) and lemon (○) leaves at a saturating light intensity (1.0×10^5 ergs/sec/cm²).

dried over calcium chloride and recirculating at 1500 c.c./min. The light intensity was 1.1×10^5 ergs/sec/cm², and was provided by a combination of mercury vapour and incandescent lamps. The results for one leaf are shown in the following tabulation:

Leaf temperature (°C)	6	15	20	25	30	35	40
CO ₂ concentration (p.p.m.)	21	27	32	43	51	65	83

The values shown in this tabulation were maintained for 30–45 min. The temperature increase from 6 to 40°C caused a fourfold increase in Γ . Leaf turgor was maintained at the higher temperature, and humidification of the gas stream entering the cuvette had no effect on Γ at 35 or 40°C. The effect of CO₂ concentration on net photosynthesis was also examined for this same lemon leaf at 20°C and at 1.1×10^5 ergs/sec/cm². A straight-line response was obtained with an intersection point on the abscissa at 32 p.p.m. This value agrees with the value for Γ obtained previously.

Leaf water stress induced by either inadequate soil moisture or from prolonged exposure of the leaves to a desiccating atmosphere caused an appreciable

increase in the Γ values of both orange and lemon leaves. Working at 35°C, values ranging from 220 to 350 p.p.m. of carbon dioxide have been obtained for lemon. Humidifying the air stream in an attempt to restore leaf turgor at this temperature caused Γ to fall from 350 to 295 p.p.m. at the end of 45 min.

(d) *Effect of Temperature and Humidity on Net Photosynthesis*

The response of orange leaf photosynthesis to temperature is shown in Figure 3(a). Photosynthesis was measured at a light intensity known to be saturating at 20°C (1.0×10^5 ergs/sec/cm²). When the air entering the cuvette was dried over calcium chloride a sharp optimum occurred at 15°C. In humidified air (relative humidity of air entering cuvette $\geq 80\%$ at 20°C) the optimum was less well defined and was displaced upwards by about 10 degC. A similar situation existed for lemon leaves [Fig. 3(b)]. In this case the optimum temperature in dry air was 20°C whereas in moist air the optimum was less well defined and the assimilation rate showed no serious decline up to 35°C.

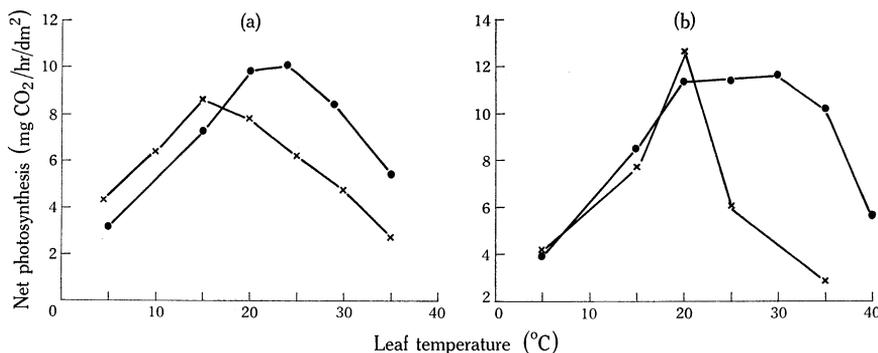


Fig. 3.—Effect of temperature on orange leaf (a) and lemon leaf (b) photosynthesis in humid (●) and in dry (×) air at a light intensity of 1.0×10^5 ergs/sec/cm².

The above data for orange and lemon leaves are taken from single experiments but this humidity effect on temperature optimum was demonstrated for the two species on a total of 16 separate occasions.

Routinely the measurements of photosynthesis at different temperatures were made on successive days for the dry and for the humidified air streams because net photosynthesis was measured for about an hour after the leaf had come to equilibrium with new experimental conditions. The temperature was initially 20°C; it was then reduced to 5°C and increased progressively. Measurements were taken at each step and the initial one was checked before proceeding to higher temperatures.

This humidity effect on photosynthesis is more accentuated in a water-stressed plant. Table 1 presents some data for a lemon plant taken from the glasshouse and left unwatered for the previous 4 days. Only the young expanding leaves on the plant gave any visual indication of stress. The data in Table 1 refer to a fully expanded leaf 17 weeks old. A temperature increase from 20 to 31°C caused a substantial reduction in photosynthesis but at 31°C an increase in humidity from 50 to

at least 85% caused a 62% increase in assimilation rate. At this same temperature and relative humidity the assimilation rate then doubled to a stable value of 5.1 mg CO₂/hr/dm² within 40 min of watering the pot to saturation.

