

Growth and photosynthesis of lettuce

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Promotor: dr.ir. J.F. Bierhuizen, hoogleraar in de tuinbouwplantenteelt.

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Growth and photosynthesis of lettuce

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
hoogleraar in de veeteeltwetenschappen,
in het openbaar te verdedigen
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des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

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ONTV. TIJDSCHR. ADM.

Woord vooraf

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De omslag van dit boekje komt uit het Groot Warmoeziers Handboek van T.F. Uilkens, Uitg. J. Noorduyt en Zoon, Gorinchem, 1852.

STELLINGEN

I

Bij de analyse van groei en fotosynthese van sla is het door de plant bedekte grondoppervlak als maat voor de lichtopname te verkiezen boven het totale bladoppervlak van de plant

Dit proefschrift

II

Er zijn geen significante verschillen in fotosynthesesnelheid op basis van de bruto fotochemische efficiëntie tussen slarassen, wanneer de milieuomstandigheden tijdens opkweek en meting gelijk zijn

Dit proefschrift

III

Selektie op planteigenschappen in een vroeg groei- en ontwikkelingsstadium van sla voor het verkrijgen van een hoog kropgewicht tijdens de oogst is niet gewenst

Eenink, A.H. en Smeets, L.: Neth. J. agric. Sci. 26: 81-98, 1978

IV

De problemen bij de groei en morfologie van kropsla zullen met meer succes geëlimineerd worden door deskundigen die de consument kunnen beïnvloeden dan door plantenfysiologen

V

De door het woord salade opgeroepen verwachting dat zich hierin ook slabestanddelen bevinden wordt steeds minder vervuld

VI

Vernieuwing van technische uitrusting en personele bezetting is noodzakelijk om impulsen tot nieuw onderzoek in een vakgebied te stimuleren

er moet ook onderzoek verricht worden naar het sterk stimuleren van beurtjaren bij appels en peren.

VIII

De gebruikswaarde van glasgroenten tendeert steeds sterker naar die van siergewassen.

IX

De sterk opkomende teelt van glasgroenten op een kunstmatig medium maakt de reclameslogan 'vers van de grond' in toenemende mate onjuist voor produkten uit de glastuinbouw.

X

Het woord dienstweigeraar voor 'iemand, die onoverkomelijke gewetensbezwaren tegen de persoonlijke vervulling van militaire dienst heeft' is onjuist, daar een beroep op de wet gewetensbezwaren militaire dienst de wil tot het vervullen van een constructieve daad tot uiting brengt.

'Growth and photosynthesis of lettuce'

Proefschrift van H.M.C. van Holsteijn

Wageningen, 28 oktober 1981

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1 General introduction

Lettuce has been cultivated and consumed as a vegetable for human nutrition for many centuries. HEDRICK (1919), for instance, mentioned lettuce cultivars (e.g. *Lactuca scariola*) used by the Persians, Greeks, Romans, and also by the Chinese in the fifth century. DODONEAUS (1554) described lettuce types such as 'tamme Lattouwe' (*Lactuca sativa*) and 'gecronckelde Lattouwe' (*Lactuca crispa*), which were cultivated in The Netherlands during the 16th century. DODONEAUS and UILKENS (1852) already reported the cultivation of heading lettuce types.

The butterhead cultivar 'Meikoningin' (May Queen) was the only heading lettuce cultivar under poor light conditions in the glass-house in The Netherlands until the early fifties (GROENEWEGEN, 1960). During the last decades new cultivars for glass-house cultivation appeared, knowledge of cultural practices, e.g. CO₂-application (VAN BERKEL, 1964) increased, technical facilities of the modern glass-house improved and its equipment became more sophisticated. The growth period in general became shorter during all seasons. Most obviously this occurred for the October and November plantings with the growth period in the winter season (DE VISSER, 1977). Usually a lettuce crop is followed by a tomato crop. Sometimes lettuce is planted a second time. This second planting became possible due to the shorter growth period. Butterhead lettuce is ranking the third position after tomato and cucumber regarding its importance in vegetable production under glass (MULDER, 1981). Data about the production of lettuce under glass during the last 30 years are shown in Table 1.

TABLE 1. Data about production and lettuce cultivars in the Netherlands.

Year	Area under glass (ha)	Production value (x fl. 1000.000)	Main cultivars
1950	-	19.5 ^e (outdoor and Dutch frames included)	Meikoningin ^g
1960	1380 ^a (298 ha Dutch frames included)	58.3 ^a (outdoor and Dutch frames included)	Proeftuins Blackpool, Regina ^h
1970	3592 ^b	124.8 ^b (outdoor and Dutch frames included)	Deciminoir, Deciso, Magiola, Noran, Plenos, Rapide ⁱ
1975	3105 ^c	123.9 ^f	Amanda Plus, Deci- minor, Deciso, Miranda, Noran ^j
1980	3285 ^d	167.0 ^d	Cynthia, Mir, Pallas, Panvit, Plus, Ravel, Renate, Salina ^k

a) Anon., 1962; b) Anon., 1970a; c) Anon., 1976; d) MULDER, 1981; e) Anon., 1952; f) Anon., 1975; g) BANGA, 1951; h) BANGA, 1960; i) Anon., 1970b; j) Anon., 1974 and k) Anon., 1980.

The area of butterhead lettuce is now more or less constant, but the production value increases and is substantial for the total vegetable production in the poor light period. In 1980 the area of iceberg lettuce under glass was about 20 ha. The area of cos-lettuce under glass can be neglected (MAASWINKEL, 1981).

The whole lettuce shoot, i.e. for butterhead lettuce the head, is harvested and consumed for human nutrition. Research on lettuce comprises studies on head formation (BENSINK, 1971; DULLFORCE, 1968), on growth (LEE, 1974; NICHOLS, 1970) and on photosynthesis (BROUWER and HUYSKES, 1968). In the winter period light is the limiting factor for lettuce production. Due to head formation parts of the newly formed leaves are excluded from light. Between the leaves competition for light (self shading) also exists, whereas the gas exchange between the leaves is hampered as well. The area, available per plant in the glass-house is restricted (mutual shading) and a rapid covering of this area

by the plant in order to intercept as much irradiance as possible can be important. BIERHUIZEN et al. (1973) concluded that a high temperature in the beginning of the growth period may be useful to reach 100% soil cover as soon as possible. An interesting problem seems whether a plant with a high rate of covering has a higher ultimate harvest weight.

Experiments for practical purpose of the growers emphasize the importance of the ultimate fresh weight and the quality of the lettuce head (e.g. VAN ESCH, 1977). A good understanding of effects of environmental conditions on growth related with time, weight, soil cover, leaf area, leaf number and photosynthesis is necessary.

Photosynthesis measurements of single leaves are difficult because of bubbled and curved leaves and the rosette habitus of the plant. With equipment suitable for the measurement of photosynthetic rates of whole plants the photochemical efficiency, maximum photosynthetic rate, light compensation point and CO_2 compensation concentration can be calculated. Gas exchange data per plant represent the overall accumulation of CO_2 , but not all plant parts contribute equally to the measured data. A basis on which the photosynthesis data of the plant will be expressed is needed to study and compare the obtained results.

Photosynthesis data are usually expressed per unit leaf area (GAASTRA, 1959), dry weight or fresh weight (BROUWER and HUYSKES, 1968; ACOCK et al., 1978) or another basis (CHARLES-EDWARDS et al., 1974). For selection on better growth and higher harvest weight photosynthesis data obtained by routine cultivation and measurement methods may improve the criteria for selection and can give a better understanding of varietal differences.

Because of the many problems involved in growth and photosynthesis of lettuce, extensive research on this topic was carried out, which is presented in the subsequent chapters. In chapter 2 the process of soil covering is studied and discussed for a number of cultivars grown under various temperatures in spring and autumn. The quantitative analysis of growth (chapter 3) deals with the growth rate in relation to time, dry weight and soil cover and with the relationship between leaf area

...and mass formation. Since equipment for photosynthesis measurements was not available at the Department of Horticulture of the Agricultural University, Wageningen, a closed system was built suitable for lettuce plants, which is described in chapter 4. Photosynthesis results obtained with this equipment are given in chapter 5, while results from measurements with whole plants in an open system are presented in chapter 6.

The chapters 2, 3, 4, 5 and 6 have already been published as separate articles. In chapter 7 an overall summary in English is given and in chapter 8 this summary is presented in Dutch.

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.
- ANON.: Tuinbouwgids 1952. Uitgave van de directie van de Landbouw, afdeling Tuinbouw, Den Haag: p. 99, 1952.
- ANON.: Tuinbouwgids 1962. Uitgave van de directie Tuinbouw van het Ministerie van Landbouw en Visserij, Den Haag: 555-556, 1962.
- ANON.: Jaarverslag 1970. Bijlagen. Produktschap voor Groenten en Fruit, Den Haag: 6-12, 1970a.
- ANON.: Twee en twintigste Rassenlijst voor Groentegewassen. Instituut voor de Veredeling van Tuinbouwgewassen, Wageningen: 101-118, 1970b.
- ANON.: Zes en twintigste Rassenlijst voor Groentegewassen. Instituut voor de Veredeling van Tuinbouwgewassen, Wageningen: 135-151, 1974.
- ANON.: Jaarverslag 1975. Produktschap voor Groenten en Fruit, Den Haag: 53-55, 1975.
- ANON.: Jaarverslag 1976. Produktschap voor Groenten en Fruit, Den Haag: p. 60, 1976.
- ANON.: Negen en twintigste Rassenlijst voor Groentegewassen. Glas-groenten. Rijksinstituut voor het Rassenonderzoek van Cultuur-gewassen, Bennekom: 84-98, 124-127, 1980.
- BANGA, O. (Ed.): Vierde beschrijvende Rassenlijst voor Groentegewassen. Instituut voor de Veredeling van Tuinbouwgewassen, Wageningen: 51-54, 1951.
- BANGA, O. (Ed.): Rassenlijst voor Groentegewassen 1960. Instituut voor de Veredeling van Tuinbouwgewassen, Wageningen: 76-83, 1960.
- BENSINK, J.: On morphogenesis of lettuce leaves in relation to light and temperature.-Meded. Landbouwhogeschool, Wageningen 71 (15):

- BERKEL, N. van: Teeltkundige aspecten van de toepassing van koolzuurgas. - Meded. Dir. Tuinb. 27: 378-384, 1964.
- BIERHUIZEN, J.F., EBBENS, J.L. and KOOMEN, N.C.A.: Effects of temperature and radiation on lettuce growing. - Neth. J. agric. Sci. 21: 110-116, 1973.
- 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.
- 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.
- DODONAEUS, R.: Cruydeboek. Jan van der Loe, Tantwerpen: 609-610, 1554.
- DULLFORCE, W.M.: Effects of light, temperature and carbon dioxide on the growth of glasshouse lettuce (*Lactuca sativa* L.). - Ph.D. Thesis, Un. of Nottingham: 1-150, 1968.
- ESCH, H.G.A. van: Plantdichtheidsproeven bij vier slarassen (heteluchteelt 1976/1977. - Intern verslag 53. Proefstation voor de Groenten- en Fruitteelt onder Glas, Naaldwijk: 1-6, 1977.
- GAASTRA, P.: Photosynthesis of crop plants as influenced by light, carbondioxide, temperature, and stomatal diffusion resistance. - Meded. Landbouwhogeschool, Wageningen 59 (13): 1-68, 1959.
- GROENEWEGEN, J.H.: Stand en betekenis van de veredeling bij sla. - Meded. Dir. Tuinb. 23: 295-299, 1960.
- HEDRICK, U.P. (Ed.): Sturtevant's notes on edible plants. J.B. Lyon Company, Albany: 321-324, 1919.
- LEE, K.K.: Growth studies with lettuce. - M.Sc. Thesis, Massey Un., New Zealand: 1-137, 1974.
- MAASWINKEL, R.H.M.: Personal communication, 1981.
- MULDER, G.: 1980 had goud in de mond. - Tuinderij 21: 14-19, 1981.
- NICHOLS, M.A.: Growth studies with lettuce. - Thesis, Massey Un., New

Zeeland: 1-106, 1970.

