

**MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 81-12 (1981)**

PHOTOSYNTHESIS OF LETTUCE

I. RESULTS WITH CULTIVAR 'AMANDA PLUS'

H. M. C. VAN HOLSTEIJN

*Department of Horticulture, Agricultural University,
Wageningen, The Netherlands*

(Received 11-III-1981)

Publication 480

H. VEENMAN & ZONEN B.V. – WAGENINGEN – 1981

PHOTOSYNTHESIS OF LETTUCE

I. RESULTS WITH CULTIVAR 'AMANDA PLUS'

INTRODUCTION

In The Netherlands the cultivation of butterhead lettuce (*Lactuca sativa* L.) in glass-houses takes place in spring, autumn and winter, and in the open field in the spring and summer season. Fundamental data on the growth of lettuce are important to obtain an optimal yield. In previous papers results of the growth analysis (VAN HOLSTEIJN, 1980b) and of the process of soil covering of lettuce (VAN HOLSTEIJN, 1980a) were presented. Data on photosynthesis of lettuce plants in relation with temperature, irradiance and CO₂-concentration are essential for a good understanding of the growth process. It is known, for instance, that in the poor light period changes in the environmental conditions during the day or during a number of days strongly affect growth. EENINK (1978) and EENINK and SMEETS (1978) concluded from research in the phytotron and in glass-houses that certain genotypes of lettuce reacted rapidly to short periods of higher irradiance and temperature resulting in a higher yield, while these genotypes gave a similar yield compared to other genotypes under constant environmental conditions. Photosynthesis measurements may give additional information on these aspects.

The quantitative growth analysis describes and analyses long term growth aspects (e.g. VAN HOLSTEIJN, 1980b; SALE, 1977), while gas exchange measurements permit an analysis of short term effects with either constant or changing conditions of irradiance, temperature and CO₂. The effect of irradiance on photosynthesis of sun and shade plants was studied by e.g. BJÖRKMAN and HOLMGREN (1966), BÖHNING and BURNSIDE (1956), CHARLES-EDWARDS et al. (1974), LOACH (1967) and LOGAN and KROTKOV (1968). The photosynthesis response of butterhead lettuce on irradiance was studied by ACOCK and HAND (1974), BROUWER and HUYSKES (1968), GAASTRA (1966), REINKEN et al. (1973) and TATSUMI and HORI (1969). SARTI (1973) presented light response curves of a cos lettuce cultivar and VAN HOLSTEIJN et al. (1977) investigated the gas exchange properties of whole shoots as affected by drought.

Gas exchange measurements can be carried out in various ways. Lettuce measurements were done on leaf discs (SARTI et al., 1977), attached leaves or leaf parts (GAASTRA, 1966; REINKEN et al., 1973; SARTI, 1973) or whole shoots (BROUWER and HUYSKES, 1968; VAN HOLSTEIJN et al., 1977; LORENZ and WIEBE, 1980; TATSUMI and HORI, 1969, 1970 and WIEBE and LORENZ, 1977). Since most plants and crops grow in plant communities or in more or less closed canopies the photosynthesis data of a single plant have to be related to its position in a canopy. Lettuce plants do not form a homogeneous canopy or row crop community and only during the early stage of growth they can be considered as solitary plants.

Since the structure of mature plants is complex and the whole shoot of the lettuce plant is harvested, measurements with whole plants are necessary. In addition the separation of a bubbled and curved leaf and in consequence the gas exchange measurement of a single leaf of a heading butterhead lettuce plant is difficult. Equipment for whole plant measurements is available (e.g. LOUWERSE and VAN OORSCHOT, 1969; VAN HOLSTEIJN, 1979).

The photosynthetic and respiratory rates are usually expressed per unit leaf area (ACOCK et al., 1978; GAASTRA, 1959, 1966; VAN HOLSTEIJN et al., 1977; REINKEN et al., 1973) or unit dry or fresh weight (ACOCK et al., 1979; BROUWER and HUYSKES, 1968; CHARLES-EDWARDS et al., 1974; SALE, 1977). BROUWER and HUYSKES (1968) expressed the photosynthetic rates of lettuce also on unit exposed leaf area (soil cover). Field chamber and assimilation chamber data are usually expressed on unit ground area (ACOCK et al., 1978; ALBERDA et al., 1977; MCCREE and TROUGHTON, 1966; SALE, 1977).

Differences in the number of leaf layers, leaf thickness or chlorophyll content still can interfere a correct comparison of the effects of environment and variety. BJÖRKMAN (1968) therefore related the soluble protein to photosynthesis and CHARLES-EDWARDS et al. (1974) and PATTERSON et al. (1977) measured the mesophyll tissue volume. The latter authors and KOLLER and DILLEY (1974) presented photosynthesis data per unit chlorophyll. Other parameters as bases of expression with specific advantages and disadvantages for a comparison of photosynthetic results are feasible. In this paper, therefore, attention is paid to this problem with the results of the butterhead lettuce cultivar 'Amanda Plus'.

Theory

Empirical and semi-empirical models have been applied to describe the relationship between environmental factors and photosynthesis of single leaves (AKITA et al., 1968; CHARLES-EDWARDS and LUDWIG, 1974; MARSHALL and BISCOE, 1980; PEAT, 1970; THORNLEY, 1976). THORNLEY (1976) modified single leaf models for the use of crop photosynthesis data and ACOCK et al. (1976b) and DUNCAN et al. (1967) used canopy models derived from leaf models. These models describing the gas exchange of a plant or canopy give a good understanding of the gas exchange properties of a plant community (ACOCK et al., 1976a, 1976b; CHARLES-EDWARDS and ACOCK, 1977; DUNCAN et al., 1967; ENOCH and SACKS, 1978; TOOMING, 1967), of the various physiological processes involved, and of the data which are still lacking.

TAKAKURA (1975) tested his model for plant growth optimisation by computer with lettuce plants, and SORIBE and CURRY (1973) simulated lettuce growth in a plastic greenhouse, but information regarding leaf or plant photosynthesis of lettuce was and is still lacking and hence appropriate models are not available. THORNLEY (1976) described a rectangular hyperbola relating the gross photosynthetic rate of a leaf to both irradiance and CO_2 :

$$P_g = \frac{\alpha I \tau C}{\alpha I + \tau C} \quad (1)$$

in which P_g is the gross photosynthetic rate, I the level of irradiance, C the carbon dioxide concentration, α the initial slope of the P - I -curve i.e. the photochemical efficiency and τ the initial slope of the P - C -curve i.e. the leaf conductance for CO_2 transfer. Maximum gross photosynthesis ($P_{m,g}$) is τC ($I = \infty$) or αI ($C = \infty$). The net photosynthetic rate (P_n) is obtained as the difference between the gross photosynthetic rate and the dark respiration (R_d):

$$P_n = P_g - R_d = \frac{\alpha I \tau C}{\alpha I + \tau C} - R_d \quad (2)$$

and the maximum net photosynthesis, $P_{m,n}$, ($I = \infty$) is $\tau C - R_d$ and $P_{m,n}$ ($C = \infty$) is $\alpha I - R_d$. ACOCK et al. (1976b, 1978) used this equation as a basis for their canopy model for green peppers and tomato, which model gave good estimates for the values of α and τ . The photorespiration (R_i) is not included as a separate component in this equation, as is done in almost similar models used by ACOCK et al. (1976a), CHARLES-EDWARDS et al. (1974) and CHARLES-EDWARDS and LUDWIG (1974). When equation (2) is used in a plant model, the parameter α will present the 'plant photochemical efficiency' and τ the 'overall plant conductance for CO_2 transfer'. The photosynthesis-irradiance response curve can be written as:

$$P_g = P_n + R_d = \frac{\alpha_g I P_{m,g,i}}{\alpha_g I + P_{m,g,i}} \quad (3)$$

The gross initial slope of the curve is α_g ($I = 0$) and the net initial slope α_n ($I = I_c$), I_c , the light compensation point when $P_n = 0$, is

$$\frac{R_d P_{m,g,i}}{\alpha_g (P_{m,g,i} - R_d)} \quad (4)$$

R_d can either be measured and used for the calculation of other parameters or estimated from the equation.

