STUDIES ON PRODUCTIVITY OF COFFEE

I. EFFECT OF LIGHT, TEMPERATURE AND CO. CONCENTRATION ON PHOTOSYNTHESIS OF COFFEA ARABICA

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SUMMARY

A study was made on the effect of light and temperature on net photosynthesis, growth and transpiration of Coffea arabica. Net photosynthesis was described as a diffusive process depending on a carbon dioxide gradient and an overall resistance. At a relative low temperature (24°C), the effect of light on net photosynthesis was comparable with that of most annual agricultural crops. Calculated internal concentration and overall resistance at 0.3 cal cm⁻² min⁻¹ were zero p.p.m. and 15 sec cm⁻¹ respectively. Above this temperature each degree rise resulted in an increase of 20 p.p.m. in internal CO₂ concentration. This effect alone accounts already for a decrease in dry matter production of approximately 7% per degree centigrade. The increase in internal CO₂ was accompanied with an increase of the overall resistance, reducing still more the dry matter production. Low rates of photosynthesis in coffee reported in literature could be explained. Increasing the external CO₂ content and thus the CO₂ gradient had only a minor effect on photosynthesis. The effect of temperature and light on growth confirmed the conclusions of net photosynthesis research. Since both factors increase transpiration substantially, the water use efficiency decreases strongly with an increase in light and in temperature above 24 °C. The results may have importance for selecting optimum growth conditions for coffee.

1. INTRODUCTION

Myna authors have pointed out that growth of a coffee plant either expressed as leaf area (ALVIM 1958), diameter of the stem (MACHADO 1952; GUISCAFRÉ-ARRILAGA, & GOMEZ 1942), or number of nodes (MONTOYA c.s. 1961) represents a good estimate of the yield. The growth of the plant is essentially a result from the dry matter production via photosynthesis and may therefore be highly dependent on light intensity. The optimum light intensity for growing coffee has been a controversial point as coffee has long been considered as a shadeloving plant. However, evidence from field experiments has shown that growth and yield can be greatly increased under full light conditions. Air temperature also is expected to have a large effect on photosynthesis of coffee via increasing the internal CO₂ content in the mesophyll (HEATH & ORCHARD 1957) which results in closing of stomates. NUTMAN (1937 a, b) has followed the pattern of photosynthesis and stomatal resistance in single leaves of a coffee plant during several days under natural field conditions. However, the separate effect of light and temperature could not be evaluated in this way. Tio (1962) investigated the effect of light also in single leaves at an air temperature of 20°C

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in the laboratory. The available data on the effect of light and temperature on photosynthesis are not sufficient, however, to permit an estimation of the potential dry matter production in several combined conditions of environmental factors.

For this reason photosynthesis experiments were carried out with whole plants under diurnal conditions of light and air temperature, the measurements were made at different periods of the day. Some additional growth experiments at different day and night temperatures were made at two light levels. The results of such experiments may give a better understanding of the growth behaviour of coffee and might serve as a basis for selecting areas for coffee growth. The experiments described here were performed at field capacity, so that soil water availability was not a limiting factor. The effect of soil water availability and coffee variety will be described elsewhere.

2. MATERIAL AND METHODS

Young cuttings of Coffea arabica were obtained from the Department of Tropical Crop Husbandry of the Agricultural University (Wageningen). The plants were cultivated in asbestos cement containers (30 × 30 × 40 cm) on a soil mixed of clay, sand and old rotten leaves (2:1:1 by volume), which moisture retention curve was known. Growth conditions in a temperature controlled glasshouse were normal daylight, and 23° and 20°C day and night temperature respectively. During the experimental period from June till September light duration at our latitude averaged 15 hours and short wave radiation within the greenhouse 300 cal day⁻¹. The plants were used for photosynthesis measurements at an age of approximately 9 months after cutting. At that stage the height was about 40 cm, per plant the total number of leaves was nearly 45, and the total leaf area varied between 820 and 1110 cm².

