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PHOTOSYNTHESIS OF LETTUCE
II. RESULTS WITH BUTTERHEAD, COS- AND
ICEBERG LETTUCE CULTIVARS

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INTRODUCTION

For many decades selection to improve yield and quality of lettuce has been carried out for outdoor and glass-house cultivation. The butterhead cultivar 'Meikoningin', for instance, is introduced since 1902 and suitable for glass-house cultivation. It was almost the only cultivar grown under glass in winter until 1950 (RODENBURG, 1960). The outdoor cultivar 'Hilde' was introduced since 1947 (HUYSKES, 1960) and the cos-lettuce cultivar 'Sucrine' was already mentioned in 1880 (RODENBURG, 1960). In The Netherlands special attention has been paid to the breeding and selection for glass-house cultivars with a higher yield, better performance and heading capacity, and resistances against diseases and tipburn (BANGA, 1939; EENINK and ALVAREZ, 1975; EENINK and GARRETSEN, 1977, GROENEWEGEN, 1952; HUYSKES, 1958, 1968; HUYSKES and RODENBURG, 1965, 1968; RODENBURG, 1960, 1968a, b) and for other lettuce types, such as iceberg lettuce (RODENBURG, 1972).

Differences in yield were related to differences in relative growth rate (SCAIFE, 1973; LEE, 1974), leaf area ratio (DULLFORCE, 1963; VAN HOLSTEIJN, 1980b), leaf number (EENINK and SMEETS, 1978; SMEETS, 1977) and leaf size (SMEETS, 1977) and with different reactions to changes in environmental conditions (EENINK and SMEETS, 1978). BROUWER and HUYSKES (1968) measured gas exchange rates of the cultivar 'Rapide' and the F_2 of 'Rapide' and 'Hamadan' and concluded that differences were caused by the exposed leaf area of a plant to light. They mentioned that the basis of expression for photosynthesis plays an important role in the calculation and explanation of the measured photosynthetic rates.

Many data are available on research between varietal differences in photosynthetic rates and yield of various crops such as grains (APEL and LEHMANN, 1969; DANTUMA, 1973; HEICHEL and MUSGRAVE, 1969), grass (CARLSON et al., 1971; CHARLES-EDWARDS et al., 1974), soybean (DORNHOFF and SHIBLES, 1970; DREGER et al., 1969), other beans (IZHAR and WALLACE, 1967), sugarcane (IRVINE, 1967), cotton (EL-SHARKAWY et al., 1965), peanut (PALLAS and SAMISH, 1974), coffee (NUNES et al., 1969) or a glass-house crop like tomato (AUGUSTINE et al., 1976; GOSIEWSKI et al., 1981; NILWIK et al., 1981). The observed differences in photosynthetic rates of the leaves, however, did not always correspond with similar differences in crop or grain yield (e.g. DANTUMA, 1973; EL-SHARKAWY et al., 1965; DE VOS, 1977). Thus, selection based on photosynthetic rate or photochemical efficiency of the measured leaves did not always result in a higher yield. Moreover, most gas exchange measurements were done on leaf level (e.g. AUGUSTINE et al., 1976; CHARLES-EDWARDS et al., 1974; DANTUMA, 1973; EL-SHARKAWY et al., 1965), while only a part of the plant and not always the leaves

were harvested. For lettuce the situation is different from most of the above mentioned crops since the whole shoot is harvested. Due to the rosette form of butterhead lettuce gas exchange measurements of single leaves are difficult and do not give a reliable estimate of plant growth.

Results of plant measurements are still difficult to interpret, as was discussed in a previous paper (VAN HOLSTEIJN, 1981). In that paper a basis of expression for the photosynthesis data of butterhead cultivar 'Amanda Plus' was developed, which procedure has been employed also for data of that and other cultivars described in this paper. The photosynthetic rates per plant will be divided by the gross photochemical efficiency (α_g) calculated per plant, and the light compensation point is multiplied with α_g . Experiments are described on the photosynthetic capacity of 3 butterhead cultivars and their relation with other plant properties under various environmental circumstances, and of a number of butterhead, cos- and iceberg lettuce cultivars, grown in spring.

MATERIALS AND METHODS

Six experiments were carried out with butterhead, cos- and iceberg lettuce (*Lactuca sativa* L.) cultivars (Table 1). In 5 experiments (1, 2, 3, 5 and 6) the butterhead cultivars 'Amanda Plus', 'Ostinata' and 'Hilde' were used. 'Amanda Plus' had also been used in previous experiments (VAN HOLSTEIJN et al., 1977; VAN HOLSTEIJN, 1981). 'Ostinata' is selected for glass-house cultivation from late spring until early autumn and 'Hilde' for outdoor cultivation from late spring until late autumn (HUYSKES, 1960). In the first spring experiment (exp. 3) the butterhead cultivars 'Decimino', 'Meikoningin', 'Rapide' and 'Valentine' were used, which were investigated in a previous experiment on the process of soil covering (VAN HOLSTEIJN, 1980a). 'Amanda Plus', 'Ostinata' and 'Hilde' were also used. In the second spring experiment (exp. 4) the butterhead cultivars 'Cynthia', 'Noran', 'Profos', 'Ravel' and 'Tornado', all selected for glass-house cultivation in spring, the cos-lettuce cultivars 'Sucrine' and 'Plucos' and the iceberg lettuce genotypes C-5 and Y-6 were used. 'Tornado' is an upright cultivar with another pattern of growth and another habitus than other butterhead cultivars. 'Sucrine' is a semi cos-lettuce cultivar and 'Plucos' a short-day glass-house cos-lettuce. The two iceberg lettuce genotypes were selected for spring glass-house conditions (VAN ESCH, 1976).

In all experiments the seeds were sown and the seedlings selected according to a procedure as described in previous experiments (VAN HOLSTEIJN, 1981). Information about sowing date, average day and night temperatures before and after transplanting into 2-litre pots, which marks the beginning of the various treatments, average level of irradiance (400–700 nm) and the dates of the gas exchange measurements is given in Table 1. Until transplanting all plants were cultivated in a Venlo glass-house. Plants of experiment 1 were grown in the phytotron of the Laboratory of Horticulture, Wageningen (DOORENBOS, 1964) without cultural problems. In the other experiments plants were cultivated under

TABLE 1. Data concerning cultivar, sowing date, start of treatment and environmental conditions of the six experiments with butterhead, cos- and iceberg lettuce cultivars. Day and night temperatures and levels of irradiance represent average values over the mentioned periods. 16 PH = 16 hours phytotron light; G = glass-house cultivation; O = outdoor cultivation.