UILKENS, T.F.: Groot Warmoeziers Handboek. Noorduyn en Zoon, Gorinchem:
847-870, 1852.

VISSER, A.J. de: De economische mogelijkheden van de jaarrondteelt en
zomerteelt van kassla. Landbouw-Economisch Instituut, Afdeling
Tuinbouw, Den Haag: 3-47, 1977.

2. GROWTH OF LETTUCE

I. COVERING OF SOIL SURFACE

INTRODUCTION

In general one can distinguish various periods in the growth cycle of a lettuce crop (*Lactuca sativa* L.) e.g. a period of germination, a period from germinating until 100 percent soil cover by the leaves and subsequently a period until harvest (BIERHUIZEN et al., 1973; BAELDE, 1972). The second period can be divided for practical purposes into two intervals viz. the one between germination, followed by emergence and transplanting and that between transplanting and 100 percent soil cover. During this latter period a rapid covering of the available soil area is important for an efficient light interception, especially during winter, when light is the main limiting factor for growth. It should be emphasized that during this growth stage the performance of the plant and its quality are of minor importance. For example a high temperature in the beginning results in a rapid covering of the soil area, thus a rapid increase in light interception per plant, but the plant has a rather poor appearance. When a lower temperature is applied later a qualitatively good head can still be harvested. In this article first some consequences of temperature, light and plant density in relation to soil cover will be discussed in more detail.

BENSINK (1971) analysed in his thesis the growth and morphogenesis of lettuce at different conditions of temperature and light. A higher temperature increased cell extension. At low light intensities, except extremely low intensities, this resulted in a plant with long leaves with a small width. A plant with such long leaves exhibits less self-shading. When the light intensity, however, is extremely low the leaves remain short. At high light intensities the initiation of leaves increases relatively faster than the leaf expansion, whereas the latter was more affected by temperature. BIERHUIZEN et al. (1973) demonstrated that the soil cover rate by lettuce plants depended exclusively on a heat sum and not on a radiation unit nor on time. They concluded from their experiments in different glass-houses that a high temperature in the beginning of the growth period of lettuce may be useful in order to reach a 100 percent soil cover as soon as possible.

Efficient light interception can be obtained when the amount of light absorbing surface per gram fresh or dry weight is high. BROUWER and HUYSKES (1968), for example, found that the difference in growth between the cultivar 'Rapide' and the F_2 of 'Rapide' and 'Hamadan' was caused by a larger light absorbing leaf surface per gram fresh weight. It is evident from their experiments that the amount of leaf area exposed to light is the most important growth parameter. When soil cover is less than 100%, growth and production are directly related to the fraction of light intercepted (SHIBLES and WEBER, 1966).

KANEMASU and ARKIN (1974) described in a simplified model how the potential net photosynthesis on a ground area basis is linearly related to the intercepted photosynthetic active radiation.

In a glass-house competition between the leaves for light occurs through self- and mutual shading of the leaves of the plants. HUGHES (1969) regarded a depression of 5 percent in growth as a criterion of mutual shading. However, this criterion is not important in horticultural practice, because the spacing of lettuce plants is economically determined (HENDRIX, 1976; KEIJZER, 1975). At a wide spacing more light per plant will be intercepted and the total weight of the lettuce head increases faster in comparison with a narrow spacing. Moreover, the harvest date will be earlier, quality and performance will improve, and the lettuce heads can be stored for a longer period (VAN ESCH, 1976). The total yield per m², however, decreases at wider spacing, although the number of marketable heads will increase (e.g. KEIJZER, 1975; VAN ESCH, 1977). At present, however, new cultivars, modern glass-houses and better growing conditions allow narrower spacing. Another procedure is to transport plants during their growing period so that from the beginning until harvest an almost closed canopy can be achieved. Nutrient film techniques make this possible, as was illustrated in a short article by SCHIPPER (1979).

Although it seems obvious that a high rate of soil cover is important for the production of lettuce, data on this aspect are lacking. Moreover, when the factors determining the soil covering are known, it may improve the selection of favourable morphological and physiological characteristics of a plant in an early stage of growth. In this part of the study of Growth of Lettuce, therefore, experiments are described in which the soil covering process of plants of several cultivars is analysed at various temperatures and three plant densities in spring and autumn for various cultivars. A mathematical description for this process is evaluated and its parameters are related to the ultimate weight at harvest.

MATERIALS AND METHODS

Spring experiment

In the experiments carried out in the early spring, the following butterhead lettuce cultivars were used: 'Meikoningin' ('May Queen'), 'Proeftuin's Blackpool', 'Rapide', 'Decimino', 'Valentine', 'Amanda Plus', 'Noran' and 'Tornado'. In the sequence of the first six cultivars, growth rate and heading ability are stronger under winter conditions, partly due to the increasing rate of leaf production and partly due to an increasing leaf size (SMEETS, 1977). This list of cultivars also represents the historical sequence up to 1976 in the use of cultivars by Dutch growers. Before 1954 'Meikoningin' was the only heading lettuce cultivar in The Netherlands (GROENEWEGEN, 1960; HUYSKES, 1968). 'Amanda Plus' has become the most popular cultivar since the early seventies, but it has the disadvantage of not being resistant against new strains of mildew (*Bremia lactucae*), which appeared in the seventies. The advantage of this rather

...growth in autumn and winter as well as in spring. 'Valentine', a compact English cultivar, has not been cultivated to a great extent in The Netherlands. 'Noran', a spring and late spring cultivar, was also used in this experiment because previous experiments were executed with this cultivar at the Department of Horticulture of the Agricultural University in Wageningen (BIERHUIZEN et al., 1973; EBBENS en KOOMEN, 1971; EVERAARTS en VAN SLOTEN, 1974). 'Tornado' was a new, upright type which starts heading rather late in its growing period and is not adapted for midwinter conditions.

On January 6, seeds of 'Valentine' and 'Tornado', and two days later seeds of the other cultivars, were sown in peat blocks of $5 \times 5 \times 5$ cm (two seeds per block). The blocks were placed in boxes in a glass-house at a day and night temperature of 18°C . The largest number of seeds germinated between 4 to 5 days after sowing whereupon the day and night temperature was lowered. Seeds which emerged earlier or later were removed. When the cotyledons of the seedlings expanded, the plants were thinned and selected. The mean day and night temperatures from germination until transplanting into the glass-house were 14.8°C and 10.5°C , respectively. During this period zineb and TMTD were sprayed weekly against mildew, botrytis, Sclerotinia, etc..

On February 23, plants were selected again and transplanted on a sandy clay soil in 3 separate compartments of a Venlo-type glass-house. The 24th of February was called day 1. The first soil cover measurements were done on day 3 and the first harvest of 'Noran' on day 4. Fertilizers were applied according to the recommendations of the Laboratory for Soil and Crop Testing, Oosterbeek, The Netherlands. The average top weight of the plants was 1.5–2.5 grams and the average leaf area was $90\text{--}120\text{ cm}^2$. Plants of 'Tornado' were smaller than those of the other cultivars.

In each compartment three plant densities, with respective distances of 20, 25 and 35 cm, were applied, later in this part indicated as 20-, 25- and 35-treatments. These densities correspond with 25, 16 and 8.16 plants per m^2 or an available ground area per plant of 400, 625 and 1225 cm^2 . Plants were considered to be solitary at the 35-spacing. In normal horticultural practice the number of plants per m^2 varies from 16–24. In autumn and winter the number is usually below 20, and in spring higher (ANON., 1978). The plots used for soil cover measurements consisted of at least 16 plants, and were surrounded with two edgerows. Additional plants of 'Noran' were planted because of the destructive measurements for the growth analysis of this cultivar (vide Part II). For this growth analysis 20 plots of 4 plants were planted, also surrounded by edge plants. All plots were distributed at random over the compartment. The same scheme was applied in all three compartments.

Three day-night temperature regimes were selected; the intermediate regime was comparable with that used in normal practice, one regime was higher and the other one lower than that in normal practice. They will be indicated as the II-, I- and III-treatments, respectively. The actual temperatures depended on the existing weather conditions outside and the heating capacity of the glass-house. CO_2 was not applied. Plants were watered by sprinkling. Manual watering was

sometimes necessary due to differences in evaporation between the various plots. During the first three weeks zineb and TMTD were sprayed once a week. The spring experiment terminated on April 29, that is day 66, when the plants in the compartment (III) with the lowest temperatures were harvested. The end harvest in compartment I took place on day 46 and of compartment II on day 54. The last harvest of plants of 'Tornado' was one week later than the other harvests.

Autumn experiment

In this experiment the following butterhead lettuce cultivars were used: 'Deciso', 'Amanda Plus', 'Dandie', 'Ravel' and 'Tornado'. 'Deciso' is exclusively an autumn lettuce and it was one of the most popular cultivars until the mid-seventies. It was used in preliminary experiments at the Department of Horticulture (MATHUSSEN, 1973; SMIT, 1974). 'Amanda Plus' and 'Tornado' were used in the spring experiment. 'Ravel' was a new, promising cultivar which, like 'Amanda Plus', can be cultivated in spring, autumn and winter. 'Dandie' has the same performance as 'Valentine' ('Valentine' is one of the parents), but is larger and grows faster. In this experiment the endive (*Cichorium endiva* L.) cultivar 'Brevo', adapted for glass-house cultivation in the late autumn and winter season, was also planted. Endive was used to test the usefulness of the mathematical description of the soil covering process by a sigmoid pattern for other rosette plants. In horticultural practice endive is planted with slightly wider spacing than lettuce.

On September 3, the seeds of 'Brevo', 4 days later the seeds of 'Tornado', and again two days later the seeds of the other cultivars were sown in peat blocks, in the same way as in the spring experiment. The day and night temperatures were 18–22°C. The seeds germinated after the fourth day. Seedlings were selected as in the spring experiment. The mean day and night temperatures from germination until transplanting in the glass-house were 22.1 °C and 17.7 °C, resp.. Twice a week zineb and TMTD were sprayed. On September 29 the plants were selected again and planted in the three compartments of the Venlo-type glass-house. The 30th of September was called day 1. The first soil cover measurement took place on day 1 and the first harvest of 'Deciso' on day 2. The average top fresh weight of a plant was 1.5–2 grams and the leaf area was 70–105 cm². The soil was fertilized in accordance with the advice of the Laboratory of Soil and Crop Testing, Oosterbeek.

The same plant densities were used as in the spring experiment. One plot consisted of 8 plants, surrounded by edge rows. Each treatment was carried out in two replications. Extra plants of 'Deciso' were necessary for the destructive measurements for the growth analysis (vide Part II). For this analysis 22 plots with two plants per plot surrounded by edge row plants, were available. All plots were distributed at random. All three compartments were planted according to the same scheme. The middle regime of the three temperature regimes was comparable with that in horticultural practice. CO₂ was not applied. Watering was carried out in the same way as in the spring experiment, but less frequent.

Pirimor was used against aphids and Phosdrin against caterpillars. The autumn experiment terminated in compartment III on the 2nd of December (day 64), in compartment I on day 50 and in compartment II on day 57.

Measurement of the soil cover percentage

The soil cover measurements were done in 3- and 4-day intervals. The observations were continued until a constant percentage of soil cover was achieved during a period of at least one week. The soil cover was determined according to the dot counting method (KVĚT and MARSHALL, 1971) with a Hasselblad camera. A tripod with a transverse tube, upon which the camera was fixed, was placed so that the camera hung above the plot (Fig. 1). In the camera a transparent plate, provided with equally spaced dots, was inserted behind the lens. The number of dots obscured by a plant were counted through the camera. Preceding the measurements of the soil cover, a standard soil area was always used for calibration. Depending on the distance between the camera and the ground surface one dot counted for 9 to 10 cm².

In the spring experiment the soil cover was measured on 16 or 18 plants per plot for the density of 20 × 20 cm, on 18 plants for the density of 25 × 25 cm, and on 12 plants for the density of 35 × 35 cm. In the autumn experiment each plot consisted of 8, 6 and 6 plants for the three densities and two plots per density were measured.