The photosynthesis- CO_2 response curve can be written as:

$$P_g = P_n + R_d = \frac{\tau_g C P_{m,g,c}}{\tau_g C + P_{m,g,c}} \quad (5)$$

The gross initial slope of the CO_2 -photosynthesis curve is τ_g ($C = 0$) and the net initial slope τ_n ($C = C_c$), C_c , the CO_2 compensation concentration when $P_n = 0$, is

$$\frac{R_d P_{m,g,c}}{\tau_g (P_{m,g,c} - R_d)} \quad (6)$$

Note that R_d in equations 3 and 4 represents another value than in equations 5 and 6.

In the ideal situation when all the light quanta are absorbed and used for the reduction of CO_2 a single constant value for the photochemical efficiency ($\alpha_{g,con}$) could be obtained for at least all C_3 -plants. RABINOWITCH (1951) and GAASTRA

(1962) concluded from their analysis of the photochemical processes that the maximum light efficiency should be about the same for leaves of different species and for leaves grown under various environmental conditions. CHARLES-EDWARDS et al. (1974) found no significant differences between photochemical efficiencies (α_n) of six temperate grass varieties. LOUWERSE and VAN DE ZWEERDE (1977) also obtained similar values of α_g of various groups of bean plants. ACOCK et al. (1976b) observed similar values of α_n between leaves measured under various circumstances and concluded that their data supported the concept of a constant potential photochemical efficiency for the photosynthesis of C₃-plants. However, this potential value ($\alpha_{g,con}$) is never obtained due to limitations of external CO₂-concentration, conductance for CO₂ or photorespiration. Measured differences between the initial slopes of the P-I-curves (e.g. BÖHNING and BURNSIDE, 1956; PEAT, 1970; for lettuce: BROUWER and HUYSKES, 1968; SARTI, 1973) are due to differences in structure and morphology of the leaf, plant or canopy.

With a correction factor all measured or estimated values of α_g can be made equal to $\alpha_{g,con}$. This means that correction is necessary either for the measured irradiance (Wm⁻²) or for the measured gas exchange rate. The corrected value for the irradiance (I_{cor}) will be expressed in Watt per plant (WPl⁻¹) and the corrected value for the photosynthesis (P_{cor}) on the basis of the real effective leaf area (EL) of the plant. This area, EL (m²Pl⁻¹), intercepts and absorbs all light quanta with efficiency $\alpha_{g,con}$. In such a concept the number of leaf layers and the leaf thickness of the plant are incorporated, whereas EL gives information on the morphology of the plant. The photosynthesis per plant P (mg CO₂ Pl⁻¹ s⁻¹), expressed on the basis of effective leaf area, is now described by: $P_{cor} = P \cdot EL^{-1}$ (mg CO₂ m⁻² s⁻¹) and I_{cor} by I · EL.

The efficiency $\alpha_{g,con}$ (mg CO₂ J⁻¹) is defined by:

$$\left. \frac{d(P_{cor})}{dI} \right|_{I=0} = \left. \frac{dP}{d(I_{cor})} \right|_{I_{cor}=0} = \left. \frac{d(P/EL)}{dI} \right|_{I=0} = \left. \frac{1}{EL} \alpha_g \right|_{I=0} \quad (7)$$

with α_g (mg CO₂ m² Pl⁻¹ J⁻¹) calculated from the obtained plant data. The conclusion from (7) is that $EL = \alpha_g / \alpha_{g,con}$ (m² Pl⁻¹). The photosynthetic rate per effective leaf area (P · EL⁻¹) is $P_{pl} \cdot \alpha_{g,con} \cdot \alpha_g^{-1}$. The effective leaf area is equal to k · A or k' · S, or another basis of expression for photosynthesis (k and k' constant). According to GAASTRA (1966) the calculated value of α_g for lettuce varies between 4 and 14% of the $\alpha_{g,con}$.

A similar theory is valid when, instead of gas exchange data per plant, data expressed per unit leaf area or soil cover are used. The photosynthetic rate per effective leaf area will be equal to $P_{pl} \cdot \alpha_{g,con} \alpha_{g,1}^{-1}$ or $P_s \cdot \alpha_{g,con} \alpha_{g,s}^{-1}$ with $\alpha_{g,1}$ and $\alpha_{g,s}$ calculated on leaf area or soil cover basis, respectively. Photosynthetic rates can then be compared using a correction factor EL⁻¹, while the measured level of irradiance in Wm⁻² can be used. Note that the corrected value of I_c will be $I_c \cdot EL = I_c \cdot \alpha_g \alpha_{g,con}^{-1}$.

In this paper the analysis of the results of gas exchange measurements is based on the above explained theory with the use of the correction factor EL^{-1} for the photosynthesis data or EL for the irradiance data.

MATERIALS AND METHODS

Two experiments were carried out with the butterhead lettuce cultivar 'Amanda Plus', one in spring (nr. 1) and one in autumn (nr. 2). Experiment 1 included plants of two sowing dates (1a and 1b) with different age groups A, B and C based on weight and leaf area. The leaf area of plants of age A varies between 4.5 and 11.5 dm^2 and the corresponding dry weight between 0.55 and 1.60 g. These values are for plants of age B between 14.0 and 28.5 dm^2 and between 1.70 and 3.90 g and for age C between 31.0 and 43.5 dm^2 and between 3.95 and 7.45 g.

In both experiments plants of different habitus were obtained with 4 different pretreatments of irradiance and temperature (Table 1). 'Amanda Plus' had been used also in previous experiments of growth and photosynthesis (VAN HOLSTEIJN, 1980a, 1980b; VAN HOLSTEIJN et al., 1977).

On January 17 seeds of the plants of experiment 1a were sown in peat blocks of $5 \times 5 \times 5$ cm in a glass-house at an average day/night temperature of 19°C. After germination the average day/night temperatures were 17/12°C, respectively. On January 24 the plants were selected. After that 11 hours artificial illumination of 35 Wm^{-2} (400–700 nm at plant level; HPLR lamps 400 W) was

TABLE 1. Data about the 4 treatments of experiments 1a, 1b, and 2 with butterhead lettuce cultivar 'Amanda Plus'. Day and night temperatures are mean temperatures and the observed levels of irradiance are also mean levels. NI is natural daylight and AI additional illumination with HPLR lamps.

Experiment	Treatment	Temperature (°C)		Irradiance (Wm^{-2})	
		day	night	NI + AI	Wm^{-2}
1a (age B and C)	I	17.0	12.5	NI + AI 66	Wm^{-2} 117.5
	II	17.0	12.5	70% of NI	: 36.0
	III	26.5	17.5	NI + AI 69	Wm^{-2} 124.0
	IV	26.5	17.5	70% of NI	: 38.5
1b (age A)	I	18.0	12.0	NI + AI 66	Wm^{-2} 117.0
	II	18.0	12.0	70% of NI	: 35.5
	III	27.0	18.0	NI + AI 69	Wm^{-2} 123.5
	IV	27.0	18.0	70% of NI	: 38.0
2	I	16.5	12.0	NI + AI 66	Wm^{-2} 84.5
	II	16.5	12.0	70% of NI	: 13.0
	III	26.0	20.0	NI + AI 68	Wm^{-2} 87.0
	IV	26.0	20.0	70% of NI	: 13.5

given. On February 18 plants were again selected and transplanted into 1.6 litre pots. In preliminary experiments it had been established that growth of 'Amanda Plus' and other butterhead cultivars until a fresh weight of 150 grams was undisturbed in these pots. On March 4 (= day 0) the plants were separated in 4 groups (I, II, III and IV) and different temperatures and irradiance levels were induced (Table 1). The HPLR lamps providing the additional illumination were situated 1.2 meter above plant level. Fertilizers were applied according to the recommendations of the Laboratory for Soil and Crop Testing, Oosterbeek, The Netherlands. Pirette was sprayed twice against diseases. Gas exchange measurements with plants of the 4 treatments of experiment 1a (age B and C) started on day 10 and ended on day 27.

Plants of experiment 1b (age A) were sown on February 22 and transplanted on March 22. On March 23 (day 19) these plants were also separated in 4 groups (I, II, III and IV; Table 1). Gas exchange measurements started on day 28 and finished on day 36. The plants of experiments 1a and 1b were used for photosynthesis-irradiance response measurements.