Experiment	Cultivars	Date of		Day/night temperature (°C)		Irradiance (Wm ⁻²)	
		sowing	start treatment	measurements	until start treatment		during treatment
1 16 PH	Amanda Plus	Sept. 19	Oct. 10	Nov. 3-5	22.0/14.7	21.0/13.0	29.1
	Ostinata	"	"	"	"	"	"
	Hilde	"	"	"	"	"	"
	Amanda Plus	Sept. 19	Oct. 10	Nov. 5-7	22.0/14.7	19.4/14.1	40.1
	Ostinata	"	"	"	"	"	"
	Hilde	"	"	"	"	"	"
	Amanda Plus	Jan. 12	Febr. 24	March 22-26	15.3/9.6	19.3/14.0	39.3
	Ostinata	"	"	"	"	16.3/9.6	51.5
	Hilde	"	"	"	"	"	"
	Hilde	"	"	"	"	16.4/9.6	52.8
2 G	Decimnor	"	"	"	"	"	"
	Meikoningin	"	"	"	"	"	"
	Rapide	"	"	"	"	"	"
	Valentine	"	"	"	"	"	"
	Cynthia	Febr. 9	March 17	April 13-22	16.1/9.8	16.7/ 9.9	58.9
	Noran	"	"	"	"	16.5/ 9.9	57.4
	Profos	"	"	"	"	17.7/10.0	63.3
	Ravel	"	"	"	"	16.7/ 9.9	58.9
	Tornado	"	"	"	"	"	58.1
	Sucrine	Febr. 7	"	"	"	17.7/10.0	63.3
3 G	Plucos	Febr. 9	"	"	"	16.5/ 9.9	57.4
	C-5	Febr. 7	"	"	"	16.7/ 9.9	58.1
	Y-6	"	"	"	"	17.7/10.0	64.0
	Amanda Plus	May 19	June 7	June 23-24	23.2/17.0	26.5/18.3	89.3
	Ostinata	"	"	"	"	26.6/18.4	87.6
	Hilde	"	"	"	"	26.5/18.3	89.3
	Amanda Plus	May 19	June 7	June 22-23	23.2/17.0	20.5/15.1	148.2
	Ostinata	"	"	"	"	"	"
	Hilde	"	"	"	"	20.1/15.9	146.1

natural daylight. In all experiments plants were sprayed twice with TMTD and in experiments 1 and 2 twice with zineb as well. Fertilization was applied once during cultivation.

Measurements of both photosynthesis and transpiration were carried out in the gas exchange assembly, an open system, described by LOUWERSE and VAN OORSCHOT (1969). Four plants of one cultivar were measured simultaneously in the 4 plant chambers. Each chamber was considered as one replicate. The shoot part was sealed off from the root part, which was kept outside the chamber at about 21 °C. Light series consisted of 6 irradiance levels in a sequence from darkness to the maximal level of irradiance, which varied between 160 and 220 Wm⁻². The irradiance was calculated at top level of the plant. The plant chamber temperature was kept at 22 ± 1 °C. One light series lasted about 2.5 hours. Each day two series were carried out. The incoming CO₂-concentration was kept at 570 mgm⁻³ and the humidity of the incoming air was constant. Plants of the same size and weight as those of age B in a previous experiment (VAN HOLSTEIJN, 1981) were used, except the plants in experiment 4 which were larger than the others. Immediately after the gas exchange measurements the fresh weight, leaf area and dry weight (after one week at 65 °C in the oven) were obtained. The leaf area was measured by a Hyaski Denke planimeter, type AAM-5. Photos of the covered soil area and the profile area were taken the evening before the beginning of the measurements. Photosynthesis, transpiration, stomatal and residual resistances were calculated according to the methods described by LOUWERSE and VAN OORSCHOT (1969).

Following the theory, explained in a previous article (VAN HOLSTEIJN, 1981), regressions were calculated through the photosynthesis data per plant with the

use of the equation $P_g = P_n + R_d = \frac{\alpha_g I P_{m,g}}{\alpha_g I + P_{m,g}}$. By this procedure the gross

photochemical efficiency (α_g), the maximal gross and net photosynthesis ($P_{m,g}$ and $P_{m,n}$), the dark respiration (R_d) and the light compensation point (I_c) were calculated. A two way analysis of variance was done with the data of 'Amanda Plus', 'Ostinata' and 'Hilde' from experiments 1, 2, 3, 5 and 6, and a one way analysis of variance was done with the data of the two spring experiments (exp. 3 and 4).

RESULTS

The calculated data of the photosynthesis-irradiance response curves, the stomatal and residual resistances, the specific leaf weight and the Tukey's Honest Significant Difference ($p < 0.01$; CARMER and SWANSON, 1973) are listed in Table 2.

The values of the gross photochemical efficiency per unit leaf area (α_g^1) are inaccurate, since only a part of the leaf area contributes to photosynthesis. The differences between α_g^1 are smaller between 'Amanda Plus', 'Ostinata' and 'Hilde'

TABLE 2. Parameters describing the response of net photosynthesis (P_n) to irradiance (I) for the cultivars of experiments 1–6. The results of experiment 3 are divided into two groups. Measurements were carried out at $22 \pm 1^\circ\text{C}$ and at an external CO_2 -concentration of 570 mg m^{-3} . α_g^1 : photochemical efficiency (in $I=0$) expressed per unit leaf area ($\text{mg CO}_2 \text{ J}^{-1}$); $P_{m,n}$ and $P_{m,n}^1$: P_n 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}); r_s and r_m : stomatal and residual resistance (s cm^{-1}). Specific leaf weight (SLW) is expressed in g m^{-2} . Values represent means of 4 plants. THSD: Tukey's Honest Significant Difference ($p < 0.01$), calculated for the results of 'Amanda Plus', 'Ostinata' and 'Hilde' (= THSD_{AOH} of experiments 1, 2, 3, 5 and 6), and the 2 spring experiments (3 and 4).

Experiment	Cultivar	Results							
		$10^3 \alpha_g^1$	$P_{m,n}$	$P_{m,n}^1$	R_d	I_c	r_s	r_m	SLW
1	Amanda Plus	3.20	180.3	8.47	4.44	6.1	11.1	19.9	14.8
	Ostinata	3.16	184.4	9.00	4.21	6.4	9.8	20.1	16.0
	Hilde	2.36	236.1	6.85	4.00	6.1	12.8	25.3	12.4
2	Amanda Plus	4.27	126.1	11.67	4.58	4.9	9.5	15.7	15.5
	Ostinata	4.09	157.4	12.22	5.06	5.3	9.3	17.3	14.4
	Hilde	3.15	100.1	8.25	5.51	6.2	12.2	24.3	11.9
3	Amanda Plus	2.92	200.2	14.39	4.63	10.7	10.7	9.8	22.5
	Ostinata	2.82	207.9	17.27	4.88	10.7	8.8	11.0	21.1
	Hilde	2.93	230.8	15.50	4.63	10.7	10.7	8.6	22.5
5	Amanda Plus	2.50	234.2	14.96	5.98	12.0	11.2	11.8	16.9
	Ostinata	2.08	249.9	15.60	5.73	14.6	9.8	15.1	17.8
	Hilde	2.05	300.6	16.00	5.72	12.3	10.9	12.5	15.2
6	Amanda Plus	1.74	285.5	19.23	5.40	17.6	11.1	15.2	19.3
	Ostinata	1.87	257.8	18.09	5.46	17.5	11.4	13.4	20.7
	Hilde	1.87	315.4	22.01	5.62	16.1	10.9	12.4	18.2
THSD _{AOH}		0.32	24.5	1.80	0.79	1.1	5.1	5.2	2.8
3	Deciminator	2.63	197.1	13.76	3.64	10.4	9.5	12.1	26.4
	Meikoningin	2.74	216.6	17.70	4.50	12.3	8.9	11.7	24.8
	Rapide	2.56	199.7	12.58	3.78	10.1	12.2	10.9	23.0
	Valentine	2.10	181.3	11.38	4.22	12.4	12.1	16.0	20.6
THSD ₃		0.28	24.3	1.79	0.62	1.2	2.9	4.0	4.9
4	Cynthia	2.12	320.7	11.05	4.23	12.8	13.9	12.3	20.6
	Noran	2.16	321.5	11.87	4.72	12.9	13.1	12.1	19.6
	Profos	1.73	261.2	11.23	4.71	13.8	13.2	17.2	22.3
	Ravel	2.13	372.4	12.98	4.47	15.1	10.8	13.1	23.4
	Tornado	3.38	369.0	15.32	4.86	11.6	9.1	9.9	26.0
	Sucrine	1.94	280.5	15.19	3.31	17.8	12.1	13.7	34.8
	Plucos	3.07	365.9	15.34	4.56	13.0	8.2	10.0	28.9
	C-5	2.32	343.4	16.15	4.51	16.6	9.8	11.8	28.3
THSD ₄		2.08	338.0	15.84	3.95	17.4	11.5	12.2	30.3
THSD ₄		0.37	52.1	2.21	0.69	1.9	3.3	3.9	5.6