Only at the density of 20 × 20 cm in the spring experiment fresh and dry weight of 8 plants per plot were harvested, when the soil cover of 100% had been reached. The fresh weight was measured immediately after cutting. The dry weights of the plants were obtained by drying during 7 days in a ventilated oven at 65°C. When the soil cover of the solitary plants became constant or decreased, the remaining plants at the density 20 × 20 cm and the plants of all other plots were harvested. Fresh and dry weights were measured for 10 plants per treatment in the spring and 8 plants per treatment in the autumn experiment.

Criteria for the performance of the head of the lettuce plants were: the appearance of diseases such as botrytis and blackrot; the quality of the head (firm, loose or leafy), of the base (well closed, bony structure) and of the leaves (soft or fluffy). No data concerning the total leaf area or the root system of the plant were collected.

Measurement of temperature and radiation

The air temperature was registered with Fuess-thermographs, which were placed in the middle of each compartment on plant level. Hourly readings were used to calculate the mean day and night temperatures. The day was considered to be from sunrise to sunset.

Measurements of the daily radiation were obtained from a nearby meteorological station of the Department of Physics and Meteorology of the Agricultural University, Wageningen. During spring and autumn the transmission for light of the three compartments was determined 4 times with a flat

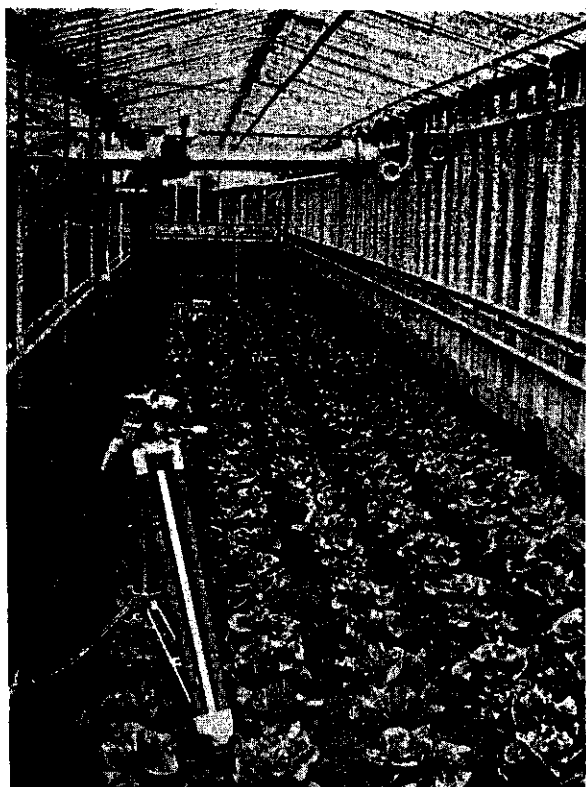


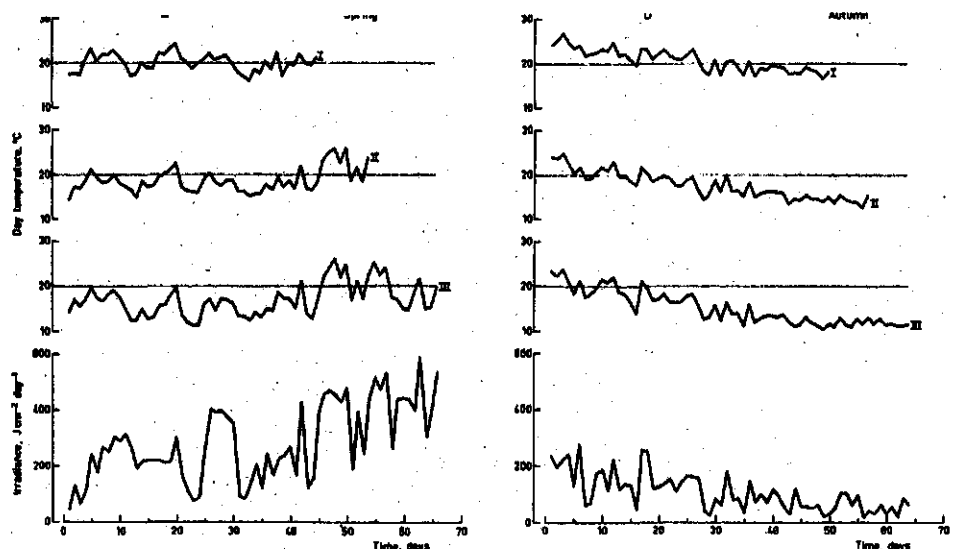
FIG. 1. General view of the set up for soil cover measurements.

photometer, type TFDL-65-2020, and once with a Kipp solarimeter. The average transmission of the Venlo-glass-house in spring was 57.5% and in autumn 58.5%. These percentages were used to calculate the radiation inside the glass-house.

In Figures 2a and 2b, the average day temperatures on plant level in the three compartments and the total short wave irradiance per day during the experiments are given. The average night temperatures in the spring experiment were respectively 7.1°C, 7.1°C and 8.2°C lower than the day temperatures in the compartments I, II and III. In the autumn experiment these figures were respectively 4.2°C, 4.1°C and 4.1°C for the used periods. The difference between day and night temperatures remained rather constant during a short period. At the same radiation level, the temperature in autumn was higher than in spring. Other environmental data such as relative humidity, CO₂-concentration, evaporation and windspeed were not regularly measured in the glass-house.

Mathematical description of the soil cover process

The relationship between soil cover and time shows a sigmoid pattern, similar to that of many biological processes (BIERHUIZEN et al., 1973). Data of the



FIGS. 2a and 2b. The average day temperature and the total short wave irradiance (per day) in compartments I, II and III of the glass-house during the spring (a) and autumn (b) experiments. Day number 1 in spring is February 24 and in autumn September 30.

preliminary experiments with the cultivars 'Noran' and 'Deciso' were used to test various equations. From these tests a four parameter sigmoid curve was selected as defined by the differential equation:

$$\frac{dS}{dt} = r.S. \left[1 - \left(\frac{S}{S_{max}} \right)^p \right] \text{ and } -1 < p < \infty \quad (1)$$

where t is the time scale (days from planting), S denotes the soil cover of the plant (cm^2) and S_{max} is the maximal area (in cm^2), covered by the plant (VAN DOORN). The family of curves defined by equation (1) includes several curves, which have been used empirically for the description of growth, e.g. the 'monomolecular' ($p = -1$), the Gompertz ($p = 0$) and the logistic (= symmetrical sigmoid) growth curves ($p = 1$). Further mathematical details are given in an extensive paper, written by RICHARDS (1969). Instead of time, t , other so-called 'environmental time scales' can be used as heat or radiation sums (NICHOLS, 1970). S is positive and increases with time. It should be noted that, in case p is restricted to be only positive and the soil cover is small compared to the maximal soil cover, equation (1) can be approximated by: $dS/dt = r.S$, which describes exponential soil cover. In this case r can be seen as the relative soil cover rate. For $p < 0$ however the initial rate of soil cover is not approximately exponential. In the following p will therefore be restricted to positive values only. The solution of (1) can be written in the form

$$S = S_{max} \left[1 + p.e.^{-p.r(t-t_0)} \right]^{-1/p}$$

where t_i denotes the number of days between planting and the inflexion point of the S-curve. Remark that $S \rightarrow 0$, only when $t \rightarrow -\infty$. For purposes of physiological interpretation it can be useful to introduce three additional parameters, namely S_i , which is the amount of soil (in cm^2), covered at the inflexion point of the curve, and L_i , which is S_i as the percentage of S_{\max} . Note that $S_{\max} \cdot e^{-1} < S_i < S_{\max}$, when $0 < p < \infty$. It is obvious that

$$S_i = S_{\max} \cdot (1 + p)^{-1/p} \quad (3)$$

and

$$L_i = S_i/S_{\max} \cdot 100 = (1 + p)^{-1/p} \cdot 100 \quad (4)$$

The parameter p in fact shows the degree in which the curve is asymmetric, because we find that $36.8 < L_i < 50\%$ as $0 < p < 1$; $L_i = 50\%$ as $p = 1$ and $50 < L_i < 100\%$ when $1 < p < \infty$. The third parameter, R_i , is the derivative of the S-curve in the inflexion point and can be defined as the rate of soil cover (in cm^2d^{-1}) at time t_i . This value represents also the maximum rate of soil cover attained during the period of soil covering.

$$R_i = \frac{S_{\max} \cdot p \cdot r}{(1 + p)^{1 + 1/p}} \quad (5)$$

Physiological interpretation of some parameters

The number of days between planting and the inflexion point denotes the length of the period in which soil covering is approximately exponential. The amount of mutual and self shading will eventually decrease the rate of soil cover and thus determine t_i . Plant density, and also environmental, ontogenetic and genetic factors, which influence plant morphology, will affect the degree of mutual and self shading. Differences in plant morphology will be expressed in parameters of the soil cover curve, like t_i . S_i is the amount of soil covered at date t_i . A high L_i seems favourable. Parameter p itself seems physiologically not meaningful and therefore L_i will be used (which is only dependent on p) in this study.

A high relative soil cover rate (r) in the beginning of the growth period of a young plant seems favourable. At that stage of growth there is no mutual shading. The value of r will only depend on temperature and cultivar. Note that S_{\max} is always 400 cm^2 at the plant density of $20 \times 20 \text{ cm}$ and almost 625 cm^2 at the density of $25 \times 25 \text{ cm}$. It can be expected that S_{\max} becomes higher than 625 cm^2 for solitary plants. In this case S_{\max} varies among cultivars and can also be influenced by temperature.

A high R_i in the inflexion point suggests that in the period immediately after t_i the soil cover rate will be high. Because of the presence of the parameters S_{\max} , p and r in R_i , R_i could be a valuable characteristic for the description of the whole S-curve. R_i is only an important parameter when the plant has not yet reached the marketable weight at time t_i . The day the maximal soil cover is reached (t_{\max}) is not mentioned in equation (1). Because of the character of the used equation, theoretically $S = S_{\max}$ only if $t = \infty$. Therefore t_{\max} is determined from the

observed data. The knowledge of this date is useful because from that date onwards all the incoming radiation is intercepted by at least one leaf layer of the plant. A low value of t_{max} , thus a short period between planting and complete soil cover, seems favourable.

For a rapid covering of the available soil, the following combination of parameters seems desirable: a high r , a high L_i , a low t_i (combined with a high S_i), a high R_i and a low t_{max} . The harvest weight (W_{end}) at the end of the growth period is needed in order to determine the relationship between the final weight of the head and one or more parameters of the curve, which describes the process of soil covering.

Calculation of the parameters of the S-curve

The above mentioned model is intrinsically non-linear in its parameters. For this reason an iterative method (method of Taylor series) was employed, in which the parameters are estimated by the least squares method in a succession of stages, as described by DRAPER and SMITH (1966, p. 267-270). Initial estimates of the parameters were made by taking those which gave the 'best fit' of the linear model:

$$\ln \left\{ 1 - \left(\frac{S}{S_{max}} \right)^p \right\} = -p.r. (t - t_i) \quad (6)$$

which was calculated for a sufficient amount of values of S_{max} and p . The iterative procedure was terminated when the differences of the parameter estimates in successive iterations were sufficiently small (0.1 for S_{max} , 0.01 for p , 0.001 for r and 0.1 for t_i). The last stage of the iterative process also provides standard errors for the parameters. The above mentioned calculations were programmed on a portable desk calculator HP 9815 by NULWIK. In general convergence was fast except for some specific treatments, which visually also showed no clear sigmoid pattern.

RESULTS

The curve fitting procedure

Table 1a shows the parameters t_i , S_i , S_{max} , r , L_i , R_i of the S-curve with their standard errors of all the treatments of the spring experiment. In this table three other parameters are presented i.e. t_{max} , which is the number of days from planting until no visual increase in soil cover occurs, W_{max} , which is the fresh weight of the lettuce head at t_{max} , and W_{end} , which is the fresh weight of the head at the end of the experiment. In Table 1a no data of the treatments 'Tornado'-III-25, 'Tornado'-III-35 are given because the soil covering process of the various plants within one plot varied too much. Data of 'Valentine'-III-35 are absent due to calculating problems. In the autumn experiment data of the treatments 'Amanda Plus'-II-35, 'Tornado'-III-35 and 'Brevo'-I-35 are not presented, since the increase in soil cover did not show a clear sigmoid pattern.

