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A NEW METHOD FOR CONTROLLING LEAF TEMPERATURES IN ASSIMILATION CHAMBERS USED FOR THE MEASUREMENT OF GAS EXCHANGE PHENOMENA

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I. INTRODUCTION

Leaf temperature in an assimilation chamber is usually measured with thermocouples. PIETERS and SCHURER (1973) demonstrated, that under certain conditions considerable systematic measurement errors occur in the determination of leaf temperature with thermocouples. Such conditions may be present in an assimilation chamber and may result in distortion of the relation between the measured rates of temperature dependent processes like photosynthesis at saturating CO_2 content, transpiration, light and dark respiration and heat exchange rates and the measured values of light intensity and temperature (PIETERS 1972, SLATYER 1971).

The assimilation chamber used in our equipment is made of an aluminium frame with double glass windows on both sides. The inside of the chamber measures 100 × 95 × 12 mm^3. One of the double windows can be taken off to give access to the interior of the chamber. The space between each pair of glass windows is part of a cooling circuit. The removable part has in some experiments been replaced by a loose frame, closed with a thin polyethylene film (lupolene H) to accomodate infrared thermometry. The leaf is held in place in the middle of the assimilation chamber by thin nylon wiring. The petiole can be laid through a slot in the aluminium frame. Thermocouples can be put into the assimilation chamber through small holes in one of its sides. The slot with the petiole and the small holes were closed with plastic paste. The air inlet and outlet each consist of twenty short steel capillaries glued into a wide pipe with a length equal to the width of the assimilation chamber.

The control of leaf temperature is often achieved by adapting the temperature of the cooling liquid pumped through the double wall of the assimilation chamber to the ligth intensity incident on the leaf. It is, however, the difference in temperature between the double wall and the leaf, which is the basis of the systematic errors in the measurement of temperature with thermocouples. In principle, the adjustment of the temperature of the cooling liquid can be achieved automatically with some sort of controller, fed by the signal of some detector of leaf temperature. The adjustment of the temperature of the cooling fluid however, is a slow process in relation to the rate of temperature changes in the leaf. Therefore, rather large oscillations in temperature may occur, so that hand operated control, although boring, gives better results.

Therefore, a control system is designed, based on infrared radiation, so that the diminution of the intensity of visible light is compensated by an increment of infrared radiation or vice versa. In this way a fast adjustment of leaf temperature is assured and the irradiation load on the leaf kept constant, which results in keeping constant the error of the thermocouple measurement of temperature. Hence, temperature is constant, although the absolute temperature is not exactly known. The drawback of not knowing the absolute temperature can be overcome by choosing another temperature detector instead of the thermocouple, e.g. a (rapid) infrared thermometer. But infrared thermometry in assimilation chambers is a rather complicated matter, which sets its own limits to the accuracy of the measurement.

II. SOME THEORETICAL CONSIDERATIONS CONCERNING INFRARED TEMPERATURE COMPENSATION

a. *General*

Application of infrared radiation for control of leaf temperatures in the assimilation chamber poses physiological and technological problems. For control of leaf temperature with infrared radiation, four components are needed:

1. A temperature measuring device with the required speed; convenient detectors are thermocouples, thermistors and a number of infrared thermometers;
2. A controller, reading the output of the detector and aiming at keeping this output at a constant value by regulating the intensity of the infrared source; this control can be done by hand with the help of a variable voltage source, like an autotransformer, or automatically with an on-off, or better, with a PID-regulated voltage source;
3. An infrared source, the intensity of which can be regulated quickly and easily by varying its feeding voltage; this infrared source must deliver a sufficient amount of energy in the desired wavelength region in an optically homogeneous beam. To this purpose, an incandescent source seems to be most suitable; a slide projector from which the heat filter has been removed is a practical solution;
4. A cooling system, which keeps the temperature of the leaf down to the desired level.

b. *Interactions between infrared radiation and the photosynthetic apparatus of the leaf*

Using a projector as a radiation source, a wavelength region has to be chosen, suitable for heating the leaf, while avoiding direct light effects on the photosynthetic apparatus. So, the beam may not contain light energy which activates systems I or II of the photosynthetic apparatus of the leaf and thus would give rise to a certain amount of photosynthesis or Emerson effects. From a physiological viewpoint it seems safe to choose a wave length of 0.78 nm as the lower limit of the infrared radiation.

c. *Interactions between infrared radiation and temperature detection*

When the infrared source emits radiation in a wavelength region for which the thermometer is sensitive, and this radiation reaches the temperature detector, the temperature measurement will be disturbed. This applies both to thermometers which operate by contact and to those operating by radiation.