than between the treatments of experiments 1, 2, 3, 5 and 6. The plants grown under low light conditions (exp. 1 and 2) showed the highest values. The α_g^1 of 'Valentine' is significantly lower than that of the other cultivars in experiment 3. In experiment 4 'Tornado' and 'Plucos' showed a high α_g^1 -value and 'Profos' and 'Sucrine' a low one, while the α_g^1 of the other butterhead cultivars and the two iceberg genotypes demonstrates intermediate values.

The maximal net photosynthesis per plant ($P_{m,n}$) was necessary for the analysis of variance (Table 3), while the maximal net photosynthetic rate per unit leaf area ($P_{m,n}^1$) is usually reported in literature. From the latter parameter ($= \tau_n^1 C$) the plant conductance for CO_2 transfer at the light saturation level (τ_n^1) and the overall plant resistance for CO_2 per unit leaf area ($= 1/\tau_n^1$) can be calculated. Plants of 'Amanda Plus', 'Ostinata' and 'Hilde' cultivated at high irradiance (exp. 3, 5 and 6) show higher values of $P_{m,n}^1$ than those grown under poor light conditions (exp. 1 and 2). Significant differences between α_g^1 - (and $P_{m,n}^1$ -) values of 'Amanda Plus' and 'Ostinata' are almost absent, while 'Hilde' deviates significantly from those two cultivars in experiments 1, 2 (and 6). A low $P_{m,n}^1$ -value of 'Valentine' and a significantly higher value of 'Meikoningin' were observed in experiment 3. The values of $P_{m,n}^1$ in experiment 4 differ between the normal butterhead cultivars 'Cynthia', 'Noran', 'Profos', 'Ravel' and 'Tornado', the non-heading cos-lettuce cultivars and the two heading iceberg lettuce genotypes.

The measured and calculated dark respiration values were in good agreement with each other. For this reason only the calculated values are presented. The differences between the R_d -values of 'Amanda Plus', 'Ostinata' and 'Hilde', of the cultivars of experiments 3 and 4 and of the treatments in experiments 1, 2, 3, 5 and 6 are small. Only during summer (exp. 5 and 6) the plants of 'Amanda Plus', 'Ostinata' and 'Hilde' demonstrate significantly higher R_d -values compared with the other plants. For all cultivars and treatments the R_d as percentage of $P_{m,g}$, both per plant, remained below 8% with small differences between the cultivars.

Small but significant differences occur between I_c -values of 'Amanda Plus', 'Ostinata' and 'Hilde' (exp. 2 and 5) and also between the butterhead cultivars in experiments 3 and 4. The effect of environmental conditions during cultivation on I_c , however, is much more pronounced as shown in the experiments with 'Amanda Plus', 'Ostinata' and 'Hilde'. Plants cultivated at a high level of irradiance showed high I_c -values.

The stomatal (r_s) and residual resistances (r_m) are calculated from the actual photosynthesis and transpiration data at the highest available level of irradiance during measurement. This level is below the calculated saturation level. No significant differences in r_s were observed between 'Amanda Plus', 'Ostinata' and 'Hilde' or between the various experiments of those cultivars (high THSD-value). Significant differences in r_m occurred with 'Hilde' (exp. 1 and 2) and between the various experiments with the 3 cultivars. A poor light period resulted in a higher r_m . Significant differences in r_s and r_m of the cultivars in the two spring experiments (exp. 3 and 4) existed. In experiment 3 'Valentine' and in 4 'Profos' had a high r_m . In experiment 4 'Plucos' and 'Tornado' had a low r_s and r_m .

The calculated data of the overall plant resistance for CO_2 transfer at the saturated level of irradiance ($1/\tau_n^1$) were compared with the sum of r_s and r_m . The value of $1/\tau_n^1$ did not exceed the sum of r_s and r_m . The correlation coefficient (r) between $1/\tau_n^1$ and the sum of the two resistances for all data together is 0.81. For experiments 1, 2, 3, 5 and 6 with 'Amanda Plus', 'Ostinata' and 'Hilde', for experiment 3 and experiment 4, r was respectively 0.83, 0.87 and 0.72. The correlation coefficients of $1/\tau_n^1$ with r_s were, in the above mentioned sequence, 0.40, 0.42, 0.86

and 0.78 and the coefficients with r_m were 0.93, 0.88, 0.61 and 0.55. The correlation between the overall resistance for CO_2 transfer and r_s is low for 'Amanda Plus', 'Ostinata' and 'Hilde' in experiments 1, 2, 3, 5 and 6, but high for the various cultivars in the two spring experiments, while for the correlation of this overall resistance for CO_2 with r_m the opposite situation occurs.

For butterhead cultivars the specific leaf weight (SLW) is mainly influenced by the cultivation conditions (experiments 1, 2, 3, 5 and 6). In experiment 3 'Valentine' has a low SLW. The SLW of 'C-5' and 'Y-6' correspond more with the SLW of the cos-lettuce than with the butterhead cultivars. A high correlation exists between SLW and r_m ($r = -0.85$), when the differences between SLW are caused by the environmental conditions during cultivation (experiments 1, 2, 3, 5 and 6). A low correlation exists, when those differences are due to the various cultivars ($r = 0.19$ and -0.17 for experiments 3 and 4, resp.).

For similar reasons as in a previous paper concerning photosynthesis (VAN HOLSTEIJN, 1981) a multilinear regression between α_g per plant and soil cover (S), leaf area (A) and dry weight (W) was carried out. The results are listed in Table 3. In all cases the correlation coefficient of α_g with S is higher than that of α_g with A or W, which is in agreement with earlier results (VAN HOLSTEIJN, 1981).