TABLES 1a and 1b. Calculated parameters with their standard errors of the soil cover curve and some primary data for all treatments and the various cultivars during spring (a) and autumn (b). The standard errors are printed in italics. I, II and III are the three applied temperature regimes. 20, 25 and 35 represent the plant densities of 20×20 , 25×25 and 35×35 cm.

Cultivar		Treatment		Results									
tempe- rature regime	plant density	t_i (days)	S_i (cm ²)	S_{max} (cm ²)	r (cm ² cm ⁻² d ⁻¹)	L_i (%)	R_i (cm ² d ⁻¹)	t_{max} (days)	W_{max} (g)	W_{end} (g)			
Amanda Plus	I	20	19.9 0.9	284.5 21.2	389.4 7.0	0.109 0.008	71.4 5.2	26.3 1.7	28	80.3 3.0	231.9 9.4		
	I	25	24.1 0.6	377.7 16.5	617.1 6.2	0.106 0.008	61.2 2.6	29.1 1.1	45		228.2 4.9		
	I	35	31.2 1.2	497.4 40.2	1027.6 33.8	0.113 0.027	48.4 3.5	25.7 1.2	56		237.3 7.2		
	II	20	23.7 1.3	283.6 28.2	393.1 9.0	0.093 0.009	72.1 7.0	22.5 1.8	37	112.2 3.8	266.4 7.6		
	II	25	26.6 1.1	332.8 16.2	625.1 12.4	0.118 0.020	53.2 3.6	22.7 2.4	52		284.3 15.9		
	II	35	30.7 0.9	479.6 31.1	1023.5 29.4	0.136 0.029	46.9 2.7	26.8 3.5	59		358.2 12.3		
	III	20	25.2 1.4	269.7 22.9	390.6 7.4	0.082 0.008	69.0 5.7	18.1 1.3	42	127.2 5.4	310.8 13.8		
	III	25	30.0 0.9	350.6 17.4	618.1 8.3	0.086 0.009	56.7 2.7	19.6 1.9	62		345.9 15.5		
	III	35	38.8 1.5	481.3 42.4	950.5 35.8	0.082 0.017	50.6 3.9	20.4 4.7	69		450.6 12.6		
Decimnor	I	20	21.3 0.8	321.0 22.1	395.6 5.1	0.092 0.004	81.1 5.5	27.3 1.8	28	99.9 3.0	260.4 10.1		
	I	25	23.9 0.8	396.1 8.3	617.8 7.1	0.104 0.009	64.1 3.5	31.7 2.3	45		296.7 9.1		
	I	35	28.1 0.9	525.5 30.5	970.6 16.6	0.114 0.015	54.1 3.0	35.6 3.0	56		325.7 10.6		
	II	20	23.6 1.6	301.8 32.4	395.4 8.9	0.097 0.009	76.3 9.9	26.0 5.2	35	109.7 3.8	299.1 9.9		
	II	25	25.1 1.0	380.7 25.7	610.5 7.7	0.105 0.012	62.4 4.2	29.7 2.8	52		351.3 11.2		
	II	35	29.0 1.2	453.8 39.9	1054.6 38.3	0.198 0.097	43.0 3.5	25.3 5.2	62		401.1 16.1		
	III	20	27.9 1.7	292.5 23.1	391.4 7.7	0.077 0.006	74.7 7.9	19.7 3.2	42	128.7 5.4	303.6 12.7		
	III	25	30.8 0.7	356.1 13.4	616.5 4.8	0.092 0.007	57.7 2.1	21.9 1.4	66		356.2 9.7		
	III	35	41.0 1.1	547.0 49.0	1024.3 36.3	0.074 0.010	53.4 3.3	23.5 4.5	69		464.6 15.1		
Meikoningin	I	20	20.1 0.7	284.2 15.2	395.1 4.2	0.101 0.005	71.9 3.8	24.6 0.9	31	98.6 3.7	222.3 7.3		
	I	25	22.7 0.7	380.8 18.8	610.8 6.1	0.114 0.009	62.3 3.0	32.2 1.4	49		287.8 4.4		
	I	35	26.4 1.0	487.4 34.9	963.5 25.4	0.125 0.023	50.6 3.3	31.3 1.9	52		324.7 10.0		
	II	20	21.7 1.3	267.1 24.0	403.6 9.6	0.089 0.010	66.2 5.7	18.9 1.3	35	108.7 1.9	259.9 11.6		
	II	25	24.2 0.8	377.6 21.1	611.7 6.3	0.107 0.010	61.7 3.4	29.7 1.5	52		318.0 5.0		
	II	35	27.8 0.7	457.9 20.4	951.4 14.2	0.132 0.019	48.1 2.0	27.1 0.9	59		370.2 9.2		
	III	20	25.2 1.3	280.3 22.1	392.8 6.2	0.082 0.007	71.4 5.5	19.5 1.6	42	129.3 2.1	251.6 8.2		
	III	25	28.3 0.7	335.4 13.3	587.0 5.5	0.091 0.007	57.1 2.2	20.0 1.6	66		335.0 11.7		
	III	35	32.3 1.5	372.4 39.4	869.6 38.8	0.165 0.087	42.8 3.7	16.8 5.5	69		414.2 10.1		

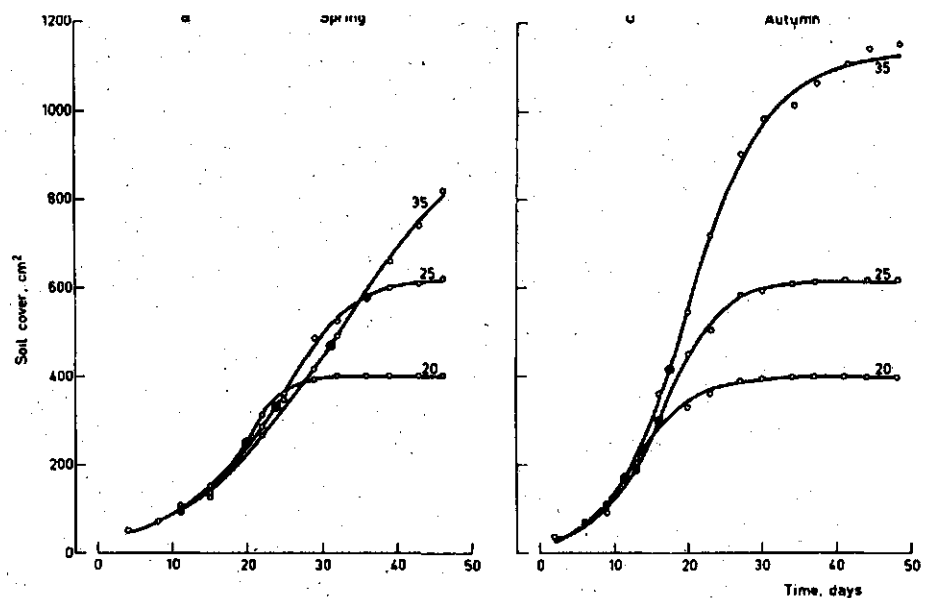
Cultivar	Treatment		Results									
	tempe- rature regime	plant density	t_i (days)	S_i (cm ²)	S_{max} (cm ²)	r (cm ² cm ⁻² d ⁻¹)	L_i (%)	R_i (cm ² d ⁻¹)	t_{max} (days)	W_{max} (g)	W_{end} (g)	
Noran	I	20	19.2 1.0	271.9 5.6	397.2 6.5	0.099 0.009	68.5 4.8	22.0 2.3	29	94.8 2.4	240.6 6.8	
	I	25	22.5 1.0	385.5 29.1	604.3 8.7	0.111 0.013	63.8 4.7	32.5 2.1	49		300.5 5.8	
	I	35	24.1 0.8	418.9 20.6	803.6 8.8	0.128 0.018	52.1 2.5	29.7 0.9	56		319.3 7.4	
	II	20	23.9 0.8	295.0 18.0	398.9 5.4	0.087 0.005	73.9 4.4	22.5 1.1	35	116.7 4.1	287.0 5.6	
	II	25	25.4 1.3	346.6 9.8	603.6 9.8	0.110 0.019	57.4 4.5	25.3 1.2	59		365.0 7.1	
	II	35	28.3 1.4	412.6 39.5	925.5 33.7	0.165 0.073	44.8 4.0	23.0 3.6	62		448.5 11.4	
	III	20	24.4 1.1	274.0 20.2	392.9 6.9	0.085 0.007	69.7 5.0	19.4 1.4	40	149.5 6.5		
	III	25	28.5 1.0	319.3 16.7	592.0 7.5	0.096 0.012	53.9 2.7	18.1 1.7	66		359.4 5.1	
	III	35	39.1 1.2	415.1 32.4	885.0 37.7	0.092 0.021	46.9 3.1	15.7 4.6	69		428.4 21.2	
Proeftuin's Blackpool	I	20	21.7 0.9	291.0 20.2	392.1 5.0	0.098 0.005	74.3 5.1	25.0 1.3	33	108.1 4.1	230.7 7.4	
	I	25	23.6 1.0	355.0 25.3	610.1 9.2	0.119 0.017	58.2 4.1	28.6 2.4	49		269.9 5.5	
	I	35	25.4 1.7	393.5 30.3	893.0 44.2	0.194 0.122	44.1 5.2	24.4 7.3	56		304.2 6.2	
	II	20	24.2 0.8	275.9 15.8	391.2 5.1	0.086 0.005	70.5 3.9	20.0 0.8	40	141.8 1.8	281.1 11.0	
	II	25	23.1 1.2	321.2 28.1	603.6 11.2	0.142 0.031	53.2 4.6	26.4 3.2	56		324.2 13.9	
	II	35	26.9 1.3	393.0 29.0	867.4 24.4	0.159 0.058	45.3 3.6	22.6 5.1	62		428.3 11.3	
	III	20	27.9 0.8	284.8 14.1	396.5 3.9	0.075 0.004	71.8 3.5	18.1 0.9	44	158.9 4.1	271.7 10.1	
	III	25	31.9 0.7	349.4 12.3	575.4 5.0	0.082 0.005	60.7 2.1	20.6 0.9	62		333.3 9.9	
	III	35	37.6 1.1	387.9 40.0	796.0 32.3	0.085 0.017	48.7 3.2	15.4 4.3	69		361.7 8.1	
	Rapide	I	20	17.6 0.6	269.9 11.0	399.9 4.7	0.088 0.004	67.5 2.7	19.2 1.0	27	77.3 1.8	207.1 4.4
		I	25	22.0 0.6	388.3 15.9	618.4 5.1	0.100 0.007	62.8 2.5	29.0 1.6	45		273.3 4.0
		I	35	25.0 1.8	447.2 54.9	971.6 46.3	0.145 0.069	46.0 5.2	25.0 4.4	56		294.4 8.8
II		20	22.9 1.4	293.6 14.7	399.0 10.9	0.076 0.006	73.6 7.1	19.5 2.8	33	103.9 2.4	258.8 9.9	
II		25	24.3 1.0	392.2 23.0	610.9 7.3	0.086 0.008	64.2 3.7	26.0 1.7	52		292.9 5.7	
II		35	28.3 0.7	513.9 34.3	977.5 16.3	0.097 0.010	52.6 2.1	28.0 3.7	56		362.8 8.4	
III		20	25.9 1.6	298.5 17.0	388.1 6.8	0.066 0.005	76.9 6.6	17.7 2.6	40	120.0 6.7	275.9 11.4	
III		25	27.7 1.1	375.0 21.2	602.1 6.3	0.082 0.008	62.3 3.5	22.7 1.4	66		329.1 9.6	
III		35	37.5 0.9	480.5 29.0	833.0 13.5	0.063 0.005	57.7 2.4	20.1 2.4	69		410.9 20.7	