In addition to this immediate enhancement of photosynthesis, high relative humidity also enabled photosynthesis to be sustained for longer periods under conditions where leaf desiccation would normally occur. This latter effect is demon-

TABLE I
EFFECT OF RELATIVE HUMIDITY AND REWATERING ON THE
PHOTOSYNTHETIC RATE OF LEMON LEAVES SUBJECTED TO
WATER STRESS

Photosynthesis was measured at a light intensity of 1.0×10^5 ergs/sec/cm² from a combination of mercury vapour and incandescent lamps, and at a normal atmospheric CO₂ concentration

Leaf Temperature (°C)	Relative Humidity of Air Entering Cuvette*	Leaf Photosynthesis (mg CO ₂ /hr/dm ²)
20	50—60%	6.5
31	50—60%	1.8
31	≥85%	2.9
31†	≥85%	5.1

* These data give the relative humidity of the air stream flowing over a sensor, held at 20°C, adjacent to the leaf cuvette.

† Pot rewatered 40 min previously.

strated in Figures 4(a) and 4(b) which show a section of the chart recording the humidity and CO₂ concentration of the air leaving the cuvette in two experiments on orange leaves. In Figure 4(a) measurements were conducted at 20°C, air with a CO₂ concentration of 300 p.p.m. entering the cuvette at a constant flow rate of 1 litre/min. Over the first 2 hr of the experiment the relative humidity of the air entering the cuvette was ≥85% and a stable photosynthetic rate of 8.7 mg CO₂/hr/dm² was maintained. Within an hour of supplying dry air to the cuvette the leaf had initiated cyclic oscillations in photosynthesis and transpiration. This can be seen from the traces of CO₂ concentration and relative humidity of the air leaving the cuvette. The peak rate of photosynthesis during each cycle was 10.5 mg CO₂/hr/dm².

The coincidence of peaks of assimilation and transpiration strongly suggests stomatal control of both processes. Over the course of this run (7½ hr) the transpiration:assimilation ratio steadily decreased. This can be gauged approximately by comparing the relative area under the peaks of the CO₂ concentration and relative humidity traces over each cycle of stomatal opening. This ratio changed from 5.14 at the outset of the run to 0.21 upon completion. When the experiment

was repeated the following day at 35°C [Fig. 4(b)] the ratio decreased from 16·55 to 0·89 during the run on dry air. At the end of this run photosynthesis and transpiration