A two and one way analysis of variance of the gross photochemical efficiencies, the maximal net photosynthesis and net photosynthetic rates at 30, 50, 70, 100 and 150 W m^{-2} , divided by α_g , the maximal net photosynthesis per unit soil cover area and the light compensation point values were carried out and the results are listed in Table 4. A two way analysis has been done with the results of 'Amanda Plus', 'Ostinata' and 'Hilde', grown in 5 experiments (nrs. 1, 2, 3, 5 and 6; Table 4a) and a one way analysis with the results of the 7 cultivars in experiment 3 (Table 4b) and of the 9 cultivars of experiment 4 (Table 4c). The analysis of variance of the net photochemical efficiencies and the maximal gross photosynthetic rates gave almost similar results as the respective gross and net values listed in this table. Therefore these values are not presented. According to the procedure followed in a previous paper (VAN HOLSTEIJN, 1981) the photosynthetic rates are divided by α_g and the light compensation point is multiplied by this parameter.

TABLE 3. The correlation coefficients of the regressions between the gross photochemical efficiency on plant basis, α_g , and soil cover (S), leaf area (A) and leaf dry weight (W) for the data of 'Amanda Plus', 'Ostinata' and 'Hilde' of experiments 1, 2, 3, 5 and 6 and for the data of experiments 3 and 4.

Treatment/Cultivar	Correlation coefficients (r) of			
	linear regression of α_g with			the multilinear model
	S	A	W	
Amanda Plus, Ostinata and Hilde	0.89	0.87	0.71	0.81
7 cultivars in experiment 3	0.81	0.66	0.61	0.68
9 cultivars in experiment 4	0.77	0.70	0.54	0.70

TABLE 4. Results of a two way analysis of variance of the data of cultivars 'Amanda Plus', 'Ostinata' and 'Hilde' in experiments 1, 2, 3, 5 and 6 (Table 4a) and the one way analysis of variance for experiments 3 (Table 4b) and 4 (Table 4c). α_g and α_d : photochemical efficiencies (in I = 0) per plant ($\text{mg CO}_2 \text{ m}^{-2} \text{ Pl}^{-1} \text{ J}^{-1}$) and per unit leaf area ($\text{mg CO}_2 \text{ J}^{-1}$); $P_{m,n} \alpha_g^{-1}$, $P_{n,30} \alpha_g^{-1}$, $P_{n,50} \alpha_g^{-1}$, $P_{n,70} \alpha_g^{-1}$, $P_{n,100} \alpha_g^{-1}$ and $P_{n,150} \alpha_g^{-1}$ (Wm^{-2}): net photosynthetic rates at saturated level of irradiance and at respectively 30, 50, 70, 100 and 150 Wm^{-2} , expressed on basis of α_g ; $P_{m,n} S^{-1}$: maximum net photosynthesis per unit soil cover area ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$); I_c and $I_c \alpha_g$: light compensation point (Wm^{-2}) and corrected light compensation point ($\text{mg CO}_2 \text{ Pl}^{-1} \text{ s}^{-1}$). Mean values with similar characters do not differ significantly from each other according to Duncan's Multiple Range Test ($p < 0.01$). ** = significant difference; ns = no significant difference.

Factor	Degrees of freedom	Results										
		$10^3 \alpha_g$	$10^3 \alpha_d$	$P_{m,n} \alpha_g^{-1}$	$P_{n,30} \alpha_g^{-1}$	$P_{n,50} \alpha_g^{-1}$	$P_{n,70} \alpha_g^{-1}$	$P_{n,100} \alpha_g^{-1}$	$P_{n,150} \alpha_g^{-1}$	$P_{m,n} S^{-1}$	I_c	$10^3 I_c \alpha_g$
a. cultivar	2	ns	**	ns	ns	**	-	ns	ns	ns	ns	ns
Amanda Plus		0.438 ^a	2.93 ^b	130.2 ^a	12.4 ^a	22.7 ^a	-	41.3 ^a	53.6 ^a	44.4 ^a	10.3 ^a	4.01 ^a
Ostinata		0.425 ^a	2.80 ^b	138.3 ^a	12.5 ^a	22.7 ^a	-	42.0 ^a	56.1 ^a	46.3 ^a	10.9 ^a	4.04 ^a
Hilde		0.455 ^a	2.47 ^a	144.7 ^a	12.6 ^b	23.2 ^b	-	42.3 ^a	55.6 ^a	37.7 ^a	10.3 ^a	4.21 ^a
experiment	4	**	**	**	**	**	-	**	**	**	**	**
1		0.714 ^d	2.91 ^c	66.8 ^a	13.9 ^d	21.7 ^a	-	34.0 ^b	41.0 ^b	26.7 ^a	6.2 ^a	4.43 ^{bc}
2		0.457 ^c	3.84 ^d	63.0 ^b	14.1 ^d	21.9 ^a	-	33.4 ^b	39.6 ^a	20.7 ^a	5.5 ^a	2.52 ^a
3		0.393 ^b	2.89 ^c	129.9 ^b	13.0 ^c	23.9 ^c	-	44.1 ^b	57.8 ^b	44.5 ^b	10.7 ^b	4.22 ^b
5		0.368 ^b	2.21 ^b	169.1 ^c	11.9 ^b	23.8 ^c	-	47.1 ^c	64.0 ^c	50.8 ^c	13.0 ^c	4.78 ^c
6		0.265 ^a	1.83 ^a	260.0 ^d	9.6 ^a	23.0 ^b	-	50.9 ^d	72.9 ^d	71.7 ^d	17.1 ^d	4.53 ^{bc}
interaction	8	**	**	ns	**	ns	-	ns	ns	ns	ns	ns
cultivar-experiment	45											
error	1											
mean	60	0.439	2.73	137.8	12.5	22.9	-	41.9	55.1	42.8	10.5	4.09
b. cultivar	6	**	**	**	-	ns	-	-	-	ns	ns	ns
Amanda plus		0.406 ^{ab}	2.92 ^b	137.0 ^a	-	27.1 ^a	-	-	-	42.1 ^a	10.7 ^{ab}	4.35 ^a
Ostinata		0.339 ^a	2.82 ^b	170.0 ^{bc}	-	28.9 ^b	-	-	-	47.0 ^b	10.7 ^{ab}	3.65 ^a
Hilde		0.436 ^b	2.93 ^b	147.1 ^{abc}	-	27.9 ^{ab}	-	-	-	44.6 ^a	10.7 ^{ab}	4.65 ^a
Decimior		0.377 ^{ab}	2.63 ^b	145.2 ^{ab}	-	28.0 ^{ab}	-	-	-	45.8 ^a	10.4 ^{ab}	3.92 ^a
Meikoningin		0.335 ^a	2.74 ^b	179.6 ^c	-	28.4 ^{ab}	-	-	-	53.3 ^a	12.3 ^b	4.14 ^a
Rapide		0.406 ^{ab}	2.56 ^{ab}	136.6 ^c	-	27.6 ^{ab}	-	-	-	44.3 ^a	10.1 ^a	4.10 ^a