The carbon dioxide content was measured with an infrared U.R.A.S. gas analyser. The airstream passed subsequently a paper dust filter, a cooling unit and a tube filled with magnesium perchlorate in order to reduce the moisture content of the air before it was analysed. Calibration was obtained with different known CO₂ concentrations. The output was registrated by a 12 point 2.5 mV Philips recorder.

A closed gas circuit was used in the photosynthesis experiments. The whole plant was enclosed in a perspex container ($30 \times 30 \times 40$ cm), which was placed upside down on top of the eternite container. At the soil surface 2 perspex plates were adjusted to each other leaving a small hole in the centre for access of the stem of the coffee plant. The whole system was sealed off with bucarid. A small volume of gas at a rate of 1 ltr/min was withdrawn via nylon tubes from the top of the perspex container, analysed and brought back to the bottom of the plant. A large volume ($50 \, \text{ltr. min}^{-1}$) was withdrawn at the top, passing a thermostat bath at 12 °C for condensation and a second thermostat bath which was set at the same temperature as that of the plant environment. The average windspeed calculated was approximately 1 cm sec⁻¹. Leakage was

tested without a plant, applying a large CO₂ gradient between the closed system and the outside air. The change in CO₂ with time was negligible in the long run compared with the changes due to photosynthesis.

A small volume of pure CO_2 was injected in the closed system in order to start the measurements at a concentration of about 600 p.p.m. The depletion of CO_2 was then recorded with time. At each desired concentration of CO_2 external, the depletion rate could be obtained with a prism and a protractor. The tangent was then converted in cm³ cm⁻² sec⁻¹ from

$$P_n = \frac{CO_2}{t} \times V \times \frac{1}{A} \times S \tag{1}$$

where P_n = net photosynthesis (photosynthesis minus respiration) in cm³ cm⁻² sec⁻¹.

$$\frac{\text{CO}_2}{t}$$
 = tangent in p.p.m. $\text{CO}_2 \text{ sec}^{-1}$

V = total volume of closed circuit in cm³

A = total leaf area in cm²

S = calibration factor

All calculations were made on a computer. Further details have been described earlier (BIERHUIZEN c.s. 1968).

Beside CO₂, also soil and air temperature were continuously registered by means of copper-constantan thermocouples on the 12 point recorder. The light intensity was recorded with a selenium photocell which had been calibrated against a Kipp solarimeter.

Most of the photosynthesis measurements were performed in a greenhouse under natural day light conditions in which the temperature fluctuated according to the intensity of the solar radiation and the capacity of its thermostat control. In order to evaluate the effect of light and temperature on CO_2 internal of coffee tissues, plants were submitted to controlled temperature and artificial light with constant intensity maintained as long as desired. A cabinet equiped with 3 H.P.L.R. Philips 400 watt high pressure mercury vapour lamps, was used. Long wave radiation was reduced by a 3 cm layer of running water between the lamps and the perspex container. Four steps of temperature treatments were imposed, increasing during four successive days. During each day, temperature was maintained constant and CO_2 consumption was recorded at four light intensities. Values of internal CO_2 concentrations were read direct from the chart curves of CO_2 depletion when P_n is nil and CO_2 external equals CO_2 internal (see eq. 2).

Some additional growth experiments under the same artificial light conditions were made at 3 day and night temperatures at full and 1/20 of full light in four replicates, in which measurements of leaf growth, transpiration and relative turgidity were made. The plants were kept near field capacity by irrigating twice a week. The soil surface was covered with a 3 cm layer of gravel

in order to prevent evaporation. Transpiration was measured by weighing. The number of leaves classed by size was noted at the beginning and at the end of the growth period. Leaf area was estimated by using an average area for leaves of each class.

The relative turgidity was measured, by saturating leaf discs on a moistened plate of agar, as described by ČATSKÝ (1960). A period of 5 hours proved to be sufficiently long for saturation of coffee discs with a diameter of 8 mm.