Cultivar	Treatment		Results								
	tempe- rature regime	plant density	t_i (days)	S_i (cm^2)	S_{max} (cm^2)	r ($\text{cm}^2\text{cm}^{-2}\text{d}^{-1}$)	L_i (%)	R_i (cm^2d^{-1})	t_{max} (days)	W_{max} (g)	W_{end} (g)
Tornado	I	20	26.0 1.5	249.0 33.0	380.8 9.8	0.139 0.025	65.4 8.5	27.1 3.1	38	144.1 8.4	298.9 1.6
	I	25	27.7 0.9	311.9 23.9	624.8 12.7	0.188 0.043	49.9 3.6	29.3 1.6	52		384.7 6.4
	I	35	32.4 1.1	459.2 41.2	997.3 35.9	0.175 0.060	46.0 3.8	31.1 2.9	59		491.6 18.6
	II	20	27.9 1.1	209.3 18.2	400.1 8.0	0.162 0.038	52.3 4.4	18.9 2.3	43	135.8 4.3	323.2 12.6
	II	25	34.7 0.6	367.8 14.5	618.4 5.1	0.102 0.008	59.5 2.3	26.1 1.0	66		432.2 11.7
	II	35	37.6 1.3	466.9 47.9	1036.4 54.3	0.151 0.060	45.0 4.0	24.9 6.3	69		538.7 7.6
	III	20	33.3 1.0	216.9 15.2	409.2 9.3	0.123 0.020	53.0 3.6	15.3 1.3	47	182.5 15.5	
	III	25									
	III	35									
Valentine	I	20	20.1 1.0	273.4 4.1	400.4 7.5	0.095 0.008	68.3 5.0	21.1 2.3	31	119.5 4.0	240.1 5.4
	I	25	25.7 0.9	418.9 24.7	609.2 6.8	0.094 0.006	68.8 4.0	32.4 1.9	49		295.5 8.4
	I	35	27.6 1.0	424.6 26.0	809.0 15.8	0.110 0.017	52.5 3.1	26.2 1.5	56		315.9 5.7
	II	20	25.8 1.0	298.3 18.0	396.4 4.2	0.076 0.004	75.3 4.5	20.0 1.3	37	135.4 3.5	292.7 9.4
	II	25	27.4 0.7	366.0 14.0	605.9 6.4	0.093 0.007	60.4 2.6	24.3 0.7	56		318.6 6.4
	II	35	28.8 1.2	395.0 28.3	809.2 19.5	0.119 0.027	48.8 3.3	22.1 2.2	62		366.3 6.1
	III	20	27.7 0.8	279.4 12.2	397.0 3.9	0.070 0.003	70.4 3.0	16.4 0.2	44	174.3 6.4	291.4 10.6
	III	25	33.1 0.5	384.0 9.3	574.4 3.0	0.070 0.002	66.9 1.6	21.4 0.8	62		335.7 8.9
	III	35							66		403.1 13.0
1b. AUTUMN EXPERIMENT											
Amanda Plus	I	20	11.5 1.5	197.9 33.4	394.6 13.0	0.254 0.138	50.2 8.3	25.3 3.8	29		145.9 7.3
	I	25	16.1 0.6	337.0 17.4	617.2 5.2	0.180 0.023	54.6 2.8	36.9 2.2	43		189.6 5.1
	I	35	18.5 0.7	529.9 32.6	1139.4 16.8	0.255 0.066	46.5 2.8	54.1 5.1	47		248.1 8.0
	II	20	12.8 1.5	206.0 27.8	396.5 10.1	0.194 0.075	52.0 6.8	21.9 1.1	33		165.7 6.8
	II	25	16.6 0.5	320.8 14.3	612.7 4.6	0.195 0.025	52.4 2.3	34.9 0.6	50		206.5 7.1
	II	35							54		297.6 9.5
	III	20	16.6 1.2	237.1 21.5	395.4 7.6	0.121 0.021	60.0 5.3	20.3 1.4	36		166.0 6.1
	III	25	18.0 0.5	316.1 9.6	603.5 4.2	0.169 0.020	52.4 2.1	29.9 1.3	50		192.9 6.8
	III	35	20.5 1.3	432.2 51.0	1040.2 43.2	0.256 0.154	43.5 4.5	34.6 5.5	54		256.4 9.7

Results

Cultivar	Treatment		Results								
	tempe- rature regime	plant density	t_i (days)	S_i (cm ²)	S_{max} (cm ²)	r (cm ² cm ⁻² d ⁻¹)	L_i (%)	R_i (cm ² d ⁻¹)	t_{max} (days)	W_{max} (g)	W_{end} (g)
Dandie	I	20	10.8 0.5	185.9 10.8	400.0	3.8	0.327 0.082	46.5 2.6	24.3 1.3	31	150.8 5.5
	I	25	14.2 0.6	319.0 16.6	612.4	4.9	0.203 0.031	52.1 2.6	35.7 1.4	43	193.9 7.8
	I	35	16.9 1.0	485.4 45.3	1049.4	21.5	0.262 0.107	46.3 4.3	50.0 4.9	47	287.5 10.3
	II	20	10.2 0.6	180.8 11.5	400.5	3.8	0.351 0.115	45.1 2.9	22.9 0.5	33	171.9 7.6
	II	25									
	II	35	19.1 1.0	483.2 40.3	1075.3	22.2	0.247 0.102	44.9 3.7	41.9 6.2	50	321.7 8.0
	III	20	11.8 0.8	190.7 12.3	399.8	4.0	0.233 0.061	47.7 3.1	19.4 0.6	40	183.6 6.1
	III	25	15.7 1.3	291.1 28.7	590.0	9.6	0.194 0.067	49.3 4.8	27.2 3.0	54	229.2 10.0
	III	35	19.0 1.6	429.9 10.5	1008.5	31.1	0.294 0.239	42.6 5.1	33.8 7.4	57	307.9 5.9
	I	20	11.1 0.9	208.0 9.8	400.8	6.2	0.204 0.055	51.9 4.6	23.2 0.5	29	154.1 6.9
	I	25	15.4 0.4	365.5 14.0	621.3	4.4	0.156 0.012	58.8 2.2	39.1 1.4	39	179.2 5.4
	I	35	18.7 1.1	548.8 14.9	1188.5	23.8	0.231 0.090	46.2 4.1	49.6 6.3	50	250.2 5.9
	II	20	11.8 0.5	217.3 10.0	398.5	2.9	0.183 0.022	54.5 2.5	24.1 0.2	31	165.1 6.7
	II	25	16.3 0.7	347.2 5.6	620.1	6.3	0.151 0.020	56.0 3.2	33.2 1.2	47	231.1 7.3
Deciso	II	35	18.7 1.3	548.0 57.3	1236.1	29.4	0.275 0.152	44.3 4.5	49.7 3.0	50	313.7 11.4
	III	20	14.5 0.8	234.5 14.9	394.7	4.6	0.134 0.017	59.4 3.7	21.9 1.6	33	161.1 4.5
	III	25	17.6 1.0	342.7 24.7	611.1	7.6	0.142 0.024	56.1 4.0	31.0 1.2	50	212.8 11.6
	III	35	18.8 1.5	483.9 12.0	1209.2	37.3	0.539 0.799	40.0 4.9	41.5 7.4	54	309.0 9.7
	I	20	16.0 1.5	233.4 25.8	399.6	8.7	0.132 0.029	58.4 6.3	20.9 2.1	33	148.7 6.1
	I	25	17.3 0.7	352.9 20.0	618.1	6.8	0.152 0.019	57.1 3.2	35.1 2.4	47	186.2 7.2
	I	35	20.4 0.8	556.9 38.1	1049.1	19.0	0.165 0.028	53.1 3.5	52.9 5.6	50	275.4 5.9
	II	20	15.1 0.7	230.2 13.5	399.1	4.8	0.144 0.018	57.7 3.3	22.1 1.6	33	167.8 4.8
	II	25	17.7 0.5	336.5 12.4	623.3	4.8	0.150 0.013	54.0 1.9	29.9 1.6	47	227.8 11.1
	II	35	22.8 0.7	590.4 32.4	1140.5	17.6	0.157 0.023	51.8 2.7	50.5 3.8	50	297.1 10.6
	III	20	19.1 1.0	270.2 9.8	392.9	4.6	0.102 0.009	68.8 4.6	22.7 2.3	40	178.9 4.9
	III	25	20.2 0.7	367.8 19.4	613.7	6.1	0.130 0.012	59.9 3.1	33.6 0.5	54	225.9 7.6
	III	35	19.7 1.5	442.7 61.0	1086.7	45.9	0.464 0.596	40.7 5.4	39.2 8.0	57	305.9 7.1
Ravel	I	20									
	I	25									
	I	35									

Cultivar	Treatment		Results									
	tempe- rature regime	plant density	t_i (days)	S_i (cm^2)	S_{\max} (cm^2)	r ($\text{cm}^2 \text{cm}^{-2} \text{d}^{-1}$)	L_i (%)	R_i ($\text{cm}^2 \text{d}^{-1}$)	t_{\max} (days)	W_{\max} (g)	W_{end} (g)	
Tornado	I	20	12.8 2.4	156.4 33.0	393.6 17.3	0.636 1.711	39.7 8.2	14.6 0.6	43		121.0 4.2	
	I	25	18.8 1.6	271.6 13.8	590.1 16.2	0.193 0.086	47.6 5.5	22.9 3.5	47		153.1 5.1	
	I	35	23.7 1.9	484.7 43.2	1175.3 121.7	0.333 0.488	41.2 7.3	34.2 7.1	47		211.9 6.3	
	II	20	15.1 1.6	168.1 19.0	382.5 8.5	0.247 0.160	43.9 4.9	13.1 1.0	50		144.3 2.9	
	II	25	19.6 0.7	298.0 14.4	571.7 4.9	0.149 0.018	54.0 2.6	26.4 0.2	54		176.1 5.7	
	II	35	21.9 1.2	414.3 39.5	948.3 25.8	0.259 0.138	43.7 4.0	32.9 2.6	57		238.6 9.1	
	III	20	16.4 1.4	170.2 16.2	374.2 5.7	0.200 0.091	45.5 4.2	12.6 0.8	54		139.6 6.7	
	III	25	18.1 1.9	233.6 33.9	506.4 13.0	0.220 0.142	46.1 6.6	20.0 2.3	57		150.4 6.0	
	III	35							61		199.6 6.6	
	Brevo	I	20	9.9 0.9	166.6 15.5	400.3 5.6	0.539 0.412	41.6 3.8	20.4 0.8	37		150.1 6.7
		I	25	15.1 0.6	303.6 18.4	618.0 5.8	0.229 0.049	49.1 2.9	33.1 0.8	46		166.5 5.6
		I	35							49		243.9 10.6
II		20	14.9 0.9	206.5 14.8	393.1 5.1	0.177 0.036	52.5 3.7	20.5 1.3	39		137.4 3.8	
II		25	15.1 0.7	279.5 17.1	603.3 5.4	0.267 0.075	46.3 2.8	29.5 1.4	53		175.2 6.0	
II		35	23.7 1.1	716.7 64.2	1672.4 46.8	0.246 0.122	43.5 3.7	53.3 2.7	56		274.9 8.1	
III		20	13.3 1.4	180.0 19.6	390.9 6.1	0.240 0.122	46.0 5.0	16.7 1.3	53		137.3 6.1	
III		25	17.3 0.9	284.6 19.2	605.1 6.1	0.204 0.060	47.0 3.2	24.2 1.8	61		157.7 5.7	
III		35	22.7 1.6	543.5 59.7	1352.3 40.6	0.421 0.510	40.2 4.3	38.1 3.7	63		209.4 8.3	



FIGS. 3a and 3b. Relation between soil cover and time in spring and autumn after planting in compartment I of the glass-house of plants of 'Amanda Plus'. Plant distances are 20, 25 and 35 cm. The lines represent the calculated regressions, the open circles are the measured data. The solid circles represent the calculated inflexion point.