Valentine										
error	21	0.334 ^a	2.10 ^a	150.8 ^{abc}	26.7 ^a			44.3 ^a	12.4 ^b	4.14 ^a
mean	1	0.376	2.67	152.3	27.8			45.9	11.0	4.14
total	28									
c. cultivar		8	**	**	-	-	ns	ns	**	**
Cynthia		0.616 ^{cd}	2.12 ^{ab}	144.6 ^b	-	-	38.2 ^a	51.3 ^{ab}	12.8 ^a	7.89 ^{abc}
Noran		0.585 ^{bcd}	2.16 ^{ab}	152.7 ^{abc}	-	-	38.6 ^a	52.5 ^{ab}	12.9 ^{ab}	7.55 ^{abc}
Profos		0.403 ^a	1.73 ^a	180.0 ^{abcd}	-	-	39.4 ^a	52.2 ^{ab}	13.8 ^{abc}	5.56 ^a
Ravel		0.610 ^{bcd}	2.13 ^{ab}	169.6 ^{abcd}	-	-	39.2 ^a	55.1 ^b	15.1 ^{abcd}	9.21 ^c
Tornado		0.813 ^e	3.38 ^c	126.1 ^a	-	-	38.3 ^a	54.5 ^b	11.6 ^a	9.43 ^c
Sucrerie		0.358 ^a	1.94 ^{ab}	217.6 ^d	-	-	40.0 ^a	52.5 ^{ab}	17.8 ^d	6.37 ^{ab}
Plucos		0.732 ^{de}	3.07 ^c	138.9 ^{ab}	-	-	38.1 ^a	37.2 ^a	13.0 ^{ab}	9.53 ^c
C-5		0.494 ^{abc}	2.32 ^b	193.1 ^{bcd}	-	-	39.3 ^a	59.0 ^b	16.6 ^{bcd}	8.20 ^{bc}
Y-6		0.444 ^{ab}	2.08 ^{ab}	211.5 ^{cd}	-	-	39.4 ^a	57.8 ^b	17.4 ^{cd}	7.73 ^{abc}
error	27	0.561	2.33	170.4			38.9	52.5	14.5	7.94
mean	1									
total	36									

The five levels of irradiance for which the rate of photosynthesis is calculated correspond with those during cultivation.

No significant differences could be shown between the α_g -values of the 3 cultivars in 5 experiments and between the net photosynthetic rates in those experiments, except for small differences for $P_{n,50}$ (Table 4a). Differences between net photosynthetic rates are caused by the environmental conditions during growth. Plants of 'Amanda Plus', 'Ostinata' and 'Hilde', grown under poor light conditions, have a lower $P_{m,n}$ and lower other photosynthetic rates (on α_g -basis) at irradiance levels above their cultivation level. However, those plants demonstrate higher rates when measured at a level lower or close to that of their growth, when compared with the plants grown under high levels of irradiance. The results of $P_{m,n}$ per unit soil area show a similar pattern as $P_{m,n}$ on α_g -basis. The low uncorrected I_c -values are also due to a low irradiance during cultivation, while the corrected values show relatively smaller differences between the experiments. For both light compensation points differences between 'Amanda Plus', 'Ostinata' and 'Hilde' are absent. Significant interaction between the cultivars and the treatments occurs only for the photochemical efficiencies and the values of $P_{n,30}$.

Relatively small, but significant differences occur between the photochemical efficiencies and maximal photosynthesis on α_g -basis of the 7 cultivars of experiment 3 (Table 4b). Almost no significant differences were obtained between the net photosynthetic rates on α_g -basis, when the plants of the various cultivars were measured at the level of irradiance close to that during cultivation. No significant differences are shown for the $P_{m,n}$ on soil cover basis and for both light compensation points in experiment 3.

Even between more heterogeneous lettuce genotypes no significant differences in net photosynthesis occur, when measured at the level of irradiance similar to that during cultivation (Table 4c). In table 4c the other parameters differ more between the cultivars than in tables 4a and b. The differences in 4c are mainly caused by the plants with another pattern of growth and heading than the butterhead cultivars. The parameters of 'C-5' and 'Y-6' do not differ significantly from each other. 'Tornado' and 'Plucos' have low $P_{m,n}$ -values on α_g -basis and 'Plucos' also on S-basis. Cos-lettuce 'Sucrine' and iceberg lettuce plants show high maximal photosynthetic rates and high uncorrected I_c -values.

In general it can be concluded from table 4 that differences between the various photosynthesis data of closely related butterhead lettuce cultivars are due to different cultivation conditions, and that after growth under similar conditions differences between photosynthesis data may only occur, when butterhead cultivars with another habitus than those generally grown in horticultural practice or other than butterhead types are investigated.

DISCUSSION

In a previous article (VAN HOLSTEIJN, 1981) problems with the interpretation of gas exchange data of whole lettuce plants have been discussed. These problems increase when besides various treatments also various cultivars are used. Cos-lettuce plants, for instance, do not form a close head like butterhead lettuce, but they have also a rosette habitus and an accumulation of many leaves on a short stem. Gas exchange data per plant represent the overall accumulation of CO_2 , while not all plant parts contribute equally to the measured total values. The SLW represents the average specific leaf weight of all leaves, while the SLW of those leaves mainly involved in the photosynthetic process is more important. The introduction of the effective leaf area (EL) by VAN HOLSTEIJN (1981) offered a reliable basis to compare photosynthetic rates and light compensation points. This procedure has also been applied in this paper. However, the plant conductance for CO_2 transfer (τ), r_s , r_m and SLW are calculated on the basis of the whole leaf area and leaf weight and not per unit EL and unit 'effective leaf weight'. In the transpiration process a similar or larger leaf area may be important than in the photosynthesis process, so that the calculation of r_s and r_m on the exact effective leaf area basis for both processes is complicated. For the use of α_g per unit leaf area (α_g^l) the above mentioned restrictions must be taken into account, too.

The small differences between calculated and measured values of R_d and the low standard errors (used in THSD) indicate that the results of the regressions are reliable. The results of α_g^l , $P_{m,n}$, $P_{m,n}^l$, I_c and SLW of 'Amanda Plus' are in good agreement with those of plants of 'Amanda Plus' (age B), grown under comparable conditions in a previous experiment (VAN HOLSTEIJN, 1981). Although irradiance and temperature effects could not be separated as was the case in the previous experiment with 4 treatments of 'Amanda Plus', the influence of the irradiance seems to be more evident than that of temperature in experiments 1, 2, 3, 5 and 6.

Photochemical efficiency

The high correlation between α_g and soil cover, both for the various experiments with 'Amanda Plus', 'Ostinata' and 'Hilde' and for the two spring experiments justifies the use of α_g and soil cover as bases of expression as developed in a previous paper (VAN HOLSTEIJN, 1981). The correlation coefficients of α_g with S and A were even higher for those 3 cultivars than those for 'Amanda Plus' (age B) in the previous experiment. The two way analysis of variance shows that the differences between photochemical efficiencies and photosynthetic rates are mainly due to environmental conditions during growth and not to varietal differences. Lower levels of irradiance result in a higher α_g as was observed in a previous experiment at 26°C, and a higher α_g^l , as reported by some authors (BJÖRKMAN and HOLMGREN, 1963; LOACH, 1967; NILWIK, 1980). A lower $P_{m,n}$ was observed by BJÖRKMAN and HOLMGREN (1963), BROUWER and HUYSKES (1968), SARTI (1973), also when these maximum values are based on α_g (VAN HOLSTEIJN, 1981). Although 'Amanda Plus' has been selected for the poor light