To diminish the effect of infrared radiation on temperature measurement, it is necessary to prevent this radiation from reaching the detector. In the case of radiation thermometers this may be attempted by placing the detector on the same side of the assimilation chamber as the infrared source, so that only reflected radiation has to be taken into account as a disturbing factor. Alternatively the detector may be placed opposite the source and the harmful radiation may be removed by absorption or interference filters (inclusive the leaf itself).

Often, for reasons of space, it is impossible or very complicated to place both the detector and the infrared source on the same side of the assimilation chamber. Therefore, only the case in which they are placed opposite to each other will be considered here, which means that the choice of the wavelength region used for infrared radiation is essential with respect to the accuracy of the temperature measurement.

The wavelength region of sensitivity of infrared thermometers is between 2.0–30 nm, dependent on the type used. Under the infrared thermometers, tried by the author, the 'Stoutjesdijk' radiometer (STOUTJESDIJK, 1966) works in the region from 2.8–30 nm, commercially available thermal image cameras in the region of 2–5.5 nm and a number of infrared point thermometers in the region of 8–13 nm.

When using glass windows in the assimilation chamber, the upper limit of transmitted radiation is around 2.8 nm. Thus, with infrared point thermometers, provided they satisfy the manufacturers specifications, no excessive troubles are to be expected from transmitted radiation. Working with the thermal image camera, it was observed that the small amount of infrared radiation between 2.0–2.8 nm, transmitted by the leaf and the assimilation chamber assembly could disturb the thermal image. In this case it is advisable to ask for a cut-on filter at 3.5 nm placed in the camera. At the cost of some loss of sensitivity of the thermal image camera (± 22%), a more reliable thermal picture can then be expected.

With the 'Stoutjesdijk' pyrometer, matters are somewhat more complicated. This instrument is based on the measurement of the difference between the amount of radiation of 0.5–2.8 nm + infrared radiation of 2.8–30 nm of the object and of radiation (transmitted by a movable glass window) + infrared radiation of this glass window of known temperature. The speed of the instrument is low, about 20 sec. for a full measurement. This is a disadvantage for the purpose of controlling leaf temperature. Furthermore, it is very sensitive to infrared radiation transmitted by the leaf. Thus, changes in the radiation from 0.5–2.8 nm also cause signals which ususally will be large compared with the signal due to the heat emission of the leaf. When such oscillations in the radiation occur within a time of the same order of magnitude as the time needed for a measurement, the accuracy of the temperature measurement is greatly impaired (see fig. **5**).

The thermocouple senses radiation also (Idle 1968, Perrier 1968). Table I gives some figures about temperature changes of a thermocouple in the assimilation chamber, under direct illumination or irradiation via a leaf, placed in or in front of the assimilation chamber, with or without recirculation of the air of the assimilation chamber. The linear air velocity in the assimilation chamber was 30 cm/sec or 2 cm/sec. It appears from the figures, that it is not easy to quantitatively interpret the temperature readings of the freehanging thermocouple: it is natural that the heat balance of the thermocouple should be strongly changed by air velocity, but also by the presence of a leaf in the assimilation chamber, even if the thermocouple does not touch the leaf surface. It is, however, not the heat balance itself which is of interest here, but the question whether the radiation sensed by the thermocouples causes errors in the temperature readings. The conclusion may be that in the visible region the direct irradiation error is negligible when the thermocouple is placed behind the leaf, especially when air velocity is high; in the infrared region, however, a measurable error is left. This is in agreement with the known optical properties of the leaf as shown in fig. 1, where between 780 nm and 1200 nm about 45% of the radiation is transmitted. In section IV an example of this error will be discussed.