This fact also became clear from the calculations because no convergence was obtained. The growth of the plants of 'Tornado' in compartment III was poor for all treatments. Plants of the plot 'Dandie'-II-25 (Table 1b) were not planted.

Figures 3a and 3b give examples of the results of the curve-fitting of the soil cover of the various treatments in compartment I in spring and autumn with the cultivar 'Amanda Plus'. The measured and calculated values are given. The inflexion point (t_i , S_i) is also shown in the Figures. All curves are asymmetrical ($p \neq 1$). The Figures demonstrate that t_{max} and S_{max} increase with a decrease in plant density. At the same plant density the process of soil-covering until the maximum area occurs more rapid in autumn than in spring due to higher temperatures in autumn. The parameters r and, for some treatments, S_{max} have high standard errors.

Time t_i and soil cover S_i at the inflexion point

The standard errors of t_i are in general small. The time of the inflexion point becomes longer when the temperature is lower or when the spacing is wider. For 'Amanda Plus', for instance, the t_i in spring is longer than the t_i in autumn because of the lower temperatures at the beginning of the growth period. Solitary plants show also an inflexion point, which is caused by self shading of the leaves within one plant. The pattern of the curve of soil covering of the

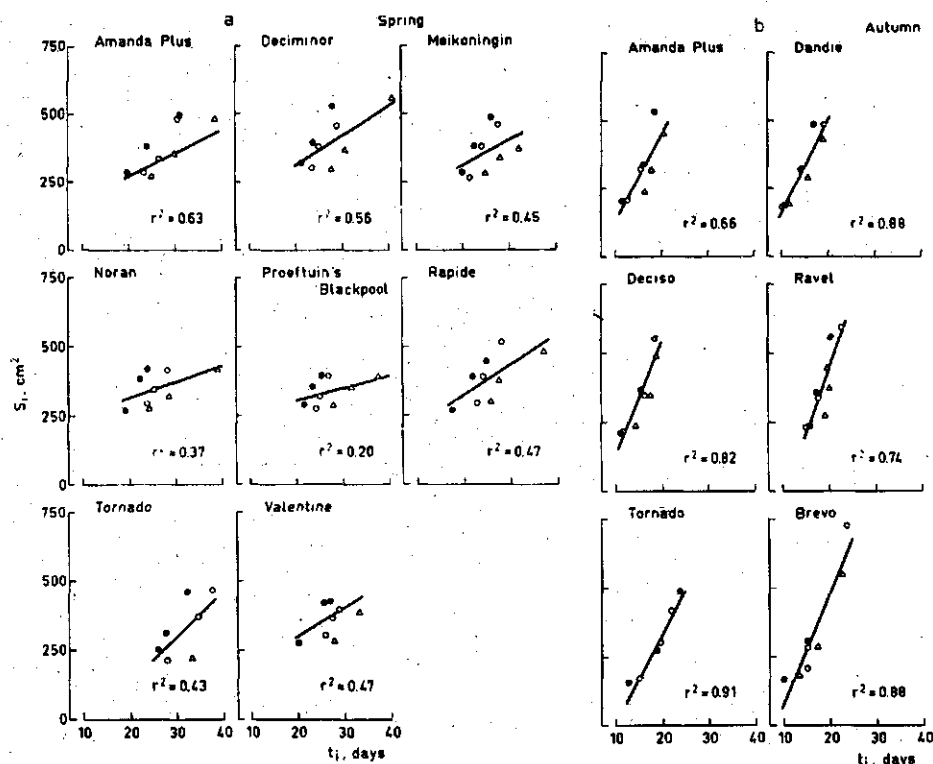
TABLES 2a and 2b. Temperature sums (heat units in degree days) of day temperatures for all treatments and cultivars in spring (a) and in autumn (b) calculated between planting and the inflexion point of the soil cover curve. I, II and III represent the temperature regimes. 20, 25 and 35 represent the plant densities of 20×20 , 25×25 and 35×35 cm.

Cultivar	Treatment								
	20	I 25	35	20	II 25	35	20	III 25	35
2a. SPRING EXPERIMENT									
Amanda Plus	407.4	470.6	616.0	425.9	480.9	554.5	390.0	470.1	598.5
Decimino	415.9	466.5	555.4	424.3	451.6	524.4	435.0	480.8	634.2
Meikoningin	391.1	443.0	519.6	393.8	434.5	502.1	421.9	441.8	534.0
Noran	369.5	439.3	470.6	429.1	457.7	511.2	377.8	445.3	603.7
Proeftuin's Blackpool	423.9	460.1	498.0	434.5	451.6	486.4	435.6	495.5	577.2
Rapide	332.7	430.0	498.3	413.2	436.4	511.2	403.0	539.9	575.4
Tornado	511.3	546.8	636.0	503.9	601.9	652.4	513.5	-	-
Valentine	407.7	505.1	532.4	465.8	495.2	520.6	431.5	510.6	-
2b. AUTUMN EXPERIMENT									
Amanda Plus	272.3	371.3	425.8	276.0	348.7	-	329.2	356.9	400
Dandie	255.3	332.6	389.9	220.8	-	397.9	244.5	312.3	373.8
Deciso	262.4	357.2	430.0	255.8	342.2	390.5	294.0	348.6	370.4
Ravel	368.9	399.1	467.6	320.0	371.5	468.2	375.5	394.5	385.8
Tornado	302.0	432.1	538.7	320.0	407.5	452.4	324.9	358.6	-
Brevo	234.8	351.4	-	316.4	320.0	483.7	273.0	343.4	437.1

solitary plants is not disturbed by competition for light interception with the neighbouring plants. The decrease of t_i at higher plant densities indicates that the inflexion point in the soil cover curve is also caused by mutual shading.

In Tables 2a and 2b the day temperature sums until t_i (heat units in degree days) are presented, in which 0°C as minimal temperature is used. Constant temperature sums until t_i were expected for the various treatments of one cultivar, but these constant sums are not shown in the Tables. Taking into account the standard error of t_i , correction for higher minimal temperatures will not result in constant heat sums, also since the sums of treatments with low mean temperatures and long periods until t_i are also not systematically higher. The mean day and night temperatures until t_i can be derived from Figures 2a and 2b. From those Figures it is evident that the mean temperature over, for instance, the first 20 days of the growth period in one compartment differs slightly from the mean temperature over the first 25 days in that compartment. Thus the differences in temperature sums between treatments of one cultivar and also probably between cultivars are caused mainly by differences in t_i . 'Tornado', for instance, has both a high t_i and a high temperature sum. In general there is a tendency to small differences in temperature sums between cultivars.

Mutual shading shortens the period of the exponential soil cover rate. In Figure 4a the linear regressions of t_i and S_i are given for all treatments in



FIGS. 4a and 4b. Calculated linear relationships between time and the soil cover area, reached at the inflexion point of the soil cover curve, for all treatments and cultivars during spring (a) and autumn (b).

● temperature regime I; ○ temperature regime II; △ temperature regime III.

spring. During spring the linear relationships between t_i and S_i are not highly significant, but other, non-linear, regressions gave no consistent higher values of the correlation coefficients (r^2) for all cultivars. Solitary plants exhibit only self shading. These plants have a higher t_i and S_i than the plants at narrow spacings. With higher temperatures the value of t_i declines for all plant densities, although S_i can remain the same or declines less than expected. The variation of the data in Fig. 4a is a result of these effects. 'Rapide' has in general a higher S_i -value during the period until t_i than other cultivars. The high t_i combined with the relatively low S_i of plants of 'Tornado' and 'Proeftuin's Blackpool' is less advantageous for the soil covering and growth of lettuce. The differences between the slopes and intercepts of the linear regressions are large between the various cultivars. 'Decimnor', 'Rapide' and 'Tornado' (however, negative intercept) have high values of the slope, which seems to be favourable for the process of soil covering. The regressions of 'Noran' and 'Proeftuin's Blackpool' show low values.

Figure 4b presents the relationship between t_i and S_i for the treatments of the autumn experiment. The correlation coefficients of the regressions are higher in

autumn than in spring and the differences in t_i are smaller. Although environmental conditions were different, the same remarks about the effects of temperature and plant density are valid for both experiments. The intercepts of the linear regression lines of all cultivars are in autumn negative and the values of the slopes are higher than in spring. 'Deciso' is one of the cultivars with a favourable low t_i and a high S_i in comparison with the other cultivars, whereas 'Tornado' combines a low value of t_i with a relatively low S_i .

We may conclude that no cultivars with a very short t_i , combined with a high S_i are present in the experiments. Moreover, with higher temperatures a certain S_i can be obtained in a shorter period.

The parameters S_{max} and r

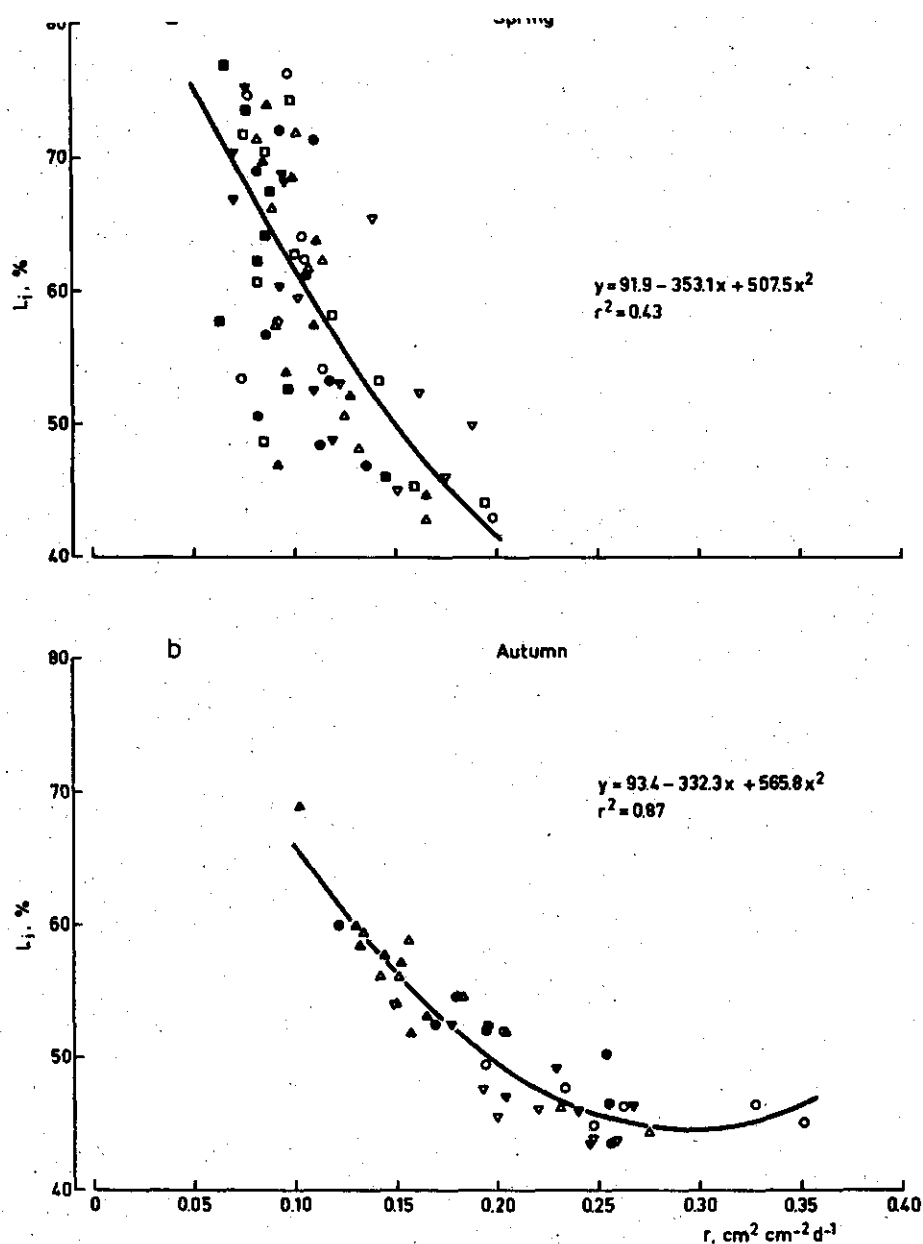
The maximal soil cover for the spacings of 20 and 25 cm is in the order of 400 and 625 cm², resp. (vide Tables 1a and 1b). Differences in S_{max} occur mainly for solitary plants. S_{max} tends to be lower at lower temperatures, when the plant forms a more compact head. The cultivar 'Valentine' has a rather low S_{max} . This cultivar is also in horticultural practice known as a lettuce with a small head.