period and 'Ostinata' and 'Hilde' for the summer period, these cultivars can not be characterised regarding their photosynthesis as shade and sun ecotypes (BJÖRKMANN and HOLMGREN, 1963), but rather as short-day and day-neutral types. Between the 7 butterhead cultivars in experiment 3 small, but significant differences occur for the photochemical efficiencies and $P_{m,n}$ on α_g -basis. BROUWER and HUYSKES (1968) also observed different efficiencies and maximal photosynthetic rates between two butterhead cultivars with data expressed per unit exposed leaf area and per unit fresh weight. Identical efficiencies of various cultivars on soil cover basis (DE VOS, 1977; TOXOPEUS, 1977) or leaf volume basis (CHARLES-EDWARDS et al., 1974) have been observed as well. 'Valentine' is a compact cultivar with a low α_g^1 , high I_c , high r_m and a low SLW. This cultivar has a low initial and overall soil cover rate and a low maximal covered soil area (VAN HOLSTEIJN, 1980a), but showed a better heading ability and growth at lower temperatures than 'Meikoningin', 'Rapide' and 'Decimino' (SMEETS, 1977). The faster growth of 'Valentine' is not based on the photosynthetic capacity, but may be due to the larger and thinner leaves.

The differences between the photochemical efficiencies and other parameters in experiment 4 are larger than those in 3, which is mainly caused by the upright cultivar 'Tornado', the cos-lettuce and iceberg lettuce cultivars. 'Tornado' has a photochemical efficiency and light compensation point deviating from those of other butterhead cultivars in this experiment. Although 'Tornado' and 'Plucos' showed a high α_g^1 , these cultivars are not suitable for winter cultivation as is known from horticultural practice. Selection for photosynthetic efficiency per unit leaf area, which is reported for other species (APEL and LEHMANN, 1969; CARLSON et al., 1971) seems not useful for lettuce. The typically lower $P_{m,n}$ for shade and higher $P_{m,n}$ for sun plants did not disappear for 'Amanda Plus', 'Ostinata' and 'Hilde' with the use of α_g as basis of expression, which means that some of the differences in leaf structure and morphology have not been corrected.

Stomatal and residual resistance

At saturating level of irradiance the CO_2 transfer from the external air to the chloroplasts determines the photosynthetic capacity. The overall plant conductance for CO_2 transfer in the gaseous and liquid phase (τ_n^1) is lower under poor light conditions (ACOCK et al., 1978; VAN HOLSTEIJN, 1981). The residual resistance (r_m) is significantly higher in experiment 1 and 2 than in other experiments with 'Amanda Plus', 'Ostinata' and 'Hilde', which is one of the reasons of the lower $P_{m,n}$. The correlation coefficient (r) between r_m of these three cultivars and $1/\tau_n^1$ is high (0.88) and between r_m and $P_{m,n}\alpha_g^{-1}$ lower (-0.50), while between r_s and $1/\tau_n^1$ and $P_{m,n}\alpha_g^{-1}$ these coefficients are respectively 0.42 and -0.16, which demonstrates the larger influence of r_m on $P_{m,n}$ than of r_s on $P_{m,n}$ in the experiments with 'Amanda Plus', 'Ostinata' and 'Hilde'. Large effects of r_m on $P_{m,n}$ have been reported by BEARDSHELL et al. (1973), FRASER and BIDWELL (1974), GAASTRA (1959) and VAN HOLSTEIJN et al. (1977), although r_m is probably overestimated (SINCLAIR et al., 1977). The various cultivation conditions did not affect r_s .

significantly. JONES and MANSFIELD (1970) found no influence of the external CO_2 -concentration, also an important environmental condition during cultivation, during growth of lettuce on r_s . In the calculations of r_s and r_m according to LOUWERSE and VAN OORSCHOT (1969) the air boundary layer resistance (r_a) has been assumed to be low and constant, which assumption seems inaccurate for lettuce plants as discussed previously (VAN HOLSTEIJN, 1981). The air boundary layer resistance for a whole plant, $r_{a,cr}$, (GAASTRA, 1966) will be underestimated and r_m overestimated. The habitus of 'Amanda Plus' and 'Ostinata' were similar, but 'Hilde' showed a more open structure when grown in poor light, which resulted in less self shading and probably a lower $r_{a,cr}$ than that for the two other cultivars.

Maximal net photosynthesis of the butterhead cultivars on α_g -basis (exp. 3) is more related with stomatal than with residual resistances ($r = -0.72$ and -0.22 , resp.). Higher correlation coefficients between these parameters were reported (DORNHOFF and SHIBLES, 1970; DUNSTONE et al., 1972; LOUWERSE and VAN DE ZWEERDE, 1977). A reason for the low coefficients in experiment 3 is the difference in basis of expression for $P_{m,n}$ (on α_g -basis) and in the basis used for the calculations of r_s and r_m (per unit leaf area). In contrast with the results of the 3 cultivars in experiments 1, 2, 3, 5 and 6 the correlation of $1/\tau_n^1$ with r_s is higher than with r_m in experiments 3 and 4. The r_s depends more on cultivar (AUGUSTINE et al., 1976) and the r_m on cultivar and treatment, and, also for lettuce, not exclusively on the cultivation conditions. The slightly lower r_s and r_m do not result in a higher $P_{m,n}$ on α_g -basis for 'Tornado', due to the high α_g and maybe high SLW. 'Sucrine' showed different values from 'Plucos', another cos-lettuce cultivar, but selected for glass-house cultivation. The low R_d of 'Sucrine' indicates a high tolerance for high temperatures. The $P_{m,n}$ on α_g -basis of the cos-lettuce and iceberg lettuce types are equal or higher than the maximal rates of the butterhead types. Maximal rates, however, are for glass-house cultivation generally not of great importance.

Specific leaf weight

SLW-values increase with an increase of irradiance (LOUWERSE and VAN DE ZWEERDE, 1977; VAN HOLSTEIJN, 1981). A positive correlation exists between SLW and $P_{m,n}\alpha_g^{-1}$ of 'Amanda Plus', 'Ostinata' and 'Hilde' in experiments 1, 2, 3, 5 and 6 ($r = 0.51$). In previous experiments (VAN HOLSTEIJN, 1981) an almost equal value was found when plants of 'Amanda Plus' were measured at 26°C . The correlation between τ_n^1 and SLW is higher ($r = 0.70$) than that in the previous experiments with 'Amanda Plus' (VAN HOLSTEIJN, 1981), since in those previous experiments the plants of different ages had similar SLW-, but different τ_n^1 -values.