On September 30 seeds of 'Amanda Plus' were sown for experiment 2 in which the same procedure was applied as in experiment 1. The average temperature was 20°C. After 5 days the day/night temperatures were 21.5/16°C, respectively, until October 31. After October 9 artificial illumination (30 Wm^{-2}) was applied during 11 hours. The plants were transplanted on October 24 and 9 days later distributed between the treatments I; II, III and IV (Table 1). During the cultivation period TMTD was sprayed 3 times. Gas exchange measurements for photosynthesis- CO_2 response curves were carried out between November 21 and December 16. Temperature and irradiance in the glass-house were measured as in previous experiments (VAN HOLSTEIJN, 1980a).

For the photosynthesis measurements the closed system as described by VAN HOLSTEIJN (1979) was used. The pot, containing the root system, was airtight sealed from the upper part of the plant and placed in a cylindrical perspex plant chamber (height 34 or 44 cm; diameter 44 cm). In the centre of the chamber the windspeed was 0.8 m s^{-1} and the relative humidity 75 to 85 %. The temperature in the chamber near the plant was measured by thermocouples. The light source above the plant chamber consisted of 5 HPLR lamps (400 W) and the level of irradiance could be reduced by movable screens with a different number of perforations. The irradiance (maximum value 215 Wm^{-2}) was measured on plant level with selenium photocells. The CO_2 -concentration was measured with an infrared gasanalyser, while the transpiration was not registered at that time.

In experiments 1a and 1b response series consisting of 8 irradiance levels were carried out in a sequence from maximum available irradiance to darkness. These series lasted 2 to 3 hours and were determined at 14° and 26°C. Sixty minutes after inserting the plant into the plant chamber the actual measurements started. Gas exchange readings were taken in the range between 580 and $500 \text{ mg CO}_2 \text{ m}^{-3}$ when a constant response was reached. Plants of similar size or weight were always selected for the two replicates.

In experiment 2 the response series were determined at 15° and 25°C at the

irradiance level of 142 Wm^{-2} (for treatment I and III) and at 65 Wm^{-2} (treatment II and IV) in the closed system according to the procedure described by NILWIK (1980b). The measurements started at a CO_2 -concentration of 1400 mg m^{-3} and lasted 2 to 3.5 hours, after which period the CO_2 compensation concentration was reached. At least 8 readings per CO_2 -series were taken with three replicates per treatment. Data at 15°C consisted of plants of treatments I, II and III and at 25°C of treatments I, III and IV.

The data of fresh weight and leaf area were collected immediately after the measurements. The dry weight of the plant was obtained by drying during 7 days in a ventilated oven at 65°C . One hour before the measurements three photos of the plant were taken. The soil cover area was calculated from one photo from above and the profile area of a plant from the average of two photos from aside.

According to equations (3) and (5) regressions were calculated through the photosynthesis data per plant from which the photochemical efficiencies α_g and α_n , the net plant conductance (τ_n), the maximal gross and net photosynthesis $P_{m,g}$ and $P_{m,n}$, the dark respiration (R_d), the light compensation point (I_c) and the CO_2 compensation concentration (C_c) were obtained. These calculations were carried out on a desk calculator HP 9518A with the actual program outlined by NILWIK (1980a). The Tukey's Honest Significant Difference was calculated to compare the calculated results of the different treatments (CARMER and SWANSON, 1973).

RESULTS

In Figure 1 an example of a response curve of the net photosynthesis to irradiance is given of plants of treatments I, II, III and IV, measured at 14°C and an external CO_2 -concentration of about 560 mg m^{-3} . The photosynthetic rates are expressed per plant (a), unit leaf area (b), unit soil cover (c) and unit dry weight (d). The values of the initial slopes, the photosynthetic rates and dark respiration thus depend on the applied unit. The sequence from high to lower levels of photosynthesis between the four treatments is almost the same for figures 1a, b and c (e.g. I, III, II and IV), although the differences between the curves are varying. When the photosynthesis is expressed per unit dry weight (1d) the sequence is II, I, IV and III.

In Table 2 various parameters, calculated from measured data of experiments 1a and 1b, are presented. Values of the P-I curves were calculated from regressions through 8 points and the values of the replicates were taken together. Tukey's Honest Significant Difference (CARMER and SWANSON, 1973) is calculated per age (A, B and C) and for all data together.

Except for the data of I_c a comparison of the results, especially those on plant basis, is difficult. In general, however, the values of α_g increase and of α_g^l decrease with an increase of age. The values of α_g and α_g^l of treatment IV are lower than other values when measured at 14°C , while those differences disappear when measured at 26°C . In general, the maximum gross photosynthesis on leaf area

TABLE 2. Parameters describing the response of gross photosynthesis (P_g) to irradiance (I) for the 4 treatments (I, II, III and IV) of the groups A, B and C of experiment 1. Measurements were carried out at 14° and 26°C and at an external CO_2 -concentration of about 560 (14°C) and 545 (26°C) mg m^{-3} . α_g and α_g^I : photochemical efficiencies (in $I=0$) expressed per plant ($\text{mg CO}_2 \text{m}^2 \text{Pl}^{-1} \text{J}^{-1}$) and per unit leaf area ($\text{mg CO}_2 \text{J}^{-1}$); $P_{m,g}$ and $P_{m,g}^I$: maximum P_g at saturating I expressed per plant ($\text{mg CO}_2 \text{Pl}^{-1} \text{h}^{-1}$) and per unit leaf area ($\text{mg CO}_2 \text{dm}^{-2} \text{h}^{-1}$); R_d : dark respiration per unit leaf weight ($\text{mg CO}_2 \text{g}^{-1} \text{h}^{-1}$); I_c : light compensation point (Wm^{-2}). Specific leaf weight (SLW) is expressed in g m^{-2} . THSD: Tukey's Honest Significant Difference ($p < 0.01$).

Treatment	Temperature	Results						
		$10^3 \alpha_g$	$10^3 \alpha_g^I$	$P_{m,g}$	$P_{m,g}^I$	R_d	I_c	SLW
age A								
I	14	0.406	4.82	179.1	21.4	7.3	8.5	19.3
II		0.323	4.37	104.2	13.7	8.2	7.2	13.2
III		0.536	4.67	196.1	17.2	6.1	6.2	15.8
IV		0.296	2.84	103.4	9.9	11.9	13.0	10.2
I	26	0.238	4.54	136.6	26.1	18.2	19.3	17.2
II		0.211	5.05	98.6	23.6	29.6	25.2	11.4
III		0.234	4.41	178.6	34.3	26.1	29.0	14.9
IV		0.488	5.33	147.1	16.1	18.7	13.0	11.3
THSD _A		0.088	1.23	37.6	7.1	6.5	4.3	2.8
age B								
I	14	0.570	3.06	302.4	16.2	4.4	7.5	18.0
II		0.778	3.05	254.3	9.8	5.2	6.3	12.4
III		0.662	2.62	285.5	11.5	3.5	6.1	15.6
IV		0.575	2.03	212.9	7.5	3.5	6.4	10.3
I	26	0.326	2.55	520.2	41.1	11.7	22.1	16.6
II		0.571	3.87	236.4	15.9	15.5	16.1	12.5
III		0.500	3.05	367.1	22.7	11.8	18.1	15.6
IV		0.542	3.16	241.3	14.6	16.1	17.1	10.6
THSD _B		0.139	0.79	94.7	7.6	4.1	4.3	3.7
age C								
I	14	0.782	2.30	320.1	9.4	3.5	9.9	21.9
II		1.004	2.71	351.7	9.4	4.1	5.6	12.8
III		0.725	1.85	274.9	7.0	3.0	6.8	14.4
IV		0.702	1.69	207.0	5.0	3.6	5.6	8.9
I	26	0.628	1.81	520.1	15.0	7.3	25.8	20.8
II		0.715	2.13	531.1	15.8	9.4	18.6	12.9
III		0.625	1.60	579.1	15.0	7.1	19.0	14.3
IV		0.786	2.07	456.0	11.9	8.1	16.8	9.9
THSD _C		0.175	0.47	81.8	2.6	2.8	4.1	5.8
THSD _{ABC}		0.136	0.87	82.9	6.2	4.9	4.2	4.1

basis decreases with age. Lettuce plants grown at lower temperatures or a higher level of irradiance showed higher $P_{m,g}^I$ -values, while a high temperature during the measurements also resulted in higher rates. The calculated results of R_d are well in agreement with the measured data (not presented here), the correlation being high ($r = 0.99$). Dark respiration rates on leaf weight basis decreased with