Table I. The temperature increase in degree Celsius of a thermocouple, freehanging in the middle of the assimilation chamber, under the influence of irradiation with white light or infrared, directly or via the leaf, and of linear air velocity.

Leaf in or in front of assimilation chamber		Irradiation with		Linear air velocity	
in	in front of	white	infrared	30 cm/sec	2 cm/sec
–	–	2.0	3.5		+
–	–	0.7	1.0	+	
	+	0.0	0.5	+	
	+	0.2	1.5		+
+		2.7	3.5		+
+		0.9	2.3	+	

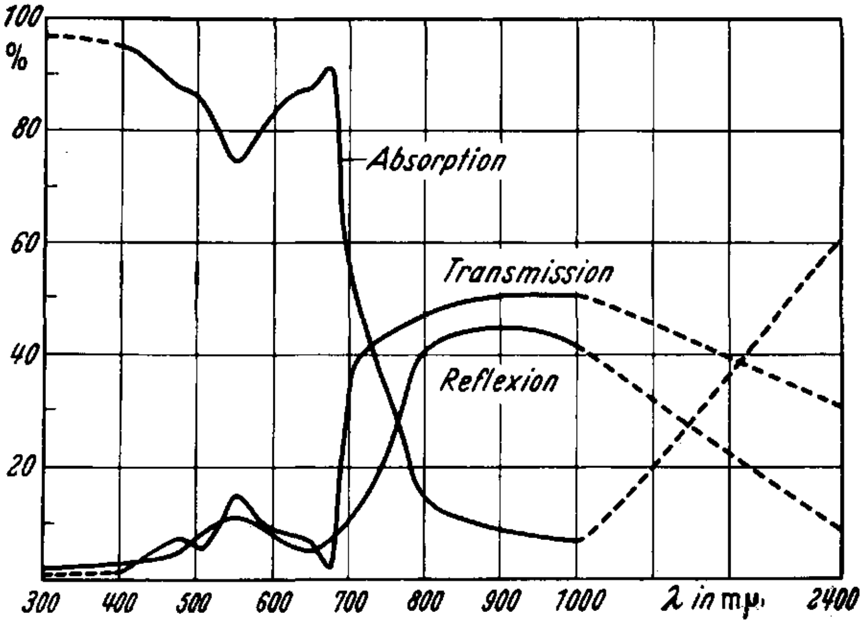

FIG. 1. Percentage of irradiation reflected, transmitted and absorbed by a green leaf in relation to wavelength. (After Walter Tranquillini, Handbuch der Pflanzenphysiologie, W. Ruhland ed., Springer Verlag V/2, 1960)

d. *The choice of the wavelength region of infrared radiation for supplying additional heat to the leaf*

From what has been said in the preceeding sections, it may be concluded that for physiological reasons 0.78 nm can be taken, as a lower limit of wavelength for the infrared radiation supplying additional heat to the leaf. However, this radiation inevitably interferes with temperature measurement by thermocouples or by the 'Stoutjesdijk' radiometer, so that these instruments should be used with due precautions. If the upper limit is chosen at 2.8 nm, which is easily realised by using glass windows in the assimilation chamber, then the thermal image camera can also be used for the temperature measurement.

e. *The cooling system*

Considering the cooling of the leaf in the assimilation chamber, two ways seem possible: either the leaf can be cooled indirectly by passing a cooling medium through the double walls of the assimilation chamber or directly by blowing air with controlled temperature with considerable linear velocity through the assimilation chamber. On the basis of heat exchange calculations, the desired linear air velocity has been estimated to be about 1000 cm/sec, but there are reasons to believe that a velocity of 250 cm/sec is sufficient in most cases. To keep measurable differences in the gas concentrations, a halfclosed recirculation system (PIETERS 1971) may be recommended. Until now it has not been tried to solve the technical problems involved in high velocity, low volume pumping in the assimilation chamber. The author works with a combination of both systems and is reasonably satisfied with a halfclosed recirculation system with a linear air velocity of 30 cm/sec, with extra cooling of the air in the recirculation system and additional cooling via the double wall of the assimilation chamber (see fig. 2).