The parameter r represents the relative soil cover rate immediately after planting into the glass-house, but r is not useful in most situations due to high standard errors. There is a tendency that r decreases at lower temperatures and increases at wider spacings. The values of r of 'Valentine' are low, compared with the values of other cultivars. The parameter r is lower in spring than in autumn.

Position of the inflexion point and slope in (t_i, S_i)

The standard errors of L_i are small. L_i is strongly influenced by plant density (effect of mutual shading) and less by cultivar and temperature. Most values of L_i are higher in spring than in autumn irrespective of cultivar. The large environmental influences on L_i make this parameter less useful as a criterion for selection between cultivars for a fast soil covering process. Since S_{max} for the plant spacings of 20 and 25 cm always gives an almost constant value i.e. 400 resp. 625 cm², it is not necessary to relate L_i to t_i . The linear regressions of the values of t_i and L_i of the widest spacing show for both experiments low values of the correlation coefficients ($r^2 < 0.10$). The same regressions without the values of 'Tornado' and 'Brevo' give still low correlation coefficients ($r^2 < 0.21$). The favourable relation of a low t_i with a high L_i , comparable with that of a low t_i with a high S_i at the narrow spacings, is not present. And a high value of t_i is not always related to a high value of L_i . Thus the best choice is for a low t_i .

Figures 5a and 5b demonstrate the non-linear relationships of L_i with r . The parameter L_i was strongly influenced by plant density and the parameter r by temperature and plant density, although the standard error of r was high. When the standard error of r was close to or exceeded the real value, this value was not mentioned in the Figures. The fit in autumn was better than in spring. A cultivar with the preferable combination of a high r and a high L_i is not present. A cultivar with the unfavourable combination of a low L_i and a low r , is also not shown. In spring 'Amanda Plus' has a rather good combination of r and L_i .



FIGS. 5a and 5b. Calculated quadratic relationships between r and L_1 for all treatments in spring (a) and in autumn (b).

Spring: ● 'Amanda Plus'; ○ 'Decimino'; △ 'Meikoningin'; ▲ 'Noran'; □ 'Proeftuin's Blackpool'; ■ 'Rapide'; ▽ 'Tornado'; and ▽ 'Valentine'. Autumn: ● 'Amanda Plus'; ○ 'Dandie'; △ 'Deciso'; ▲ 'Ravel'; ▽ 'Tornado'; and ▽ 'Brevo'.

values, whereas 'Tornado' (because of low L_i) and 'Proeftuin's Blackpool' (because of low r) have a less favourable combination of the parameters. In autumn 'Amanda Plus' has an intermediate position between other cultivars, like 'Ravel' and 'Dandie'.

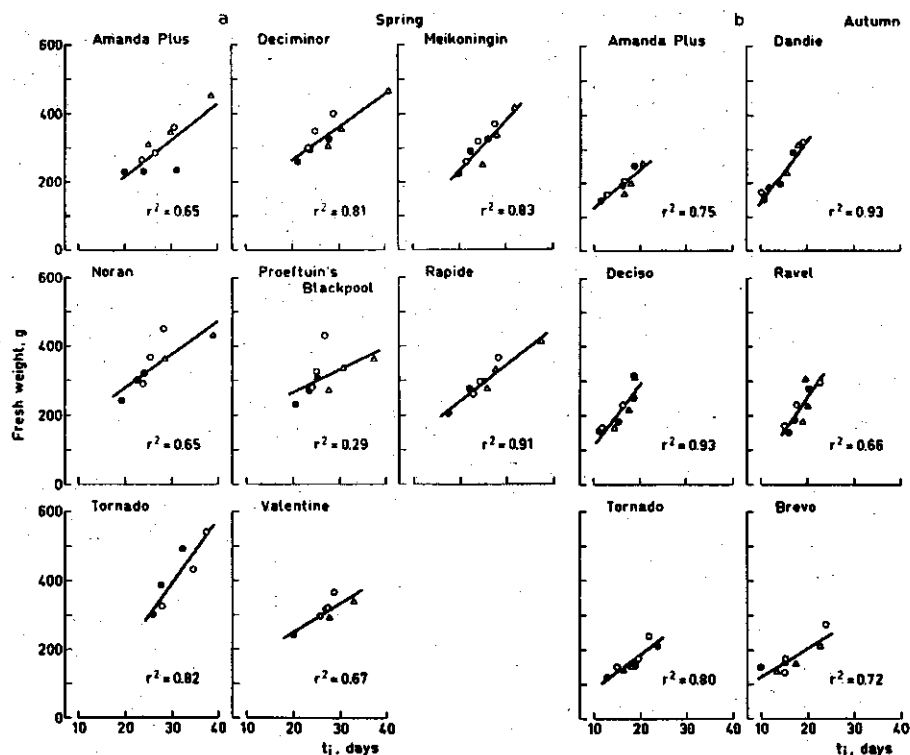
The slope R_i increases at lower plant densities and with higher temperatures. This is more evident in autumn than in spring. The values of R_i are higher in autumn than in spring (see 'Amanda Plus'). 'Decimnor' has in spring slightly higher values than the other cultivars, while 'Proeftuin's Blackpool' has low values. In autumn cultivar 'Tornado' has a low value of R_i . The parameter R_i is not as meaningful as was expected as an overall characteristic of the curve, because of the small differences between the values, mainly in spring.

Correlation of some soil cover parameters with end harvest weight

The fresh weight of the lettuce head at the end of the experiments, W_{end} , depends partly on the harvest date, as in spring and autumn the plants of the three compartments were not cut on the same day. Higher weights at lower temperatures are partly caused by those different harvest dates. Wider spacings result in higher end weights. The total amount of intercepted radiation during the period of complete soil cover is higher in spring than in autumn. Plants in spring, therefore, had much more benefit from the radiation during the weeks before harvest than those in autumn. Generally the end weight in spring was higher.

The relationships between W_{end} and L_i , t_i and W_{max} deserve attention for breeding reasons. The relationships of t_i and W_{max} with W_{end} also give information about the relationships between S_i and t_{max} with W_{end} . The correlation coefficients (r^2) of the linear regressions between L_i and W_{end} of all cultivars together are 0.04, 0.12 and 0.07 for the plant densities 20, 25 and 35 cm, resp. in spring, and 0.12, 0.33 and 0.13 for those plant densities in autumn. The correlation coefficients are slightly higher when calculated without the data of 'Tornado' and 'Brevo'. Cultivars with approximately the same L_i (which depends mainly on plant density) can reach different values of W_{end} . Lower temperatures give a lower fresh weight at a certain L_i . Since the relationship of L_i with W_{end} is not clear and because of the relatively high standard errors of r , also no significant relation between r and W_{end} can be expected.

Figures 6a and 6b present linear relationships between t_i and W_{end} . A longer t_i , caused by wider spacing and/or lower temperatures, gives a higher W_{end} . The correlation coefficients and the values of the slopes and intercepts vary much between the cultivars in spring as well as in autumn. The linear fit of 'Amanda Plus' differs in spring more from the fits of other cultivars in spring than from the linear fit of 'Amanda Plus' in autumn. The differences of the values of 'Tornado' are rather large between spring and autumn. Non-linear regressions do not give a better fit for the cultivars. The correlation coefficients (r^2) of the linear regressions of t_i and W_{end} per temperature regime for the temperature regimes I, II and III were in spring resp. 0.53, 0.72 and 0.78 and in autumn resp. 0.41, 0.35 and 0.25.



FIGS. 6a and 6b. Calculated linear relationships between time at the inflexion point and the fresh weight at the final harvest for all treatments and all cultivars in spring (a) and in autumn (b). ● temperature regime I; ○ temperature regime II and △ temperature regime III.

The parameter W_{\max} is only available for the 20 cm spacing in spring. From Table 1a it is obvious that W_{end} gives higher values when W_{\max} is higher. Selection on W_{\max} seems favourable, but, because of the positive relation between t_{\max} and W_{\max} this is misleading.

DISCUSSION

In a Venlo glass-house some environmental factors can often not be conditioned to a great extent and the climate within such a glass-house is not homogenous. As a result of this much variation in the data and the results of the experiments can be expected. In these experiments the difference in actual temperature regimes was relatively small, especially in the autumn experiment. The last harvest date was late in comparison with normal horticultural practice (KLAPWIJK, 1978a, 1978b) and the end weight was in many treatments also higher than the commercial weight. In both experiments rather large plants were planted in the glass-house.

The measurement of the soil cover by the dot counting method was easy and fast. Differences in soil cover between various treatments seem large during the first weeks of growth, due to the high soil cover rate, but the large differences in cm^2 of covered soil present only a small difference in the number of days.

In general the fitting of the soil cover by a four parameter sigmoid curve is feasible, as was shown by calculations with results of 'Noran' and 'Deciso' in preliminary experiments, but also for other cultivars or rosette plants, like endive. Some parameters such as t_i , S_i and L_i have low standard errors. The standard errors of r are high. The four parameter curve is not sufficient flexible to describe the process of soil covering accurately for all treatments. For those treatments the soil covering process did not occur according to a sigmoid pattern. This resulted in high standard errors of the parameters or no convergence in the calculations (e.g. in autumn experiment the treatments 'Amanda Plus'-II-35, 'Tornado'-III-35 and 'Brevo'-I-35). Other causes of the high standard errors are: the relatively high inaccuracy of the dot counting method for the measurements of small plants, the difficulty to obtain and measure the exact value of S_{\max} of the solitary plants and the unequal distribution of the primary data throughout the whole curve. More measurement dates are needed during the beginning of the soil covering process (the exponential part). Moreover, when the period from planting until t_{\max} is long the fit becomes less accurate. Since the shape of the curve is chosen because of the preliminary results of the soil cover measurements with the butterhead cultivars 'Noran' and 'Deciso', the fitting of this curve is more difficult for 'Tornado', which is an upright lettuce type with another pattern of soil covering and growth, and 'Brevo', an endive cultivar. The use of a minimal soil cover percentage of 36.8% ($p > 0$) in the calculations was appropriate. As a result of this choice a physiological interpretation of r remained possible. Since all plants start to grow as solitary plants, the value of r had to be the same for all plant densities. There is a tendency; however, that r increases with wider spacing, but because of the high standard errors most values of r are identical. The uncorrected time scale did not appear to be suitable in uncontrolled conditions (NICHOLS, 1970). NICHOLS tried to compensate for these fluctuating conditions by using 'environmental time scales' for the description of growth. Time scales based on the heat unit concept were not suitable enough either, especially the exponential growth stage during which the soil cover is less than the maximal value. A better correlation was obtained between growth and the corrected solar radiation, although temperature was important as well.

BIERHUIZEN et al. (1973) concluded from glass-house experiments with 'Noran' at a plant density of 20×20 cm that temperature determines the soil cover rate. This conclusion could not be confirmed in the spring and autumn experiments described in this article, although an influence of the temperature is evident. Growth and soil covering are not identical processes, but from NICHOLS' experiments it seems also justified to conclude that temperature does not exclusively determine the soil cover process. A problem for the comparison of the temperature sums until t_i is that at date t_i the parameter S_i can have various

autumn of, for example, 'Amanda Plus' is not useful. The use of radiation sums for the experiments with soil cover as described by NICHOLS (1970) was not sufficient to solve the time problem accurately, not even when the radiation was corrected on a soil cover base and for a minimal and maximal radiation. The use of radiation sums in this study was tried but was not more successful than the use of temperature sums.