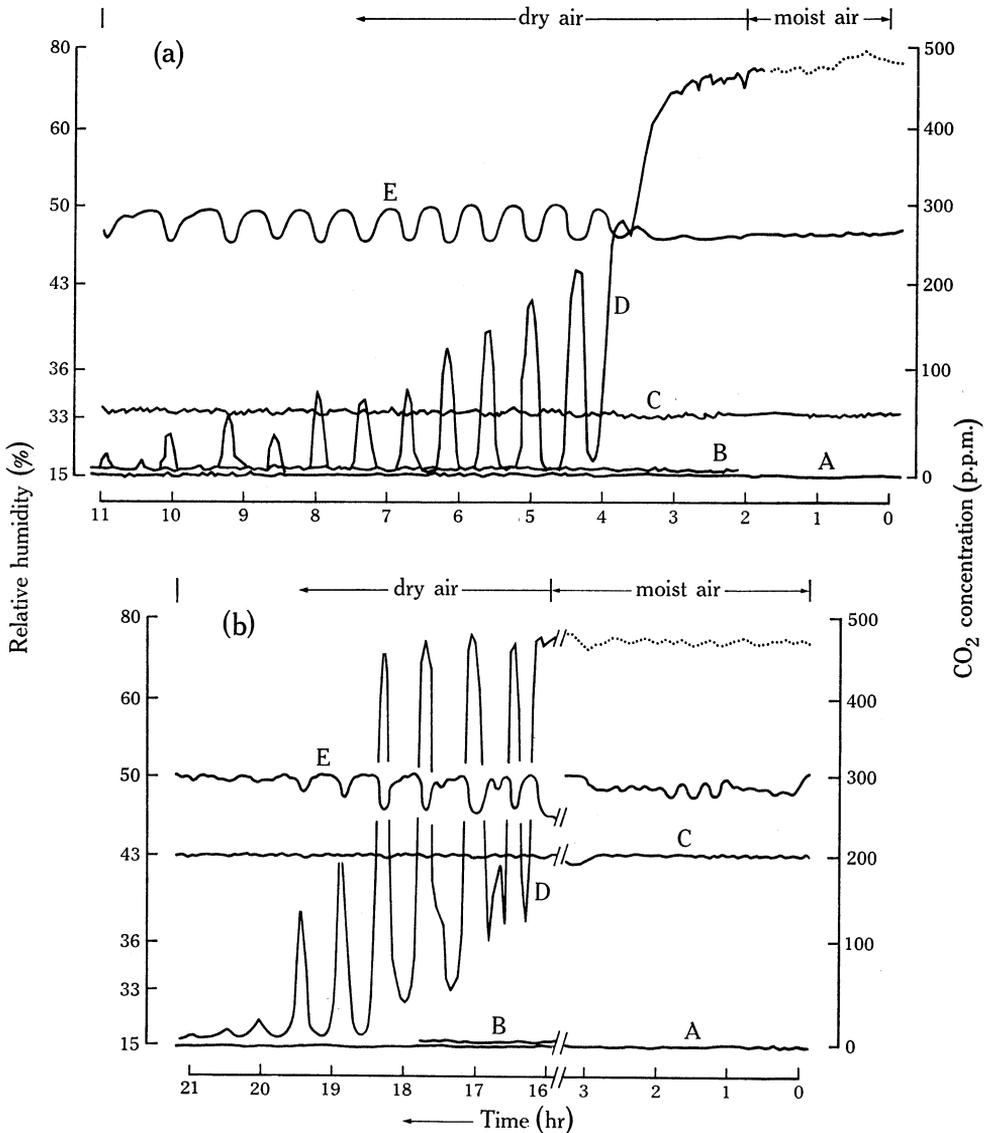


Fig. 4.—Cyclic oscillations in photosynthesis and transpiration in orange leaf at 20°C (a) and 35°C (b), in moist followed by dry air as indicated on the figures. *A*, recorder zero (the temperature probe which normally occupied this channel was not activated); *B*, zero for the humidity sensor in the dry air stream entering the cuvette; *C*, temperature recorder [set at 20°C (a) or 35°C (b)]; *D*, humidity of air leaving cuvette; *E*, CO₂ concentration of air leaving cuvette.

were barely detectable. In this second experiment the same leaf was used and the flow rate of 1 litre/min was maintained but at the higher temperature there was a reduction in photosynthesis and an accompanying increase in transpiration.

The eventual fall in assimilation rate was not necessarily due to a leaf factor *per se* because when humid air was supplied to a leaf held at 20°C, i.e. conditions which allow maintenance of leaf turgor, photosynthesis continued undiminished for 25 hr.

IV. DISCUSSION

(a) *Assimilation Rate*

Low photosynthetic capacity is a typical feature of the citrus leaves examined to date. Expressed on an area basis, mean assimilation rates at light saturation and near optimum temperature are about one-half to one-third of the rates quoted in the literature for deciduous tree species such as apple (Heinicke 1966; Kozlowski and Keller 1966). Our own work has confirmed this order of difference.

The mean photosynthetic activity of orange leaves, expressed as assimilation number (mg CO₂ fixed/mg chlorophyll/hr), was 3.64, with a minimum of 1.87 for some mature leaves on a potted plant grown out-of-doors. Lemon leaves gave an average assimilation number of 2.87 for fully expanded, unhardened, glasshouse-grown leaves, with a maximum of 5.53 for some immature pale-green leaves. By contrast Hill and Wittingham (1955) give a value of 14.0 for sunflower. In the present work, vine leaves (Sultana) and apple leaves (Granny Smith seedlings) from a fully exposed situation have achieved assimilation numbers of 6.44 and 6.82 respectively, while corn grown in the glasshouse yielded a value of 11.60.

(b) *CO₂ Compensation Point*

Assuming that Γ gives a relevant index of internal CO₂ concentration, the CO₂ compensation point for well-hydrated citrus leaves suggests that the gradient from the outside of the leaf to the sites of fixation compares favourably with most other mesophytes. The tropical grasses must be regarded as exceptions because they have $\Gamma = 0$ (Meidner 1962; and confirmed in the present work for maize using the same conditions as those for citrus).

In citrus, Γ increased sharply with leaf desiccation and sometimes reached values in excess of normal atmospheric CO₂ concentration. Arid conditions would therefore be unfavourable to net photosynthesis as verified by the experimental data presented here. By analogy Heath and Orchard (1957) report an increase in Γ in onion leaf of 225 p.p.m. (from 20 to 245 p.p.m.) when the temperature was increased from 10 to 35°C.