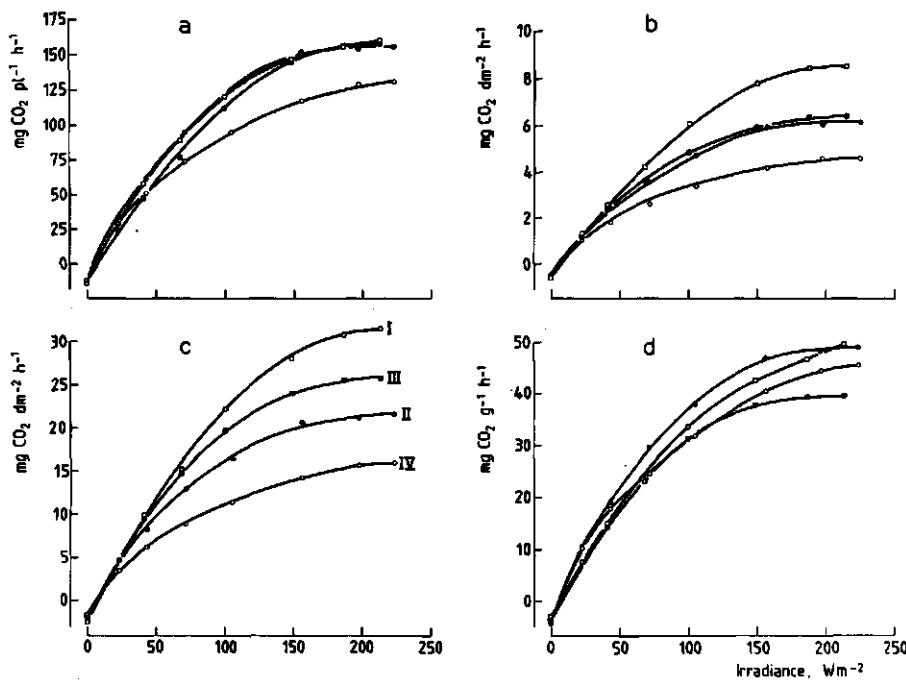


FIG. 1. Curves through measured data describing the response of net photosynthesis to irradiance of the 4 treatments (I, II, III and IV) of experiment 1, age B. The photosynthetic rates (mg CO₂ h⁻¹) are expressed per plant (a), per unit leaf area (b), per unit soil cover (c) and per unit dry weight (d). The measurements were carried out at 14°C and an external CO₂-concentration of about 560 mg m⁻³. □ = I; ● = II; ■ = III; ○ = IV.

increasing age and lower measurement temperatures. The R_d -values per plant of age A were in the order of magnitude of 14% (at 14°C) and 17% (at 26°C) of $P_{m,g}$ per plant, with lower percentages at increasing age. The I_c -values depend strongly on the temperatures during measurements. The values measured at 14°C, a temperature applied in the poor light season in glass-houses, are between 5 and 13 Wm⁻² for all treatments. Differences between the parameters are more obvious between age A and B and between age A and C than between age B and C. High SLW-values are due to low temperatures and a high level of irradiance during growth.

The effective leaf area of plant, EL, is assumed to be related with one or more plant characteristics: $EL = \alpha_g \alpha_{g,con}^{-1} = k \cdot A$ or $k \cdot S$, etc.. A multilinear regression has been carried out between α_g on plant basis with soil cover (S), leaf area (A), average profile area (Pa) and dry weight (W) for all plants of experiment 1. From linear regressions it became evident that the best fit of α_g occurred with soil cover. The S was taken as the first independent variable, A as second one and W as the last one in the multilinear regression model. The same sequence of plant characteristics was applied in a regression model with growth rate in a previous paper (VAN HOLSTEIJN, 1980b). The profile area was listed after leaf area in the model.

TABLE 3. The correlation coefficients of the regressions of the gross photochemical efficiency on plant basis (α_g) with the soil cover (S), leaf area (A), profile area (Pa) and leaf dry weight (W) for all plants of experiment 1 and for the three separate age-groups.

Group	Correlation coefficients (r) of				
	linear regressions of α_g with				the multilinear model
	S	A	Pa	W	
A, B, C	0.93	0.92	0.91	0.86	0.90
A	0.84	0.87	—	0.88	0.92
B	0.85	0.79	—	0.77	0.76
C	0.66	0.56	—	0.44	0.62

The correlation coefficients are listed in Table 3. Addition of the Pa to the multilinear regression of all data did not improve this model ($p < 0.01$) significantly and therefore Pa was not added to the models per age-group. The correlation coefficients of α_g with S, A and W decrease with increasing age, while this effect is more pronounced for the correlation of α_g with A and W than with S.

The results of a 3-way analysis of variance of the gross photochemical efficiencies, maximal gross photosynthetic rates per unit leaf area, maximal net photosynthetic rates, net photosynthetic rates at irradiance level of 35 and 100 W m^{-2} and of the light compensation points are listed in Table 4. According to the theory presented in the introduction the photosynthetic rates are divided by α_g and the corrected light compensation points multiplied by this parameter. Instead of EL ($= \alpha_g \alpha_{g,con}^{-1}$) only the factor α_g has been used, since $\alpha_{g,con}$ has a constant value. The values of $P_{n,35}$ and $P_{n,100}$ are chosen since these levels of irradiance correspond with those during cultivation.

For almost all parameters differences between factors age and measurement temperature exist, while the influence of temperature during cultivation on the parameters is less. For photosynthetic rates on α_g -basis the differences between age are mainly due to plants of age A. The level of irradiance during cultivation has a larger influence on photosynthesis than the temperature level, as applied in these treatments, while temperature during the measurements contributes strongly to the different maximum rates. No significant difference occurs between the $P_{n,35}$ -values of the four treatments. At a high level of irradiance (100 W m^{-2}) the temperature during measurements did not affect the net photosynthetic rates. The corrected light compensation point ($I_{c,cor}$) is mainly affected by age and temperature during measurement and not by environmental conditions during growth, while I_c is more influenced by the conditions during growth than by age.

In Table 5 the calculated results of the CO_2 -series of experiment 2 are listed. Tukey's Honest Significant Difference (CARMER and SWANSON, 1973) is calculated for all treatments together. Values of the P_n -C-curves were calculated from regressions through at least 8 points and the values of the 3 replicates were taken together. The τ_n - and τ_n^1 -values of plants of treatment I and III are slightly lower

TABLE 4. Results of a 3-way analysis of variance of the data of experiment 1 for the factors age (A, B and C), treatment (I, II, III and IV) and temperature during measurement (14° and 26°C). α_e and α'_e : gross photochemical efficiencies (in I = 0) expressed per plant (mg CO₂ m⁻² P₁ J⁻¹) and per unit leaf area (mg CO₂ J⁻¹); P_{m,n}^{α-1}, P_{m,n}^{α'-1} and P_{m,n}^{α,α'} (W m⁻²) are the net photosynthetic rates at saturated irradiance level and at 35 and 100 W m⁻² expressed on basis of α_e ; P_{m,n}^{α,α'}: maximum gross photosynthesis per unit leaf area (mg CO₂ dm⁻² h⁻¹); I₀ and I₁ α_e: light compensation point (W m⁻²) and corrected light compensation point (mg CO₂ P₁ J⁻¹ s⁻¹). ** = significant difference ($P < 0.01$); ns = no significant difference. Mean values with similar characters do not differ significantly from each other according to the Duncan's Multiple Range Test ($P < 0.01$).