The SLW depends more on experimental conditions (exp. 1, 2, 3, 5 and 6) than on cultivar ('Amanda Plus', 'Ostinata' and 'Hilde'), but the influence of SLW on photosynthesis is less than, for instance, that reported by PEARCE et al. (1969) for 13 alfalfa clones. They found a high correlation ($r = 0.79$) for the various SLW-values with photosynthesis caused by as well environmental as genetical differ-

ences. For the 7 butterhead cultivars in experiment 3 there existed no correlation between $P_{m,n}\alpha_g^{-1}$ and SLW ($r = 0.06$), a result reported earlier (DUNSTONE et al., 1972; PALLAS and SAMISH, 1974). The opposite conclusion, however, is more frequently noted for various cultivars and species (CHARLES-EDWARDS, 1978; DORNHOFF and SHIBLES, 1970; IRVINE, 1967). A better correlation existed between $P_{m,n}\alpha_g^{-1}$ and SLW in experiment 4 ($r = 0.59$), but selection with the help of SLW seems not very useful, since the correlation between SLW and the maximum photosynthesis does not give information about the correlation between SLW and photosynthetic rate at a low irradiance, the correlation coefficients are still low, and a high SLW does not seem favourable under poor light conditions. The correlation coefficients (r) between SLW and the overall plant conductance for CO_2 in experiments 3 and 4 are respectively 0.19 and 0.84. The coefficient from experiment 4 corresponds with results of AUGUSTINE et al. (1979), who observed a high correlation between leaf thickness and the carboxylation efficiency, one of the factors included in τ_n^1 .

Light compensation point

The large influence of irradiance and the small varietal influence on I_c in experiments 1, 2, 3, 5 and 6 with 'Amanda Plus', 'Ostinata' and 'Hilde' is also observed by others (LOACH, 1967). Small but significant differences were reported by NILWIK et al. (1981) for tomato genotypes. A preceding period with a high level of irradiance seems to be unfavourable for a subsequent period with less light, but this negative effect is usually compensated in practice by a decrease in the glass-house temperature. Plants grown under poor light conditions will react positively on a period with a high level of irradiance due to the low I_c at that moment. When the temperature under these circumstances rises, I_c will increase as well (VAN HOLSTEIJN, 1981).

Cultivars with a similar habitus and pattern of growth have similar I_c -values. The high values of 'C-5', 'Y-6' and 'Sucrine' (exp. 4) show that these cultivars are less adapted to the winter and early spring season. The two iceberg lettuce genotypes gave identical results for all parameters, although 'C-5' has been selected from other genetic material than 'Y-6' (VAN ESCH, 1976).

Significant differences between photosynthetic rates of the heading and non-heading cultivars in experiments 3 and 4 are absent, when measuring at levels of irradiance close to those of cultivation. However, with the use of α_g as basis of expression for the photosynthetic rates differences between the various treatments of one cultivar and between the cultivars remain at saturating level of irradiance. For butterhead lettuce selection is not useful through differences between photosynthetic rates and parameters describing the photosynthetic process. The differences disappear or change when the results are based on a reliable basis, and when the results are obtained under similar environmental conditions during the measurement as during growth. Study of the morphology and photosynthetic capacities of lettuce plants will be simplified, and the cultivation of lettuce in the poor light period will be easier, when non-heading cultivars would become of more commercial interest.

SUMMARY

In 6 experiments the response of photosynthesis to irradiance of whole lettuce shoots was measured in an open system at 22°C and a CO₂-conc. of 570 mgm⁻³. The butterhead lettuce cultivars 'Amanda Plus', 'Ostinata' and 'Hilde' were used in 5 experiments (nrs. 1, 2, 3, 5 and 6). Seven butterhead cultivars were used in a spring experiment (nr. 3) and 5 butterhead, 2 cos- and 2 iceberg lettuce cultivars in another spring experiment (nr. 4). The gross photochemical efficiency per plant (α_g) and per unit leaf area (α_g^1), the maximal net photosynthesis per plant ($P_{m,n}$) and per unit leaf area ($P_{m,n}^1$), the dark respiration per unit leaf weight (R_d) and the light compensation point (I_c) were calculated by curve-fitting. The stomatal (r_s) and residual resistances (r_m) and the specific leaf weight (SLW) were calculated on the basis of total leaf area (A). A multilinear regression of α_g with soil cover, leaf area and leaf weight gave a good fit for all experiments and for each separate plant characteristic the soil cover gave the best correlation with α_g .

In a two way analysis of variance $\alpha_g, \alpha_g^1, P_n$ at 30, 50, 100 and 150 Wm⁻² and at saturating level, expressed on basis of $\alpha_g, P_{m,n}$ per unit soil cover, I_c and corrected $I_c (= I_c \alpha_g)$ were analysed for the 3 cultivars in 5 experiments. A one way analysis for the same parameters was carried out for experiments 3 and 4, but only P_n at the level of irradiance during growth (50 and 70 Wm⁻², resp.) and $P_{m,n}$ were analysed. For 'Amanda Plus', 'Ostinata' and 'Hilde' α_g^1 is more influenced by treatment than cultivar, while in experiments 3 and 4 varietal differences also appeared. $P_{m,n} \alpha_g^{-1}$ increased after a higher irradiance during growth. Differences between P_n and other parameters increased, when the cultivars differed more in habitus, growth and genetical background (exp. 4). Measurements at the irradiance level of growth showed no difference between the photosynthetic rates at α_g -basis of the cultivars. Results of the analysis of $P_{m,n}$ per unit soil cover were identical to those of $P_{m,n}$ per α_g . The influence of irradiance on I_c is more pronounced than that of cultivar. Differences in r_m existed for 'Hilde' compared with 'Amanda Plus' and 'Ostinata', and for the cultivars in the other experiments. A period with low irradiance resulted in a high r_m . Differences in r_s existed only in experiments 3 and 4. SLW is mainly influenced by cultivation conditions (irradiance) and then correlated with r_m , while those SLW-differences caused by cultivar are almost not correlated with r_m . The 2 cos-lettuce cultivars gave different results, while the 2 iceberg genotypes always gave similar results. Cos- and iceberg lettuce seemed less adapted for growth in winter.

Selection on higher yield of butterhead lettuce with the use of parameters describing the photosynthetic process seems hardly useful, certainly when photosynthesis is measured at circumstances identical to those during growth.

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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.
- APEL, P. und LEHMANN, CHR. O.: Variabilität und Sortenspezifität der Photosyntheserate bei Sommergeste. – *Photosynthetica* **3**: 255–262, 1969.
- 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.
- AUGUSTINE, J. J., STEVENS, M. A. and BREIDENBACH, R. W.: Physiological, morphological and anatomical studies of tomato genotypes varying in carboxylation efficiency. – *J. amer. Soc. Hort. Sci.* **104**: 338–341, 1979.
- BANGA, O.: Bijdrage tot het rassenonderzoek van kropsla. – *Meded. Tuinbouwvoorlichtingsdienst* **14**: 1–103, 1939.
- BEARDSSELL, 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.
- BJÖRKMÄN, O. and HOLMGREN, P.: Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. – *Physiol. Plant.* **16**: 889–914, 1963.
- 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.
- CARLSON, G. E., PEARCE, R. B., LEE, D. R. and HART, R. H.: Photosynthesis and photorespiration in two clones of orchardgrass. – *Crop Sci.* **11**: 35–37, 1971.
- 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.: An analysis of the photosynthesis and productivity of vegetative crops in the United Kingdom. – *Ann. Bot.* **42**: 717–731, 1978.
- 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.
- DANTUMA, G.: Rates of photosynthesis in leaves of wheat and barley varieties. – *Neth. J. agric. Sci.* **21**: 181–187, 1973.
- DOORENBOS, J.: Het fytotron van het Laboratorium voor Tuinbouwplantenteelt der Landbouwhogeschool. – *Meded. Dir. Tuinb.* **27**: 432–437, 1964.
- DORNHOFF, G. M. and SHIBLES, R. M.: Varietal differences in net photosynthesis of soybean leaves. – *Crop Sci.* **10**: 42–45, 1970.
- DREGER, R. H., BRUN, W. A. and COOPER, R. L.: The effect of genotype on the photosynthetic rate of soybean (*Glycine max* (L) Merr.). – *Crop Sci.* **9**: 429–431, 1969.
- DULLFORCE, W. M.: Analysis of growth of winter glasshouse lettuce varieties. – *Rep. Un. Nottingham, Sch. Agric.* 1962: 57–64, 1963.
- DUNSTONE, R. L., GIFFORD, R. M. and EVANS, L. T.: Photosynthetic characteristics of modern and primitive wheat species in relation to ontogeny and adaptation to light. – *Austr. J. biol. Sci.* **26**: 295–307, 1972.
- EENINK, A. H. and ALVAREZ, J. M.: Indirect selection for tetraploidy in lettuce (*Lactuca sativa* L.). – *Euphytica* **24**: 661–668, 1975.
- EENINK, A. H. and GARRETSEN, F.: Inheritance of insensitivity of lettuce to a surplus of exchangeable manganese in steam-sterilized soils. – *Euphytica* **26**: 47–53, 1977.
- EENINK, A. H. and SMEETS, L.: Genotype x 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.