3. RESULTS

3.1. Effect of light, temperature and CO₂ on net photosynthesis

Fig. 1 shows an example of net photosynthesis as a function of light, obtained in a coffee plant grown under natural day light. The curves are BLACKMAN type curves (1905) where the initial slope seems to be the same with different saturation plateaus imposed by the internal CO₂ concentration of the tissues. The figure shows that the rate of photosynthesis is approximately linear with

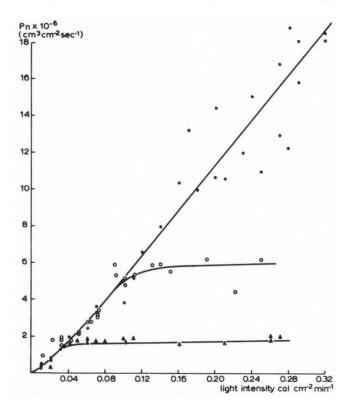


Fig. 1. The effect of light intensity under natural conditions on net photosynthesis of Coffea arabica at an external CO₂ concentration of 300 p.p.m. and an internal CO₂ concentration of 0 (••••), 70 (○○○) and 180 (▲▲▲) p.p.m.

light in the whole range studied e.g. up to 0.3 cal cm⁻² min⁻¹, when CO₂ internal of the tissues is approximately nil. With a CO₂ internal of about 70 p.p.m., saturation is reached at about 0.1 cal cm⁻² min⁻¹, whereas this decreases to an extreme low light intensity of 0.04 cal cm⁻² min⁻¹ in case the CO₂ internal of the tissues is as high as 180 p.p.m. The maximum rate of photosynthesis estimated in our experiments was in the order of 20×10^{-6} cm⁻² sec⁻¹.

Photosynthesis can be described as a diffusive process according to

$$P_n = \frac{[CO_2]_{ext} - [CO_2]_{int}}{R}$$
 (2)

where: P_n is again net photosynthesis in cm³ cm⁻² sec⁻¹

 $[CO_2]_{ext}$ - $[CO_2]_{int}$ is the difference of the CO_2 concentration of the external air and the CO_2 concentration in the tissues in p.p.m. $\times 10^{-6}$

R is the total resistance in the pathway of CO₂ in sec cm⁻¹

The data of fig. 1 enable us to evaluate the resistance in each of the three curves of the figure. At a light intensity of 0.3 cal cm⁻² min⁻¹, the total resistance at 0, 70 and 180 p.p.m. was respectively 15, 38 and 60 sec cm⁻¹. It is evident there-

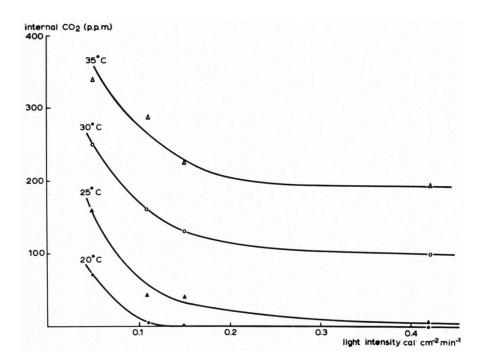


Fig. 2. The effect of artificial light and temperature on the internal CO₂ concentration of Coffea arabica.

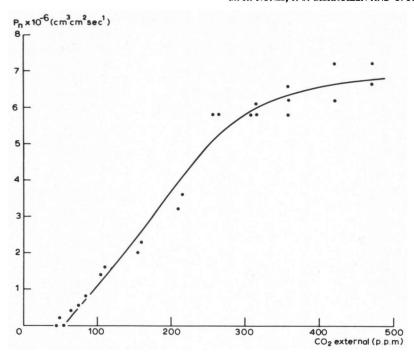


Fig. 3. The effect of external CO₂ concentration on net photosynthesis.

fore that the resistance increases as well as the CO_2 internal and both factors contribute to the difference in maximum P_n between the three curves. The increase in total resistance may be attributed to closing of stomates due to the high CO_2 internal concentrations.