f. *Infrared transmitting cooling liquid*

In order to apply the infrared thermometry, one of the walls of the assimilation chamber must be constructed of material, which is highly transmissive for the direct heat emission of the leaf in the region of sensitivity of the infrared thermometer. When this condition is not fulfilled, serious difficulties arise in the calculation of leaf temperature. Polyethylene film of 0.04 mm (Lupolene H) transmits at least 90% of the infrared radiation and seems a reasonable solution of the problem. Hence, only one of the double walls is left for additional cooling. Radiation between 0.4 and 2.8 nm must be transmitted by this double wall and the cooling liquid, so that water is not suitable. Tetrachloromethane which readily transmits infrared radiation, has been chosen as the cooling medium.

III. PRACTICAL REALISATION

a. *General*

Fig. 2 gives a schematic picture of the entire installation. Fig. 2 III shows how the projectors of visible light (P1) and of infrared radiation (P2) are placed in respect to the leaf (8) in the assimilation chamber (A). The projectors are used without front lenses. This has the advantage that a larger part of the emitted radiation reaches the assimilation chamber, but the disadvantage that the light distribution is less homogeneous than when a complete optical system is used. Also the oblique position with respect to the assimilation chamber of the projectors of visible radiation is not fully satisfying.

The manual regulation of the intensity of visible light proceeds via an electronic A.C. stabilizer (S) and an autotransformer (T). The automatic regulation of infrared radiation via the thermocouple (7), measuring the temperature of the leaf (8), a controller (C) and the regulated voltage (V). The measured temperature is recorded (R). The infrared transmitting polyethylene film (Lupolene H) is held in place by the removable lid of the assimilation chamber (6).

Fig. 2 I and 2 II show the pumping circuits of the cooling fluid (tetra) and of the recirculated air respectively. The cooled tetra is pumped by a teflon membrane pump (L) through the heat exchanger for cooling the recirculated air (H2), through the double wall of the assimilation chamber (9) to the refrigerator and heat exchanger (CU + H1). The air is circulated through the manifolds (16) through the assimilation chamber by the membrane pump (G), after the pumping heat being removed in the heat exchanger (H2). The primary airstream enters and leaves the assimilation chamber via the narrow, perforated tubes (15).

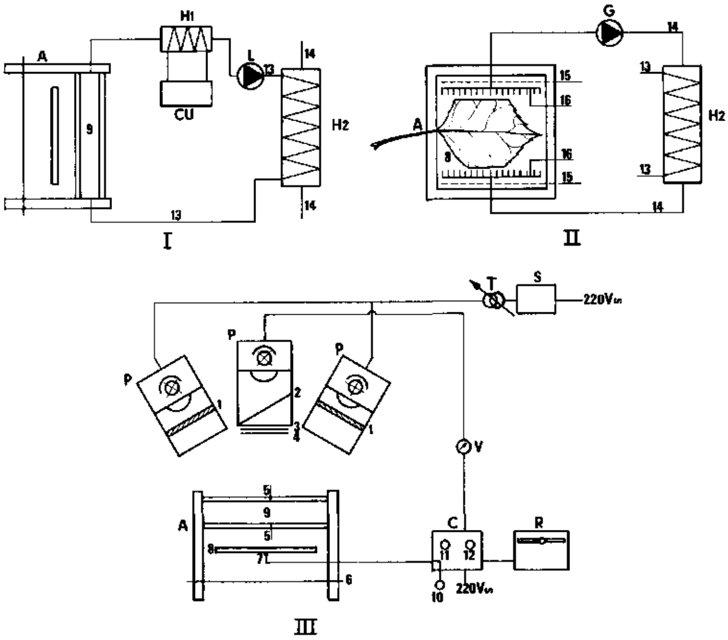

FIG. 2. Scheme of the installation for the infrared temperature compensation system. I. Pumping circuit of tetra, II. Pumping circuit of recirculated air, III. Irradiation of the assimilation chamber and electronic control unit. A = assimilation chamber, CU = alcohol cooling machine, H_1 = heat exchanger for the temperature regulation of the tetra, H_2 = heat exchanger for cooling the recirculating air, L = tetra pump, G = air recirculation pump, S = A. C. electronic voltage stabilizer, T = autotransformer, R = recorder, C = electronic controller of the infrared temperature compensation system, V = voltmeter of the regulated output, P = projector.