TABLE 5. Parameters describing the response of net photosynthesis (P_n) to external CO_2 -concentration for the 4 treatments (I, II, III and IV) of experiment 2. Measurements were carried out at 15° and 25°C and at 65 (for II and IV) and 142 Wm^{-2} (I and III). The τ_n and τ_n^1 are conductances for CO_2 (in $\text{C} = \text{C}_c$) expressed per plant ($\text{m}^3\text{Pl}^{-1}\text{s}^{-1}$) and per unit leaf area (m s^{-1}); $P_{m,n}$ and $P_{m,n}^1$: maximum P_n at saturating C expressed per plant ($\text{mgCO}_2\text{Pl}^{-1}\text{h}^{-1}$) and per unit leaf area ($\text{mgCO}_2\text{dm}^{-2}\text{h}^{-1}$); C_c : CO_2 compensation concentration ($\text{mgCO}_2\text{m}^{-3}$). Specific leaf weight is expressed in gm^{-2} . THSD: Tukey's Honest Significant Difference ($p < 0.01$).

Treatment	Temperatuur (°C)	Results					
		$10^3\tau_n$	$10^3\tau_n^1$	$P_{m,n}$	$P_{m,n}^1$	C_c	SLW
I	15	0.190	0.869	244.6	11.2	94.2	19.9
	25	0.136	0.687	305.9	15.6	176.1	17.3
II	15	0.110	0.735	104.8	6.7	58.8	11.5
III	15	0.260	1.234	212.5	10.1	101.5	15.3
	25	0.184	0.906	270.9	13.4	169.1	16.6
IV	25	0.088	0.378	132.8	5.7	110.2	9.4
THSD		0.013	0.214	63.4	3.3	22.9	4.7

at an increased temperature during measurements and lower temperatures during growth. For plants grown at low irradiance (II and IV) a high temperature during growth (IV) and/or measurement results in low values of τ_n and τ_n^1 . Temperature affects maximum P_n , resulting in higher values for $P_{m,n}$ and $P_{m,n}^1$ at higher measurement temperatures (for I and III), but lower values when the temperature during cultivation is higher (III). The calculated C_c -values correspond with the values registered by the infrared gas analyser and the correlation between the calculated and measured values was high ($r = 0.97$). C_c depends strongly on temperature during measurement.

DISCUSSION

Gas exchange data of whole plants or shoots are more difficult to interpret than those of single leaf measurements. Special problems arise for butterhead lettuce due to its short stem and the production of a head with bubbled and curved leaves, which exclude new formed leaves partly from irradiance (BENSINK, 1971; DULLFORCE, 1968). Moreover, in practice the plants do not grow as solitary plants. The canopy is not homogeneous, even not at narrow spacings at the end of the growth period. The leaves and the number leaf layers are unequally distributed over the 'canopy'. Plants achieve a high 'leaf area index' in the centre during heading stage, while the exterior of the plant consists of one or a few leaf layers only. Because of the complex structure of lettuce plants a comparison between plants (e.g. BROUWER and HUYSKES, 1968; VAN HOLSTEIJN et al., 1977) is difficult. Four treatments were given during cultivation in order to obtain

distinct differences in plant structure and habitus and to analyse the effect of those differences on photosynthesis.

From actual data as well as from calculated results it became evident that no saturation of photosynthesis was obtained at 225 Wm^{-2} . For single leaves the level of irradiance saturation has been determined at 42 Wm^{-2} (REINKEN et al., 1973) and between 200 and 240 Wm^{-2} for cos lettuce (SARTI, 1973). BROUWER and HUYSKES (1968) and VAN HOLSTEIJN et al. (1977) did not observe saturation levels for whole shoots at 209 resp. 154 Wm^{-2} .

Figure 1 shows that differences between the photosynthesis light response curves depend on the basis of expression. On weight basis the sequence of the photosynthesis levels changes and some differences decrease as shown by BROUWER and HUYSKES (1968). The small difference between calculated and measured values of R_d and the low standard errors for most parameters indicate that the use of equations (3) and (5) on plant level gives reliable results. ACOCK et al. (1976b, 1978) also obtained reliable results with other crops, for which they used a crop model based on a similar leaf model.

Photochemical efficiency

Although differences between gross (in $I = 0$) and net (in $I = I_c$) photochemical efficiencies exist, the conclusions in this paper based on α_g are valuable for α_n as well, since the correlation between α_g - and α_n -values was high ($r = 0.99$). The high correlation between α_g and S and the good fit of the multilinear regression of α_g with 4 plant characteristics justify the outlined theory about the application of α_g to define a basis of expression for the photosynthetic rates and a corrected value for I_c . The correlation coefficient of α_g with the 3 plant characteristics decreased with increasing age, which might be ascribed to a higher number of leaf layers, the more complex structure of the older plant, and the senescence of the older leaves of the plant.

In older plants a relatively smaller part of the total leaf area intercepts light and contributes to the positive net photosynthesis than in young plants. The data of the photochemical efficiencies on the basis of leaf area are therefore inaccurate, but they permit rough comparison with other data. The highest α_g^1 -values are observed in the group with the younger plants and the lowest ones in group C. These data are similar with those on leaf level (LUDLOW and WILSON, 1971b; PEAT, 1970) and plant level (NILWIJK, 1980a). Moreover, young lettuce plants have a more open structure, which can result in a higher photochemical efficiency as shown by NILWIJK (1980a) for sweet pepper plants. Typical sun and shade-effects on α_g^1 or α_n^1 as reported for single leaves by some authors (BJÖRKMAN and HOLMGREN, 1966; BÖHNING and BURNSIDE, 1956; LOACH, 1967; SARTI, 1973) are not noticeable for all treatments. In single leaves structural and morphological differences like leaf thickness, structural changes in chloroplasts and chlorophyll content are responsible for these effects. Other authors (CHARLES-EDWARDS et al., 1974; LUDLOW and WILSON, 1971a) reported no influence of the level of irradiance during cultivation on α_g or α_n . For single plant measurements contrasting results are also reported. NILWIJK (1980a) observed differences in α_n^1

mainly caused by the spatial structure of the sweet pepper plant as a result of pretreatment and BROUWER and HUYSKES (1968) found different α_n -values on soil cover basis for two applied treatments, but identical photochemical efficiencies on plant or canopy level were observed by ACOCK et al. (1976a) and LOUWERSE and VANDE ZWEERDE (1977). The efficiencies calculated from plant data in these experiments with lettuce are lower than those from single lettuce leaves (SARTI, 1973) or other leaves (ACOCK et al., 1979) and those calculated from other plant or canopy data which are corrected for number of leaf layers (ACOCK et al., 1976a; NILWIK, 1980a).

Dark respiration

The $P_{m,g}$ of the photosynthesis-irradiance response curve depends on the 'overall plant conductance' for CO_2 (τ_g) and the CO_2 -concentration, which is the same for all measurements in experiment 1. The $P_{m,n}$ depends also on the estimated dark respiration (R_d). These estimated R_d -values per plant never exceeded 17% of the $P_{m,g}$ per plant but this percentage increased at values below $P_{m,g}$. LOGAN (1970) found similar percentages for birch trees over the whole season. The lower percentage of the older groups was not expected for lettuce, since the plants of age B and C possess more aged leaves and a higher number of leaves excluded from the light source. Dark respiration decreases with age (LUDLOW and WILSON, 1971b) and the lower rates with increasing age for lettuce can be a result of that effect. MCCREE and TROUGHTON (1966) and LUDWIG et al. (1965) concluded from canopy data that the respiration of the lower and older leaf layers was extremely low. For lettuce, however, the 'shade' leaves consist of a mixture of old leaves and newly formed leaves within the head of the plant.

Plant conductance for CO_2

The plant conductance for CO_2 (τ) determines to a great extent $P_{m,g}$ ($= \tau_g C$) and $P_{m,n}$ ($= \tau_n C$) in light series. The carboxylation efficiency is incorporated in this 'overall conductance for CO_2 ', which represents an average value for all leaves of the plant. These values can differ considerably as was reported by ACOCK et al. (1978) for leaves in a tomato canopy. A higher plant conductance means a high carboxylation efficiency and/or a low resistance for the transport and diffusion of CO_2 from the external air to the carboxylation sites. On leaf level the total resistance can be divided in the boundary layer resistance (r_a), the stomatal resistance (r_s) and the residual resistance (r_m) (BIERHUIZEN and SLATYER, 1964; GAASTRA, 1959; LUDLOW and WILSON, 1971a). For lettuce plants the r_m , i.e. the residual resistance, can be considered as the most important factor (VAN HOLSTEIJN et al., 1977), which is in agreement with data of BEARDSHELL et al. (1973), FRASER and BIDWELL (1974), GAASTRA (1959, 1962), and, at an irradiance level below 50 W m^{-2} , of NILWIK and TEN BÖHMER (1981).