Fig. 2 shows that both light and temperature are influencing the CO_2 internal of the tissues. However, the effect of temperature is more important. With a light intensity higher than 0.15 cal cm⁻² min⁻¹, which is the normal situation in the field, the internal CO_2 of the tissues can be expressed as a linear function of temperature. Below 24°C, the internal CO_2 concentration is zero. Above this value, the internal CO_2 rises linearly with 20 p.p.m. (r = 0.796) for each degree centigrade.

According to these results it can be concluded that for each degree centigrade above 24°C a decline is to be expected of about 10% in dry matter production, therefore above 34°C dry matter production approaches zero. At lower light intensities than 0.1 cal cm⁻² min⁻¹ there is an additional CO₂ internal increase, which can rise even higher than 300 p.p.m. (fig. 2). At such environmental conditions and an external CO₂ concentration in the air of 300 p.p.m. net photosynthesis is even negative.

An example of the effect of external CO_2 on net photosynthesis in coffee is shown in fig. 3. At low CO_2 concentrations P_n is almost a linear function

of CO_2 external. The intercept of the curve with the abscissa corresponds with the internal CO_2 of the tissues. The saturation point seems to occur already between 400 and 500 p.p.m. The tangent represents the reciprocal of the total resistance (equation 2). Examination of a number of curves of $P_n = f$ (CO_2 external) in coffee proves that rapid stomatal closure may occur after injection of high concentrations of CO_2 into the perspex chamber. However, direct measurements of stomatal opening were not made to prove this.

3.2. Growth and transpiration at three day/night temperature combinations and two light levels

Some data of a growth experiment in the temperature controlled glasshouse are presented in fig. 4.

The highest leaf growth occurred at a day/night temperature treatment of 25/20°C. It declined somewhat at a lower temperature (20/12°C) but was 50% less at the highest temperature treatment (32/25°C).

The effect of light on leaf growth was not significantly different. The plants grown at the high temperature treatment showed some morphological disturbances in the leaves like curling between veins and a smaller leaf area. The average area of a mature leaf at the highest temperature was 20.3 cm², whereas it was 22.3 cm² in the other temperatures.

The transpiration rate of plants grown both at full light (daily average 300 cal cm⁻² min⁻¹) and in the shade decreased sharply with decreasing temperatures, whereas the difference in transpiration between plants at high and medium temperatures in the shade was small. Plants under shade transpired approximately 1/3 less than the correspondent ones under full light.

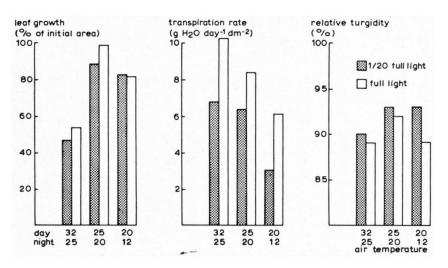


Fig. 4. The effect of 3 day/night temperature treatments and two light levels on leaf growth, transpiration rate and relative turgidity.

Measurements of stomatal opening were carried out respectively with a porometer (BIERHUIZEN c.s. 1965) and an infiltration mixture of isopropanol and water (WORMER 1965). Stomates of leaves grown under comparable illumination in full light and in the shade were chosen and measured at 10 a.m. and 4 p.m. The stomatal opening at 20/12 °C was greater under full light, it was the same both under full light and shade at 25/20° and larger under shade conditions at 32/25 °C.