1. projector visible radiation with heatfilter, 2. projector infrared irradiation with cold light mirror (45°), 3. RG 8, 4. RG 780, 5. glass window, 6. infrared transmitting polyethylene film (lupolene H), 7. measuring junction of thermocouple, 8. leaf, 9. double wall assimilation chamber, 10. reference junction thermocouple in melting ice, 11. knob sensitivity of the amplifier, 12. knob electronic reference temperature, 13. pumping circuit tetra, 14. pumping circuit of recirculated air, 15. entrance and exit of direct main flow of air through assimilation chamber, 16. entrance and exit manifolds of recirculated air.

b. *Temperature detector and controller*

A thermocouple (7) was used as a detector with a controller (C) designed by the Technical and Physical Engineering Research Centre at Wageningen. Nowadays several controllers are commercially available which are adapted to the use of thermocouples. The controller used had a bandwidth of 0.5 °C if the regulated output varies between 0 and 220 V. The reference junction of the thermocouple is placed in melting ice (10). Any temperature between 9° and 36 °C can be chosen (12) and is held constant within 0.2 °C.

c. *Infrared source*

A Leitz Prado 500 projector is used without heat filter and front lens as a radiation source (P2). The visible part of the radiation has to be removed. To this end a cold light mirror (7.5 × 7.5 cm^2, Balzers n° 93, 45°) was put in the place of the removed heat filter at an angle of 45° to the axis of the light bundle (2). In this way, a large portion of the visible radiation was deflected from the bundle needed for heating the leaf. In front of the projector, two Schott filters RG 8 (3) and RG 780 (4) were placed without additional cooling. The heat load on these filters is acceptable. Instead of the RG 780, a saturated solution of iodine in tetrachloromethane in a glass box of 2 cm width may also be used.

d. *Tetrachloromethane as a cooling medium*

The tetrachloromethane (fig. 2 I), used as a cooling medium, must be temperature regulated, and pumped through the double wall of the assimilation chamber. When designing the thermostatic bath and circulation system, it had to be kept in mind that no material which will be attacked by this solvent can be used, that direct heating of the tetra had to be avoided, and that the vapour is poisonous. Therefore, heating and cooling are performed via heat exchangers with hot water and cold ethanol. A narrow tube connects the gasphase of the thermostat and the outer atmosphere. The circulation pump (L) is a membrane pump, made of teflon (Asti circulation pump). For the connections (13), copper tubing and brass fittings are used. The glass windows (5) in the assimilation chamber are glued onto the aluminium frame of the assimilation chamber with Araldit AV 129 from Ciba, Switzerland. This epoxy resin has proved to be resistent to tetra.

IV. SOME EXPERIENCES WITH THE INFRARED TEMPERATURE CONTROL OF THE LEAF IN THE ASSIMILATION CHAMBER

Representative examples of photosynthesis – light curves of leaves of corn and poplar in air enriched with CO_2 to 0.5% and measured with application of the automatic temperature control, is given in fig. 3. For a description of the apparatus used for the measurement of photosynthesis, the reader may be referred to PIETERS 1971. In both cases light saturation is reached to a large extent. In literature examples may be found, where the photosynthesis – light curves at CO_2 saturation do not reach the light saturation level (GAASTRA, 1959). It is not improbable that also in these cases, this is due to light dependent temperature errors in the measurement with thermocouples.

It is known that light saturation of the photosynthetic apparatus of corn leaves is difficult to atttain, even in normal air (HESKETH, 1967). This may be explained by the fact that the photosynthetic apparatus of corn may be CO_2-saturated already at CO_2 concentrations lower than 0.03% and thus may reveal temperature dependency (PIETERS, unpublished). Still, fig. 3 demonstrates that, even at the high intensities used, no full light saturation seems to be reached.