On plant and canopy level the transport process is more complicated and other CO_2 sources outside the leaf occur. Another resistance, $r_{a,cr}$, the plant or crop resistance determining the transport of CO_2 from the atmosphere to the leaves, can play a more significant role (GAASTRA, 1966). This $r_{a,cr}$ is considered to be

low for most crops, but for lettuce plants which have a more dense leaf package this resistance can be more important. VAN HOLSTEIJN et al. (1977) paid no attention to the role of $r_{a,cr}$ in their experiments, since they used a constant value on leaf basis for r_s and calculated r_s - and r_m -values on basis of the leaf area of all leaves of the plant. The level of irradiance below saturation and the calculation methods of r_m according to GAASTRA (1959) also contributed to an overestimation of r_m (and r_s) by VAN HOLSTEIJN et al. (1977). JONES and MANSFIELD (1970) measured detached leaves of lettuce and they observed values of the total resistance above 30 sec m^{-1} , but the applied level of irradiance (14.4 W m^{-2}) was below saturation for lettuce leaves. The average total conductance on leaf basis (from $P_{m,g}^1$) decreases with age, which can be caused by the more complex structure of the plant, by more self shading, as found by ACOCK et al. (1978) with canopy data, and slightly by the increase of mesophyll and stomatal resistances (LUDLOW and WILSON, 1971b). A decrease in conductance for CO_2 means an increase in total resistance for the transport of CO_2 .

The higher conductance at 26° compared to 14°C indicates that for these photosynthesis measurements the optimum τ -value is found above 14° and probably near 26°C , as observed by NILWIJK (1980b) for sweet pepper, where the optimum value in most situations was obtained at 24°C . For long term growth, however, a lower temperature seems to be favourable for a high conductance for CO_2 transfer. A distinction between the temperature effect of growth and the gas exchange measurement is more difficult to draw in Table 5, due to the restricted number of conductance data. Only a slight influence of the environmental factors in these experiments on r_s is expected (JONES and MANSFIELD, 1970). Different τ -values therefore are also caused by plant structure, more self shading, the influence of $r_{a,cr}$ and the role of internal factors affecting r_m . AUGUSTINE et al. (1976), for instance, concluded that differences in carboxylation efficiencies between genotypes were determined by anatomical and biochemical factors, which are expressed in r_m and BJÖRKMAN (1968) observed differences in carboxydismutase activity of several species grown in strong and weak light.

Specific leaf weight and photosynthesis

The leaf area ratio (LAR) and the specific leaf weight (SLW), calculated from plant data, are considered as less reliable estimates for a morphological characteristic like leaf thickness (VAN HOLSTEIJN, 1980b), but can be used as indicators for some morphological properties. Only small differences between SLW-values of ages A, B and C were observed for treatment I, II, III and IV. The differences between the values of the 4 treatments were significant. Temperature and level of irradiance during cultivation both affect leaf thickness. The influence of leaf thickness on $P_{m,g}$ in these experiments is not always similar, since the correlation coefficient (r) between SLW and $P_{m,n} \alpha_g^{-1}$ at 14° is 0.73 and at 26°C it is 0.55. In other experiments with single plants or canopies usually a higher positive relation between SLW and the maximal photosynthetic rates is observed (LOUWERSE and VAN DE ZWEERDE, 1977; NILWIJK, 1980b). The correlation coefficients (r) between τ_n^1 and SLW for plants measured at 14° and 26°C are 0.57 and 0.63,

respectively. These coefficients may have been negatively influenced by the ages of the plants in experiment 1, since plants of the 3 age groups gave almost similar SLW-values but different plant conductances for CO_2 .

The analysis of variance of net photosynthetic rates on the basis of α_g of irradiance level of 35 and 100 Wm^{-2} shows no significant differences between group B and C. The absence of any significant differences between the corrected $P_{n,35}$ -values of the 4 treatments suggests a similar assimilation of the 'sun' and 'shade' plants at that level of irradiance, which is in contrast to some other results obtained from plant or canopy measurements and expressed on leaf unit basis (BROUWER and HUYSKES, 1968; LOGAN and KROTKOV, 1968; LOUWERSE and VAN DE ZWEERDE, 1977; PATTERSON et al., 1977). Their observed differences between sun and shade plants are due to the various structures and morphologies of the plants and the leaves and the applied basis of expression for the photosynthetic rates, and not to fundamental differences in photosynthetic processes. The spatial structure of the lettuce plant compensates for the differences in leaf structure and morphology at that level of irradiance.

Light compensation point

The influence of measurement temperature is larger than the effects of treatment and age on I_c . Lettuce plants seem to adapt well to the applied irradiance levels in this experiment. The level of irradiance in the winter season approaches the light compensation point. Age and plant structure affect the light interception and self shading and thus I_c . Moreover, young plants have a relatively high number of just unfolded leaves, and this results in higher I_c -values (LUDLOW and WILSON, 1971b). Observed light compensation points are averages of the compensation points of all leaves of the plant. Reported values of single leaves are lower than the values in this experiment (DULLFORCE, 1971; HEATH and MEIDNER, 1967). The maintenance of a low temperature seems to be essential at poor light conditions in order to obtain a low respiratory rate and a low I_c , since an increase of 1°C increases I_c with one Wm^{-2} , a slightly lower value than found by NILWIK (1980a) with sweet pepper plants.

Photosynthesis and CO_2 compensation concentration

The maximal P_n -values of the CO_2 -series are mainly determined by differences in the estimated photochemical efficiencies (from: $P_{m,n} = \alpha_n I$). The P_n -values of treatment I and III, measured at 142 Wm^{-2} , are influenced by temperature during cultivation and during the gas exchange measurement (LOACH, 1967; NILWIK, 1980b). Calculation of $P_{m,n}$ on the basis of data over a range between 80 and $1400 \text{ mgCO}_2 \text{ m}^{-3}$ (in experiment 2) can give misleading results, since a higher CO_2 -concentration can cause an increase in the stomatal resistance for lettuce (JONES and MANSFIELD, 1970) and residual resistance (NILWIK and TEN BÖHMER, 1981; WITWER and ROB, 1964).

The calculated values of C_c are in agreement with the observed data. The C_c -values, which provide an average estimate of the CO_2 -concentration in the intercellular spaces for the whole plant, are slightly higher than the values

reported by HEATH and MEIDNER (1967) for detached leaves at comparable temperatures. BRAVDO (1971) also observed higher CO_2 compensation concentrations of leaves and stem together as compared with concentrations of single leaves. The leaves which intercept direct light have lower C_c -values than the young and old 'shade' leaves (NILWIK, 1980b). The shade part of the plant and the stem contribute more to R_d (BRAVDO, 1971) and form an extra CO_2 source, although the contribution of the stem for lettuce is low and also R_d has a low value. A higher temperature during the measurements causes a higher C_c (HEATH and MEIDNER, 1967; NILWIK, 1980b), due to an increase in photorespiration in the leaves which intercept irradiance and to a higher R_d of the other plant parts. A significant influence of the treatment temperature on C_c is not expected (NILWIK, 1980b).

With the use of the effective leaf area (EL) for an analysis of the photosynthesis data the interpretation of the results is still complex. More extensive studies of the morphology of a lettuce plant are essential to solve the problems of light interception, CO_2 transport and diffusion from the external air to the carboxylation sites. The 'ideal' plant seems to be a plant with an open structure, a low $r_{a,cr}$, without a head and with a good light interception of all the leaves, but at the moment such a plant shape is not of commercial interest.

SUMMARY

In two experiments photosynthesis of whole lettuce shoots was measured in a closed system. During cultivation in both experiments 4 treatments of different irradiances and temperatures were applied to obtain plants with different habitus. In experiment 1 the response of photosynthesis to irradiance (I) was measured for plants of 3 ages at 14° and 26°C. In experiment 2 the response of photosynthesis to CO_2 -concentration (C) was measured at 15° and 25°C.