- EL-SHARKAWY, M. A., HESKETH, J. D. and MURAMOTO, H.: Leaf photosynthetic rates and other growth characteristics among 26 species of *Gossypium*. – *Crop Sci.* **5**: 173–175, 1965.
- ESCH, H. G. A. VAN: Personal communication, 1976.
- 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.: Some physiological aspects of CO₂-application in glasshouse culture. – *Acta Hort.* **4**: 111–116, 1966.
- GOSIEWSKI, W., NILWIK, H. J. M. and BIERHUIZEN, J. F.: Photosynthesis of different tomato genotypes. I. The influence on temperature. – *Scientia Hort.*, 1981 (in press).
- GROENEWEGEN, J. H.: Nieuwe slarassen voor de teelt onder glas. – *Meded. Dir. Tuinb.* **15**: 22–28, 1952.
- HEICHEL, G. H. and MUSGRAVE, R. B.: Varietal differences in net photosynthesis of *Zea mays* L. – *Crop Sci.* **9**: 483–486, 1969.
- 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: Photosynthesis of lettuce. I. Results with cultivar 'Amanda Plus'. – *Meded. Landbouwhogeschool, Wageningen* **81** (12): 1–21, 1981.
- 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.
- HUYSKES, J. A.: Het kweken van zwaardere rassen. – *Meded. Dir. Tuinb.* **21**: 210–213, 1958.
- HUYSKES, J. A.: Gebruikswaardeonderzoek van het nieuwe zomerras 'Hilde'. – *Meded. Dir. Tuinb.* **23**: 232–236, 1960.
- HUYSKES, J. A.: Glasslaveredeling en teeltontwikkeling als cyclisch proces. In: *Rassen in Wording*. W. E. J. Willink, Zwolle: 141–144, 1968.
- HUYSKES, J. A. en RODENBURG, C. M.: *De techniek van de veredeling van glassla*. W. E. J. Willink, Zwolle: 1–86, 1965.
- HUYSKES, J. A. en RODENBURG, C. M.: Het kweken van slarassen voor de kasteelt in de zomer. – *Zaadbelangen* **14**: 280–281, 1968.
- IRVINE, J. E.: Photosynthesis in sugarcane varieties under field conditions. – *Crop Sci.* **7**: 297–300, 1967.
- IZHAR, S. and WALLACE, D. H.: Studies on the physiological basis for yield differences. III. Genetic variation in photosynthetic efficiency of *Phaseolus vulgaris* L. – *Crop Sci.* **7**: 457–460, 1967.
- JONES, R. J. and MANSFIELD, T. A.: Increases in the diffusion resistances of leaves in a carbon dioxide-enriched atmosphere. – *J. exp. Bot.* **21**: 951–958, 1970.
- LEE, K. K.: Growth studies with lettuce. MSc. Thesis, Massey Un., New Zealand: 1–137, 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.
- 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.
- NILWIK, H. J. M.: Photosynthesis of whole sweet pepper plants. I. Response to irradiance as influenced by cultivation conditions. – *Photosynthetica* **14**: 373–381, 1980.
- NILWIK, H. J. M., GOSIEWSKI, W. and BIERHUIZEN, J. F.: Photosynthesis of different tomato genotypes. II. The influence of irradiance and external CO₂ concentration. – *Scientia Hort.*, 1981 (in press).

- NUNES, M. A., BIERHUIZEN, J. F. and PLOEGMAN, C.: Studies on the productivity of coffee. III. Differences in photosynthesis between four varieties of coffee. – Acta Bot. Neerl. 18: 420–424, 1969.
- PALLAS, J. E. JR. and SAMISH, Y. B.: Photosynthetic response of peanut. – Crop Sci. 14: 478–482, 1974.
- PEARCE, R. B., CARLSON, G. E., BARNES, D. K., HART, R. H. and HANSON, C. H.: Specific leaf weight and photosynthesis in alfalfa. – Crop Sci. 9: 423–426, 1969.
- RODENBURG, C. M.: Varieties of lettuce. An international monograph. W. E. J. Willink, Zwolle, 1–228, 1960.
- RODENBURG, C. M.: Ervaringen bij het kweken van minder randgevoelige rassen. – Zaadbelangen 22: 272–274, 1968a.
- RODENBURG, C. M.: Stand van de veredeling van kortedagsla. – Groenten en Fruit 23: 1452–1453, 1968b.
- RODENBURG, C. M.: Ervaringen bij de ijsslaveredeling voor de voorjaarsteelt. – Zaadbelangen 26: 500–503, 1972.
- SARTI, A.: Growth and photosynthetic activity of *Lactuca sativa* L. *romana*, cultivated in three day light intensities. – Lab. radiobiochimica ed Ecofisiologia Vegetali, C.N.R., Roma: 1–13, 1973.
- SCAIFE, M. A.: The early relative growth rates of six lettuce cultivars as affected by temperature. – Ann. appl. Biol. 74: 119–128, 1973.
- SINCLAIR, T. R., GOUDRIAAN, J. and DE WIT, C. T.: Mesophyll resistance and CO₂ compensation concentration in leaf photosynthesis models. – Photosynthetica 11: 56–65, 1977.
- SMEETS, L.: Analysis of the differences in growth between five lettuce cultivars marking the development in lettuce breeding for winter production. – Euphytica 26: 655–659, 1977.
- TOXOPEUS, H.: Stubble turnips. In: ALBERDA et al.: Crop photosynthesis methods and compilation of data obtained with a mobile field equipment. – Agr. Res. Rep. 865, CABO, Wageningen: 42–44, 1977.
- VOS, N. M. DE: Wheat. In: ALBERDA et al.: Crop photosynthesis methods and compilation of obtained data with a mobile field equipment. – Agr. Res. Rep. 865, CABO, Wageningen: 22–30, 1977.