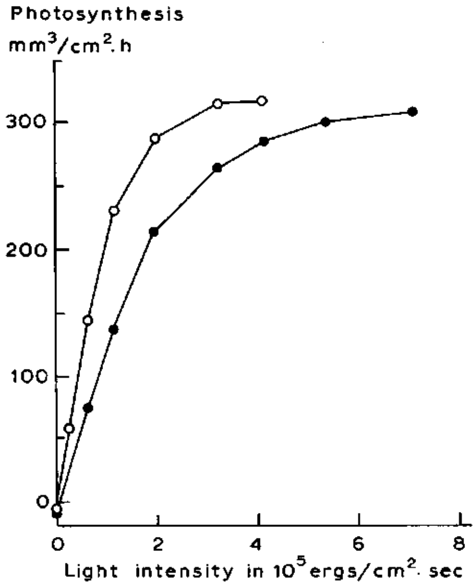

FIG. 3. Photosynthesis versus light curves at saturating CO_2 concentration in the ambient air, showing a high degree of light saturation of a attached leaf disk of *Populus euramericana* 'robusta' (○) and a detached leaf disk of *Zea mays* (●). Temperature control with the infrared temperature compensation system.

At least two factors are responsible for this phenomenon:

1°. The band width of the controller, and

2°. an appreciable sensivity of the thermocouple for the infrared radiation transmitted by the leaf.

The former factor (1°) is bound to the feedback mechanism in general and can be improved by increasing the amplification of the signal of the thermocouple fed to the controller, for which, however, a limit is set by the signal noise ratio and the stability of the system. Moreover, correction of the recorded temperature error may be applied by changing the reference voltage of the controller by hand.

The second factor (2°) implies that the thermocouple absorbs more energy from the infrared radiation than from the visible radiation. The higher the infrared radiation is, the larger positive temperature error of the thermocouple will result. Since the temperature of the junction is controlled, the leaf will be lowered to an extent related to the amount of infrared radiation, given to the leaf. This property of thermocouples may be demonstrated when for the control of leaf temperature, infrared thermometers which are insensitive for the infrared radiation are used instead, as e.g. the PRT4, Barnes Engineering. Then, photosynthesis remains constant in the region of light saturation while at the same time the temperature readings of the thermocouples increase, or vice versa (table II). This positive error of the thermocouple works out to be a negative error in leaf temperature, which is added to the negative one already present.

TABLE II. Control of leaf temperature with a thermocouple and with the infrared point thermometer PRT 4 in comparison to the leaf temperature measured with the PRT 4 and a thermocouple respectively, to show the influence of the infrared compensation on the temperature measurement with the thermocouple.

Visible irradiation as % of the maximum (max. = 700000 erg.cm^{-2}.sec^{-1})	Leaf temperature measured with		Control with	Photosynthesis in % of maximum rate
	Thermo.c.	PRT4		
100	19.3	21.0	PRT4	100
80	19.6	21.0		99
59	19.8	21.0		98
38	20.2	21.0		90
19	20.3	21.0		50
0	20.6	21.0		0
100	15.9	18.2	Therm.c.	100
80	15.9	18.0		98
59	15.9	17.8		92
38	15.9	17.6		82
19	15.9	17.3		55
0	15.9	17.3		0

Irradiation of the leaf in the assimilation chamber gives rise to the development of a temperature gradient over the leaf in the direction of the airstream. With the thermal image camera, this gradient was estimated to be about 2.5 °C/10 cm at the highest illumination level and a flow rate of 30 cm/sec. Still, the magnitude and form of this gradient is not exactly known because of technical and methodological difficulties encountered with the use of an instrument of that type in determining leaf temperatures in assimilation chambers. Knowledge of the magnitude and form of the gradient is of importance for the calculation of the average leaf temperature. It will be clear that with the automatic temperature control described here, the mean temperature of the leaf depends on where the thermocouple is placed in the temperature gradient over the leaf. When placing the thermocouple near the air entrance, photosynthesis was found 20% higher than when placing it near the exit because of the differences thus introduced in the actual leaf temperature. Assuming a Q_{10} of 2.2 this means a temperature difference of 2.3 °C. This effect has to be taken into consideration when comparing individual leaves. An additional feature of infrared temperature compensation is, that within one individual measurement not only temperature is constant, but also the temperature gradient.