Attention was paid to the basis of expression for the photosynthetic rates, obtained per plant. The basis, effective leaf area (EL), is equal to soil cover (S), leaf area (A) and leaf weight (W) and to the gross photochemical efficiency (α_g), since $EL = \alpha_g \alpha_{g,con}^{-1}$ with $\alpha_{g,con}$ as the constant value of α_g when all light quanta are absorbed. A multilinear regression model of α_g with S, A and W gave high correlation coefficients, while addition of the profile area did not improve the model significantly.

In experiment 1 the gross photochemical efficiency per plant (α_g) and per unit leaf area (α_g^1), the maximal gross and net photosynthesis ($P_{m,g}$ and $P_{m,n}$) per plant and per unit leaf area ($P_{m,g}^1$), the dark respiration (R_d) per unit leaf weight and the light compensation point (I_c) were calculated by curve-fitting. In a 3-way analysis of variance some of these parameters, the net photosynthetic rates on α_g -basis at 35 and 100 Wm^{-2} and at light saturation, I_c and the corrected I_c ($= I_c \cdot \alpha_g$) were analysed. The values of α_g^1 and $P_{m,g}^1$ decreased with increasing age. The α_g -value was not affected by treatment and measurement temperatures. The photosynthetic rates on α_g -basis gave only lower values for the group of young plants. The effect of treatment on P_n diminished at 35 Wm^{-2} , but increased at

100 Wm⁻² and became more distinct at the saturated level of irradiance. The corrected P_n at 35 Wm⁻² is higher at 14° than at 26°C. This difference disappeared at 100 Wm⁻² and at saturating I the $P_{m,n}$ was higher at 26° than at 14°C. I_c is strongly influenced by measurement temperature. Corrected I_c -values were affected by age and not by treatment.

In experiment 2 the net conductance for CO₂ per plant (τ_n) and per unit leaf area (τ_n^1), the $P_{m,n}$ and $P_{m,n}^1$, and the CO₂ compensation concentration (C_c) were calculated. An increase in measurement temperature decreased τ_n and τ_n^1 , but affected the maximum photosynthetic rates positively. C_c depends strongly on temperature during measurement.

Observed differences between the parameters are discussed, also in relation to the stomatal and residual resistances and morphological properties of the plant such as specific leaf weight and plant structure.

ACKNOWLEDGEMENTS

I wish to thank Prof. Dr. Ir. J. F. BIERHUIZEN for reading and critisizing the manuscript. I am much indebted to Drs. H. J. M. NILWIK for the inspiring discussions and for his assistance in solving the mathematical problems. I also wish to thank Mrs. BERNADET TER HORST for her assistance in experiment 1. Acknowledgement is due to Mr. H. VAN LENT for his preparation of Figure 1.

REFERENCES

ACOCK, B., CHARLES-EDWARDS, D. A., FITTER, D. J., HAND, D. W., LUDWIG, L. J., WARREN WILSON, J. and WITHERS, A. C.: The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis. An experimental examination of two canopy models. – *J. exp. Bot.* **29**: 815–827, 1978.

ACOCK, B., CHARLES-EDWARDS, D. A. and HAND, D. W.: An analysis of some effects of humidity on photosynthesis by a tomato crop under winter light conditions and a range of carbon dioxide concentrations. – *J. exp. Bot.* **27**: 933–941, 1976a.

ACOCK, B., CHARLES-EDWARDS, D. A. and SAWYER, S.: Growth response of a chrysanthemum crop to the environment. III. Effects of radiation and temperature on dry matter partitioning and photosynthesis. – *Ann. Bot.* **44**: 289–300, 1979.

ACOCK, B. and HAND, D. W.: The effect of day temperature and CO_2 concentration on net photosynthesis. – *Ann. Rep. G.C.R.I.*, Littlehampton: 49, 1974.

ACOCK, B., HAND, D. W., THORNLEY, J. H. M. and WARREN WILSON, J.: Photosynthesis in stands of green pepper for application of empirical and mechanistic models to controlled-environment data. – *Ann. Bot.* **40**: 1293–1307, 1976b.

AKITA, S., MURATA, Y. and MIYASAKA, A.: On light-photosynthesis curves of rice leaves. – *Proc. Crop Sci. Soc. Jap.* **37**: 680–684, 1968.

ALBERDA, TH. et al.: Crop photosynthesis: methods and compilation of data obtained with mobile field equipment. – *Agr. Res. Rep. 865*, CABO, Wageningen: 1–46, 1977.

AUGUSTINE, J. J., STEVENS, M. A., BREIDENBACH, R. W. and PAIGE, D. F.: Genotypic variation in carboxylation of tomatoes. – *Plant Physiol.* **57**: 325–333, 1976.

BEARDSELL, M. F., MITCHELL, K. J. and THOMAS, R. G.: Effects of waterstress under contrasting environmental conditions on transpiration and photosynthesis in soybean. – *J. exp. Bot.* **24**: 579–586, 1973.

BENSINK, J.: On morphogenesis of lettuce leaves in relation to light and temperature. – *Meded. Landbouwhogeschool, Wageningen* **71** (15): 1–93, 1971.

BIERHUIZEN, J. F. and SLATYER, R. O.: Photosynthesis of cotton leaves under a range of environmental conditions in relation to internal and external diffusive resistances. – *Aust. J. biol. Sci.* **17**: 348–359, 1964.

BJÖRKMAN, O.: Carboxydismutase activity in shade-adapted and sun-adapted species of higher plants. – *Physiol. Plant.* **21**: 1–10, 1968.

BJÖRKMAN, O. and HOLMGREN, P.: Photosynthetic adaptation to light intensity in plants native to shaded and exposed habitats. – *Physiol. Plant.* **19**: 854–859, 1966.

BÖHNING, R. H. and BURNSIDE, C. A.: The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants. – *Am. J. Bot.* **43**: 557–561, 1956.

BRAVDO, B. A.: Carbondioxide compensation points of leaves and stems and their relation to net photosynthesis. – *Plant Physiol.* **48**: 607–612, 1971.

BROUWER, R. and HUYSKES, J. A.: A physiological analysis of the responses of the lettuce variety 'Rapide' and its hybrid with 'Hamadan' to day-length and light intensity. – *Euphytica* **17**: 245–251, 1968.

CARMER, S. G. and SWANSON, M. R.: An evaluation of the pairwise multiple comparison procedures by Monte Carlo methods. – *J. Amer. Statist. Assoc.* **63**: 66–74, 1973.

CHARLES-EDWARDS, D. A. and ACOCK, B.: Growth response of a chrysanthemum crop to the environment. II. A mathematical analysis relating photosynthesis and growth. – *Ann. Bot.* **41**: 49–58, 1977.

CHARLES-EDWARDS, D. A., CHARLES-EDWARDS, J. and SANT, F. I.: Leaf photosynthetic activity in six temperate grass varieties grown in contrasting light and temperature environments. – *J. exp. Bot.* **25**: 715–724, 1974.

CHARLES-EDWARDS, D. A. and LUDWIG, L. J.: A model for leaf photosynthesis by C_3 species. – *Ann. Bot.* **38**: 921–930, 1974.

DULLFORCE, W. M.: Effects of light, temperature and carbon dioxide on the growth of glasshouse lettuce (*Lactuca sativa* L.). – Ph.D. Thesis, Un. Nottingham: 1–150, 1968.

DULLFORCE, W. M.: The growth of winter glasshouse lettuce with artificial light. – *Acta Hort.* **22**: 199–210, 1971.

DUNCAN, W. G., LOOMIS, R. S., WILLIAMS, W. A. and HANAU, R.: A model for simulating photosynthesis in plant communities. – *Hilgardia* **38**: 181–205, 1967.

EENINK, A. H.: Energiebesparing in de slateelt door veredeling. – *Landb. Tijdschrift* **90**: 483–487, 1978.

EENINK, A. H. and SMEETS, L.: Genotype \times environment interactions with lettuce (*Lactuca* L.) in relation to the development of genotypes for growing under poor energy conditions. – *Neth. J. agric. Sci.* **26**: 81–98, 1978.

ENOCH, H. Z. and SACKS, J. M.: An empirical model of CO₂ exchange of a C₃ plant in relation to light, CO₂-concentration and temperature. – *Photosynthetica* **12**: 150–157, 1978.