The relative turgidity measured at midday is higher in plants under shade, as was expected. Plants grown at high temperature have the lowest values. There is a strikingly low turgidity, however, in plants grown at low temperature and high light intensity. This result may be attributed to reduction in root permeability or root growth due to low night air temperatures (which could have reached 9–10°C) and hence low soil temperatures, resulting in an impairment of water absorption with transpiration during the day. Inhibitory effects of low temperature in root growth are reported by STERN c.s. (1968) in cotton and by FRANCO (1958) in coffee.

4. DISCUSSION

The maximum rate of photosynthesis observed was in the order of magnitude of 20×10^{-6} cm³ cm⁻² sec⁻¹, which is about three times higher than the maximum reported by NUTMANN (1937a) in coffee fields of Tanganyika, and 2.5 times higher than the maximum reached by Tio (1962) under laboratory conditions.

The present study, however, clearly demonstrates that maximum photosynthesis rate can be achieved in the particular situation of zero CO₂ internal (fig. 1, top). The results of Tio are well confirmed with the order of magnitude of the line in the middle of fig. 1. As Tio has not recorded leaf temperature it is possible that a rise of some degrees in leaf temperature occurred in his experiments due to direct radiation of high intensity over the leaf (20°C has been reported under certain conditions in coffee by Alvim 1958). Of course actual leaf temperature depends on the microclimate and the plant and soil factors, which in turn determine the energy balance of the canopy. Burning of coffee leaves due to direct radiation is a common feature. In our opinion such a temperature rise which results in an increase in CO₂ internal could mainly account for the lower rate of photosynthesis recorded. The depressive effect obtained under light intensity above 6000 foot candles could be explained in this way as well. A similar explanation can be given for the midday drop in photosynthesis.

In coffee areas where the average daily temperature is above 22° C and light intensity higher than 0.15 cal cm⁻² min⁻¹ it is expected that maximum curves will not be obtained or only early in the day. The pattern of the curve will change gradually therefore, from top to central or even the lower line of fig. 1.

In comparing net photosynthesis of coffee with that of other plants, it is obvious that potentially the same rate can be obtained. In cotton for example internal concentration and total resistance are of the order of 20 p.p.m. and

10 sec cm⁻¹ respectively (Bierhuizen c.s. 1968). In coffee such values are zero and 15 sec cm⁻¹. However, in coffee internal CO₂ usually rises very rapidly in the course of the day with a simultaneous rise in the overall resistance. This means that generally net photosynthesis in coffee is a quarter of that of most annual agricultural crops. Since above 24°C a rise of one degree results in an increase of 20 p.p.m. in internal CO₂, air temperature is a dominant factor concerning dry matter production of coffee, contrary for example to cotton in which between 25 and 35°C the effect of air temperature was found to be negligible. The internal CO₂ of the tissues may depend also on other factors than temperature. Experiments on respiration of coffee plants leads us to suspect that CO₂ respired can be fixed again in the dark especially after a long dark period. This phenomenon, which will be a further point of research, induces a changing in the CO₂ content of the tissues and may be of great importance to explain some obscure results in the behaviour of photosynthesis of coffee plants and in the rythmic autonomous stomatal movements (Nunes & Rodrigues, unpublished results) as well.

The curves of P_n against CO_2 external, show that the CO_2 saturation point is rather low compared with values around 0.1% found for many other crops (Hoover c.s. 1933 for wheat, Singh & Lal 1935 for sugar cane, Gaastra 1959 for sugar beet, turnip, tomato and cucumber).

The results of the growth experiment at three day/night temperatures (20/12, 25/20 and 32/25°C) and two levels of light are in good agreement with the results of the photosynthesis measurements affirming the conclusion that above 25°C, temperature has a large inhibitory effect. Moreover, a reduction to 1/20 of full light at 25°C or 20°C has a far less decreasing effect on production than an increase in temperature from 25 to 32°C. On the other hand increasing temperature and light increase transpiration considerably. This means that water use efficiency (dry matter production in grams per gram water used) decreases largely with an increase of light and temperature. Therefore, a more detailed study of the water relations in coffee was carried out, to be published elsewhere.

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