Study of fast phenomena of gas exchange like induction effects, is only possible by using a quick system of temperature control, since only then will an abrupt change in illumination have no consequences for mean leaf temperature. Fig. 4a shows the constancy of the temperature with the

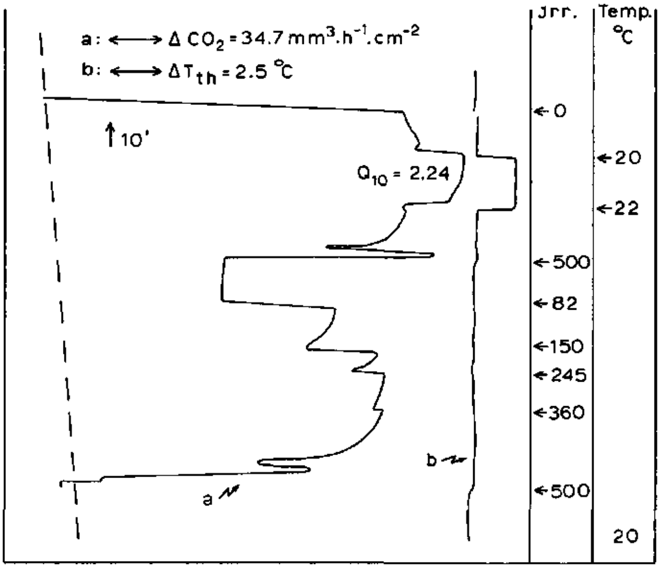

FIG. 4a. Part of a registrogram, showing the rate of photosynthesis of a leaf of *Populus euramericana* 'robusta' and the infrared temperature compensation. The thermocouple temperature is practically constant at all irradiation levels. The effect of the bandwidth of the PID-controller is shown at the change from 0 to 500 × 10³ erg/cm²sec (or vice versa). Some induction effects of the photosynthetic apparatus are shown. A practically immediate temperature change is shown to be possible and the effect on photosynthesis demonstrated. Dashed line is the baseline of the katharometer.

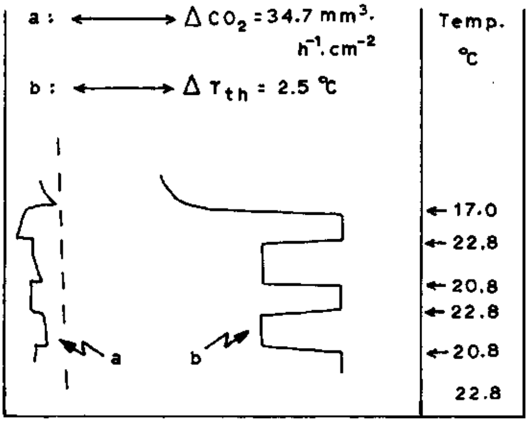

Fig. 4b. Part of a registrogram, showing the dark respiration of a leaf of *Populus euramericana* 'robusta' at changing temperatures. The abrupt changes in the temperature are produced with the automatic infrared temperature compensation system. Dashed line is the baseline of the katharometer.