FRASER, D. E. and BIDWELL, R. G. S.: Photosynthesis and photorespiration during the ontogeny of the bean plant. – *Can. J. Bot.* **52**: 2561–2570, 1974.

GAASTRA, P.: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. – *Meded. Landbouwhogeschool, Wageningen* **59** (13): 1–68, 1959.

GAASTRA, P.: Photosynthesis of leaves of field crops. – *Neth. J. agric. Sci.* **10**: 311–324, 1962.

GAASTRA, P.: Some physiological aspects of CO₂-application in glasshouse culture. – *Acta Hort.* **4**: 111–116, 1966.

HEATH, O. V. S. and MEIDNER, H.: Compensation points and carbondioxide enrichment for lettuce grown under glass in winter. – *J. exp. Bot.* **18**: 746–751, 1967.

HOLSTEIJN, H. M. C. VAN: A closed system for measurements of photosynthesis, respiration and CO₂ compensation points. – *Meded. Landbouwhogeschool, Wageningen* **79** (10): 1–14, 1979.

HOLSTEIJN, H. M. C. VAN: Growth of lettuce. I. Covering of soil surface. – *Meded. Landbouwhogeschool, Wageningen* **80** (7): 1–27, 1980a.

HOLSTEIJN, H. M. C. VAN: Growth of lettuce. II. Quantitative analysis of growth. – *Meded. Landbouwhogeschool, Wageningen* **80** (13): 1–24, 1980b.

HOLSTEIJN, H. M. C. VAN, BEHBOUDIAN, M. H. and BONGERS, H. C. M. L.: Water relations of lettuce. II. Effects of drought on gas exchange properties of two cultivars. – *Scientia Hort.* **7**: 19–26, 1977.

JONES, R. J. and MANSFIELD, T. A.: Increases in the diffusion resistance of leaves in a carbon dioxide enriched atmosphere. – *J. exp. Bot.* **21**: 951–958, 1970.

KOLLER, H. R. and DILLEY, R. A.: Light intensity during leaf growth affects chlorophyll concentration and CO₂ assimilation of soybean chlorophyll mutant. – *Crop Sci.* **14**: 779–782, 1974.

LOACH, K.: Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. – *New Phytol.* **66**: 607–621, 1967.

LOGAN, K. T.: Adaptations of the photosynthetic apparatus of sun and shade grown yellow birch (*Betula alleghaniensis* Britt.). – *Can. J. Bot.* **48**: 1681–1688, 1970.

LOGAN, K. T. and KROTKOV, G.: Adaptations of the photosynthetic mechanism of sugar maple (*Acer saccharum*) seedlings grown in various light intensities. – *Physiol. Plant.* **22**: 104–116, 1968.

LORENZ, H. P. and WIEBE, H. J.: Effect of temperature on photosynthesis of lettuce adapted to different light and temperature conditions. – *Scientia Hort.* **13**: 115–123, 1980.

LOUWERSE, W. and VAN OORSCHOT, J. L. P.: An assembly for routine measurements of photosynthesis, respiration and transpiration of intact plants under controlled conditions. – *Photosynthetica* **3**: 305–315, 1969.

LOUWERSE, W. and VAN DE ZWEERDE, W.: Photosynthesis, transpiration and leaf morphology of *Phaseolus vulgaris* and *Zea mays* grown at different irradiances in artificial and sun light. – *Photosynthetica* **11**: 11–21, 1977.

LUDLOW, M. M. and WILSON, G. L.: Photosynthesis of tropical pasture plants. II. Temperature and illuminance history. – *Aust. J. biol. Sci.* **24**: 1065–1076, 1971a.

LUDLOW, M. M. and WILSON, G. L.: Photosynthesis of tropical pasture plants. III. Leaf age. – *Aust. J. biol. Sci.* **24**: 1077–1087, 1971b.

LUDWIG, L. J., SAEKI, T. and EVANS, L. T.: Photosynthesis in artificial communities of cotton plants

in relation to leaf area. I. Experiments with progressive defoliation of mature plants. – Aust. J. biol. Sci. **18**: 1103–1118, 1965.

MARSHALL, B. and BUSCOE, P. V.: A model describing the dependence of net photosynthesis on irradiance. I. Derivation. – J. exp. Bot. **31**: 29–39, 1980.

MCCREE, K. J. and TROUGHTON, J. H.: Non-existence of an optimum leaf area index for the production rate of white clover under constant conditions. – Plant Physiol. **41**: 1615–1622, 1966.

NILWIK, H. J. M.: Photosynthesis of whole sweet pepper plants. I. Response to irradiance and temperature as influenced by cultivation conditions. – Photosynthetica **14**: 373–381, 1980a.

NILWIK, H. J. M.: Photosynthesis of whole sweet pepper plants. II. Response to carbon dioxide concentration, irradiance and temperature as influenced by cultivation conditions. – Photosynthetica **14**: 382–391, 1980b.

NILWIK, H. J. M. and TEN BÖHMER, H.: An improved closed system for continuous measurement of photosynthesis, respiration and transpiration. – Meded. Landbouwhogeschool, Wageningen **81** (4): 1–9, 1981.

PATTERSON, D. T., BUNCE, J. A., ALBERTE, R. S. and VAN VOLKENBURGH, E.: Photosynthesis in relation to leaf characteristics of cotton from controlled and field environments. – Plant Physiol. **59**: 384–387, 1977.

PEAT, W. E.: Relationships between photosynthesis and light intensity in the tomato. – Ann. Bot. **34**: 319–328, 1970.

RABINOWITCH, E. I.: Photosynthesis and related processes. Vol. II. Interscience Publ. Inc., New York, 1951.

REINKEN, G., WEISS, B. and ZISCHKA, W.: Die Photosynthese der wichtigsten Gemüsearten unter Glass. – Ber. Versuchen Untersuchungen II: 45–67, 1973.

SALE, P. J.: Net carbon exchange rates of field-grown crops in relation to irradiance and dry weight accumulation. – Aust. J. Plant Physiol. **4**: 555–569, 1977.

SARTI, A.: Growth and photosynthetic activity of *Lactuca sativa* cv. *romana*, cultivated in three day light intensities. – Lab. Radiobiologia ed Ecobiologia Vegetali. C.N.R., Roma: 1–13, 1973.

SARTI, A., LOUASON, G. and CORNIC, G.: A study of the Kok-effect on *Lactuca sativa* cv *romana*. – Phytotronic Newsletter **16**: 38–43, 1977.

SORIBE, F. I. and CURRY, R. D.: Simulation of lettuce growth in an air-supported plastic greenhouse. – J. agric. Engin. Res. **18**: 133–140, 1973.

TAKAKURA, T.: Plant growth optimisation using a small computer. – Acta Hort. **46**: 147–156, 1975.

TATSUMI, M. and HORI, Y.: Studies on the photosynthesis of vegetable crops. I. Photosynthesis of young plants of vegetables in relation to light intensity. – Bull. Hort. Res. Stat. Hiratsuka, Kanagawa, Ser. A**8**: 127–140, 1969. (Eng. summary and subtitles.)

TATSUMI, M. and HORI, Y.: Studies on photosynthesis of vegetable crops. II. Effect of temperature on the photosynthesis of young plants of vegetables in relation to light intensity. – Bull. Hort. Res. Stat. Hiratsuka, Kanagawa, Ser. A**9**: 181–188, 1970 (Engl. summary and subtitles).

THORNLEY, J. H. M.: Photosynthesis. In: Mathematical Models in Plant Physiology. A quantitative approach to problems in plant and crop physiology. Academic Press, London: 92–110, 1976.

TOOMING, H.: Mathematical model of plant photosynthesis considering adaptation. – Photosynthetica **1**: 233–240, 1967.

WIEBE, H. J. und LORENTZ, H. P.: Wirkung von Wechseltemperatur und lichtabhängiger Temperaturregelung auf des Wachstums von Kopfsalat. – Gartenbauwiss. **42**: 42–45, 1977.

WITTWER, S. H. and ROB, W.: Carbon dioxide enrichment of greenhouse atmospheres for food crop production. – Econ. Bot. **18**: 34–56, 1964.