(c) *Temperature and Humidity Effects on Photosynthesis*

Although citrus thrives in a hot, dry environment under irrigation, leaf photosynthesis has a low-temperature optimum. Admittedly, though, the environmental factors which promote maximum leaf photosynthesis do not necessarily favour the production of quality fruit, and this latter requirement is the determining one for commercial production. The low-temperature optimum of citrus leaf photosynthesis does, however, provide a corollary for the work of El-Sharkawy and Hesketh (1964) who provided evidence that leaves with the highest photosynthetic rates also have the highest temperature optimum. Temperature effects on

photosynthesis appear to be variable. Bierhuizen and Slatyer (1964) showed no significant temperature effect on cotton when temperatures were increased from 30 to 40°C, and Waldron, Glasziou, and Bull (1967) obtained a temperature coefficient of 1.1 between 8 and 30°C for sugar-cane. Other reports in the literature (Mitchell 1936; Went 1950; Pharis and Woods 1960; Ormrod 1961; Warren Wilson 1966) do give optimum temperatures for photosynthesis of approximately 20°C. The sharp decrease in citrus photosynthesis at higher temperatures in dry air cannot be readily attributed to increased respiration. In the present case dark respiration increased almost linearly with temperature from 20 to 35°C (temperature coefficient = 2.0) but this increase could not possibly account quantitatively for the decrease in net photosynthesis above 20°C in dry air.

The sensitivity of citrus leaf photosynthesis to temperature is substantially altered by the relative humidity level. This effect was encountered fortuitously during an attempt to rehydrate a lemon leaf which had stopped transpiring at high temperature. The data from experiments of Thompson, Stolzy, and Taylor (1965) subsequently became available with some comparable observations on rough lemon leaves.

(d) Resistances to Gaseous Diffusion

Short-term effects of humidity, where an increase in relative humidity of the air stream has enhanced photosynthesis, especially at high temperature and in water-stressed plants (reported here and also by Thompson, Stolzy, and Taylor 1965), could be interpreted as a reduced mesophyll resistance to CO₂ diffusion such as that described by Gaastra (1962). While it is difficult to distinguish between stomatal and mesophyll resistance to diffusion, the data of Figures 4(a) and 4(b) provide evidence of stomatal control and also of a high mesophyll resistance to CO₂ diffusion. The decreased humidity elicited a rhythmic opening and closing of the stomata with associated effects on transpiration and photosynthesis. These cyclic oscillations in photosynthesis and transpiration would require a common response by approximately 3 million stomata (stomatal density 60,000/cm²; see Reed and Hirano 1931) for the leaf in question.

An analysis of this situation, using the same approach as that of Slatyer and Bierhuizen (1964), points to a high mesophyll resistance to CO₂ diffusion. Transpiration is expressed as

$$T = c/(r_a + r_l),$$

where T = total flux, c is the difference in water vapour concentration at the evaporating sites and in the free air, r_a is the external resistance to diffusion, and r_l is the diffusion resistance within the leaf. Photosynthesis is then expressed as

$$P = c'/(r'_a + r'_l + r'_m),$$

where c' is the CO₂ concentration difference between the chloroplasts and the free air, $(r'_a + r'_l + r'_m)$ is the total resistance to CO₂ transfer, and r'_m is the resistance to CO₂ transfer through the mesophyll cells to the chloroplasts. Depending on its magnitude, r'_m (the mesophyll resistance) will govern the relative extent of stomatal

control of transpiration and photosynthesis. If r'_m is small and does not represent a significant resistance to CO_2 diffusion, then r'_l would control photosynthesis and would have commensurate effects on both photosynthesis and transpiration. If, however, r'_m is large, then changes in stomatal diffusion resistance (included in r_l and r'_l) will have a more profound effect on transpiration than on photosynthesis. This situation existed in the data shown in Figures 4(a) and 4(b). In this case the ratio of transpiration over photosynthesis decreased steadily during the exposure of the leaves to dry air. Presumably r'_l became larger during successive cycles of stomatal opening and closure and, since CO_2 diffusion was dominated by the large r'_m , the effect of dehydration was to cause a relatively greater reduction in transpiration than in photosynthesis. Barrs and Klepper (1967), using leaves of cotton and pepper plants, have reported similar oscillations of photosynthesis and transpiration. They also described related oscillations in the turgidity of the cotton leaf which take it from a flaccid to an erect state over the course of a single cycle. The citrus leaves examined in the present work did not show this latter characteristic.

V. ACKNOWLEDGMENTS

Thanks are due to Dr. J. V. Possingham, Mr. D. McE. Alexander, and Mr. D. H. Maggs for their criticism of the manuscript. Grateful acknowledgment is also made to Mrs. E. Törökfalvy for expert technical assistance.

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