use of the infrared temperature compensation method under changing illumination of the leaf of *Populus euramericana* 'robusta', and the rate of photosynthesis. The induction effects of photosynthesis show up, undisturbed by concurrent temperature changes. An abrupt change of temperature can be produced by turning the knob for the reference temperature on the electronic controller. The Q_{10} of this CO_2-saturated photosynthesis is estimated to be 2.24. Fig. 4b gives a picture of the reaction of dark respiration of the same leaf upon abrupt temperature changes. Fig. 4c depicts the rate of photosynthesis of a detached leaf disk of corn at a number of light intensities. The Q_{10} of photosynthesis of corn is estimated to be 2.29. Also here the infrared temperature control proves to function correctly. A last remark which may be of interest, is that fluctuations in the temperature of the cooling liquid are also automatically corrected by the infrared radiation so that only minor fluctuations in leaf temperature are left. So, when the differential of the thermostatic bath of the tetra is large (in this case about 1.5 °C) large oscillations in the compensating radiation occur, which will be detected by the 'Stoutjesdijk' pyrometer. In this situation, the 'Stoutjesdijk' pyrometer can not be used for the accurate measurement of temperature (fig. 5).

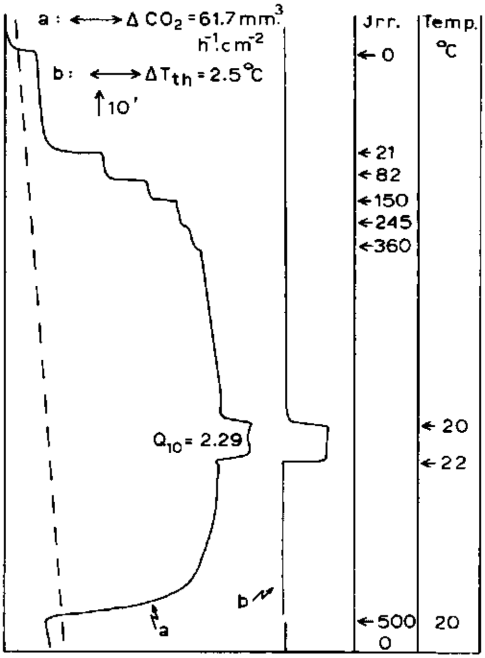

FIG. 4c. Part of a registrogram showing the rate of photosynthesis of a leaf of *Zea mays* and the infrared temperature compensation. No induction effects are demonstrated. Dashed line is the baseline of the katharometer.

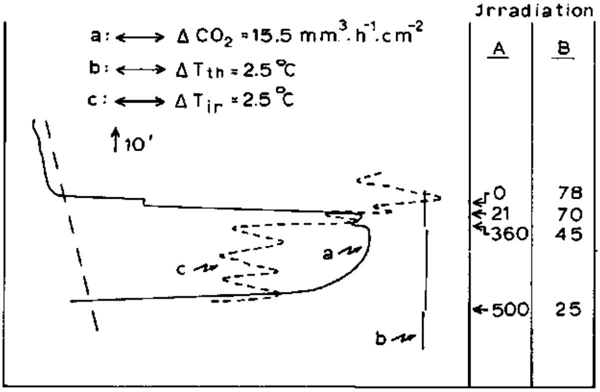

FIG. 5. Part of a registrogram showing the rate of photosynthesis of *Populus euramericana* 'robusta' (line a), leaf temperature as measured by the thermocouple (line b), and the 'leaf temperature' signal of the 'Stoutjesdijk' radiometer (line c). The figures in the table show how infrared (B, volt) compensates visible (A) light (erg. cm^{-2}. sec^{-1}). Line c shows how strongly the compensating infrared radiation is sensed by the pyrometer. The oscillations in the infrared radiation are caused by the compensation of the large differential in the temperature of the cooling fluid in the double wall of the assimilation chamber. Dashed line is the baseline of the katharometer.

V. CONCLUSION AND SUMMARY

A system is described for the automatic and instantaneous control of the temperature of a leaf in the assimilation chamber by supplying infrared radiation: the infrared compensation system. This system has proved to function correctly.

It is advisory to use fast pyrometric techniques for the detection of absolute leaf temperature, because thermocouples may underestimate the leaf temperature.

Interaction of the infrared radiation from the compensation system and the temperature detection must be held within acceptable limits. In this respect the infrared point thermometer PRT 4 from Barness Engineering is suitable, because it insensitive to this short wave infrared radiation.

If there exists a temperature gradient over the leaf in the assimilation chamber, the mean temperature of the measured region must coincide with the mean temperature of the entire leaf.

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