The depression in soil cover at the 20 and 25 cm spacings is, compared with the solitary plants, more than the 5%, which HUGHES (1969) considered as a criterion for mutual shading. HUGHES studied the depression in growth, while in this Part the depression in covered soil area is observed. The lower t_i at the 20 and 25 spacings, compared with the t_i of the solitary plants, is caused by mutual shading. The inflexion point of the soil cover curve of solitary plants is determined by self shading of the leaves of the plant itself. Higher temperatures result in a higher value of S_i at a certain value of t_i than lower temperatures do. At higher temperatures the effect of mutual shading becomes visible in a later stage of the soil covering process.

The effect of mutual shading is less at lower temperatures because cell extension is less, leaves are shorter and the relative width of the leaves is higher (BENSINK, 1971). Self shading, however, is stronger in that case, as the leaves are overlapping each other to a greater extent.

No cultivars in these experiments were used which had the desired combination of the soil cover parameters for a rapid cover of the soil. No clear and very useful relationships exist, unfortunately, between end fresh weight and the parameters of the soil cover curve. For instance, at one temperature regime it seems difficult to select a high W_{end} based on t_i , especially in autumn. The correlations between W_{end} and some of the parameters could be better in horticultural practice than in these experiments. The final harvest date was chosen when the solitary plants achieved maximum soil cover. This implies that the plants at the densities of 20 and 25 cm, which densities are more similar to those applied in normal practice, were harvested too late. One other reason is that the concept of soil cover is twodimensional and to regard this as a measure for the light intercepting surface of the plant is oversimplified. Growth of a plant is a threedimensional process during which light is intercepted from all directions. Especially during winter, the threedimensional structure of a plant is essential. Plant height and leaf thickness are also important parameters for the growth of a plant. The microclimate around a plant and between the leaves will play a part too. A plant with an open structure has a better gas-exchange, and is less affected by diseases. EENINK and SMEETS (1978) concluded from glass-house experiments with various genotypes that the correlations between plant growth characteristics and the fresh weight in an early stage of growth and those at harvest are low. The correlation will even be less when the length of the growth period increases, as shown in this article. The growth period between t_{max} and t_{end} is important for W_{end} .

It is possible and interesting from a physiological point of view to describe the soil cover process of a plant by a four parameter sigmoid curve, although its relation with the marketable head is low. With data of that curve the harvest time or the end weight can not be predicted. A high temperature in the beginning of the growth period may be useful in order to reach a hundred percent soil cover as soon as possible, but it is no guarantee for a high marketable yield. At present it does not seem possible to select genotypes with favourable characteristics in the early stage of growth on the basis of the parameters of the soil cover curve, unless genotypes with much larger differences than shown between butterhead cultivars are used.

Lettuce (*Lactuca sativa* L.) is an important glass-house crop under the poor light conditions during winter in the Netherlands. Despite many experiments fundamental data about the whole process of growth are scanty. Two experiments, one in spring with 8 cultivars and one in autumn with 5 cultivars, were carried out in order to study the process of soil covering by lettuce plants. In both experiments 3 plant densities and 3 temperature regimes were applied. The process of soil covering can be described by a four parameter sigmoid curve with the parameters r , the initial relative soil cover rate; S , the soil cover and S_{\max} , the maximal area which can be covered; t , time in days from planting and p , which determines the position of the inflexion point (t_i , S_i). As other parameters L_i ($= S_i/S_{\max}$) and R_i , the soil cover rate in the inflexion point, are introduced.

Especially with treatments with long growing periods (low temperatures, solitary plants) problems with curve-fitting occurred. All curves appeared to be asymmetrical. The parameters p and r were less useful, mainly because of their high standard errors. Lower temperatures and wider spacings result in higher t_i - and S_i -values and a lower r . S_{\max} tends to decrease at lower temperatures. When the growing period is short or the plant density high, L_i becomes high. Differences between cultivars exist in the spring as well as in the autumn experiment, but no cultivar showed the optimal combination of parameters for a fast soil covering process. The correlation of some soil cover parameters (t_i , S_i , L_i , S_{\max}) with the final harvest weight of the lettuce head was low, especially between the parameters, which give information about the early stage of growth, and the final weight. This was partly due to the late harvest date in the experiments.

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REFERENCES

- ANON.: Planten, plantafstanden en teeltduur. Tuinderij Leidraad 7. – Tuinderij 18 (25): 12–13, 1978.
- BAELDE, I.: Temperatuur en de groei van sla. – Tuinderij 12 (22): 16–17, 1972.
- BENSINK, J.: On morphogenesis of lettuce leaves in relation to light and temperature. – Meded. Landbouwhogeschool, Wageningen 71 (15): 1–93, 1971.
- BIERHUIZEN, J. F., EBBENS, J. L. and KOOMEN, N. C. A.: Effects of temperature and radiation on lettuce growing. – Neth. J. agric. Sci. 21: 110–116, 1973.
- 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.
- DOORN, W. van: Personal communication.
- DRAPER, N. R. and SMITH, H.: Applied Regression Analysis, Pp. 267–270. John Wiley & Sons, New York, 1966.
- EBBENS, J. L. en KOOMEN, N. C. A.: Invloed van temperatuur en licht op groei van sla in verschillende kastypen. – Verslag ingenieursproef Tuinbouwplantenteelt: 1–55, 1971.
- 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.
- ESCH, H. G. A. van: Plantdichtheidsproeven bij vier slarassen (winter 1975). – Verslag 745. Proefstation voor de Groenten- en Fruitteelt onder Glas, Naaldwijk: 1–11, 1976.
- ESCH, H. G. A. van: Plantdichtheidsproeven bij vier slarassen (heteluchtteelt 1976/1977). – Intern verslag 53. Proefstation voor de Groenten- en Fruitteelt onder Glas, Naaldwijk: 1–6, 1977.
- EVERAARTS, A. P. en SLOTEN, D. H. van: De invloed van temperatuur en straling op de groei en ontwikkeling van sla in een late voorjaarsteelt. – Verslag ingenieursproef Tuinbouwplantenteelt: 1–35, 1974.
- GROENEWEGEN, J. H.: Stand en betekenis van de veredeling bij sla. – Meded. Dir. Tuinb. 23: 295–299, 1960.
- HENDRIX, H. A. M.: Plantafstanden en hun economische betekenis bij sla. – Groenten en Fruit 32: 100–101, 1976.
- HUGHES, A. P.: Mutual shading in quantitative studies. – Ann. Bot. 33: 381–388, 1969.
- HUYSKES, J. A.: Slaveredeling en teeltontwikkeling als cyclisch proces. Pp. 141–144. Rassen in wording. Tjeenk Willink, Zwolle, 1968.
- KANEMASU, E. T. and ARKIN, G. F.: Radiant energy and light environment of crops. – Agric. Meteor. 14: 211–225, 1974.
- KEIJZER, J. A. A.: Hoe bepalen we de juiste plantdichtheid bij sla? – Tuinderij 15 (20): 16–17, 1975.
- KLAPWIJK, D.: De groeiduur van sla. I. – Tuinderij 18 (22): 38–41, 1978a.
- KLAPWIJK, D.: De groeiduur van sla. III. – Tuinderij 18 (24): 24–27, 1978b.
- KVĚT, J. and MARSHALL, J. K.: Assessment of leaf area and other assimilating plant surfaces. In ŠESTÁK, Z., ČATSKÝ, J. and Jarvis, P. G. (ed.): Plant Photosynthetic Production. Manual of Methods. Pp. 520–521. Dr. W. Junk N.V. Publ., The Hague, 1971.
- MATHIJSSEN, M. C. M.: De invloed van licht en temperatuur op de groei en ontwikkeling van herfstsla. – Verslag ingenieursproef Tuinbouwplantenteelt: 1–34, 1973.
- NICHOLS, M. A.: Growth studies with lettuce. – Thesis Massey University, New Zealand: 1–106, 1970.
- NILWIK, H. J. M.: Personal communication.
- RICHARDS, F. J.: The quantitative analysis of growth. In STEWART, F. C. (ed.): Plant Physiology, Vol. V.A. Academic Press, New York, 1969.
- SCHIPPER, P. A.: Vijftig procent opbrengstverhoging bij sla mogelijk? – Tuinderij 19 (8): 26–27, 1979.
- SHIBLES, R. M. and WEBER, C. R.: Interception of solar radiation and dry matter production by various soybean planting patterns. – Crop Sci. 6: 55–59, 1966.
- 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.
- SMIT, C. D.: Invloed van licht en temperatuur op de groei en ontwikkeling van herfstsla. – Verslag ingenieursproef Tuinbouwplantenteelt: 1–18, 1974.

3 GROWTH OF LETTUCE

II. QUANTITATIVE ANALYSIS OF GROWTH

INTRODUCTION

Since the cultivation of lettuce (*Lactuca sativa* L.) in glass-houses is of great importance during the winter period, many experiments have been carried out over the past 30 years with the purpose of obtaining optimal growth in the poor-light period. These experiments were made specifically for practical purposes of the growers. Usually only the fresh weight of the lettuce head at the end of the commercial growth period was measured, and often much emphasis was laid on the performance and the quality of the lettuce head (e.g. VAN ESCH, 1977; KRIZEK et al., 1974). Sometimes more harvest periods in an earlier stage of growth were included (BIERHUIZEN and PLOEGMAN, 1966; VAN ESCH, 1973), but in general detailed quantitative data on the growth of lettuce are scarce.

A growth analysis using frequent destructive harvests leads to a good understanding of the effect of environmental conditions on growth during the entire period from transplanting until harvest. With such an analysis the daily increase in the growth of the plant can be calculated. The commercial grower is especially interested in the yield, expressed in grams of fresh weight, and in the quality of the marketable head, and not in the dry matter percentage of the lettuce head. In a quantitative analysis of growth, however, the dry weight of the plant is generally used (KVĚT et al., 1971; e.g. for lettuce: DULLFORCE, 1968; NICHOLS, 1970).

Theory of quantitative analysis of growth

BLACKMAN (1919) described the dry matter accumulation of the whole plant as a law of continuous compound interest. Since then a quantitative approach of the growth of plants has been applied numerous times, especially for field crops. For the growth analysis of these outdoor crops, plants were often grown under controlled conditions (COCKSHULL and HUGHES, 1969; EAGLES, 1967, 1969; EVANS and HUGHES, 1961; FUKAI and SILSBURY, 1977; HUGHES and COCKSHULL, 1969; HUGHES and EVANS, 1962; WATSON, 1952; WILSON and COOPER, 1969). In general young plants were used (e.g. HURD and THORNLEY, 1974; THORNLEY and HURD, 1974) and in the case of older plants often only a short growth period was analysed.

RADFORD (1967) reviewed and defined the formulae of the classical growth analysis, the growth rate (GR), the relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR). The growth rate of a plant at any instant in time (t) is defined as 'the increase of plant material per unit of time i.e. $GR = dW/dt$ (W = weight). This GR is the most simple growth characteristic. The relative growth rate (RGR) of a plant at an instant in time (t) is defined as 'the

$= (1/W)(dW/dt)$. The net assimilation rate (NAR) of a plant at an instant of time (t) is defined as 'the increase of plant material per unit of assimilatory material per unit of time' i.e. $NAR = (1/A)(dW/dt)$ (A = leaf area). The leaf area ratio (LAR) of a plant at an instant in time (t) is defined as 'the ratio of the assimilatory material per unit of plant material present' i.e. $LAR = A/W$. The relationships of A with time and W with time are important. In case W and A vary with time without discontinuity, the only requirement for the analysis according to RADFORD (1967) is that fitted growth curves are available which adequately describe the W versus t and the A versus t relationships over the period in question. In the first place a good fit of the growth curves is important and not their physiological interpretation. These growth curves are needed for a further analysis of growth. The derived functions (RGR, NAR, LAR) can be deduced accurately from these functions without additional assumptions. RADFORD described, for instance, exponential and polynomial regressions relating A and W with time. HUGHES and FREEMAN (1967) and NICHOLS and CALDER (1973) discussed and improved the application of regression analysis. HUGHES and FREEMAN used frequent small harvests and the natural logarithms of W and A instead of simply W and A, thus making the variability of the primary data more homogeneous. They fitted polynomials of the relationships of $\ln(A)$ and $\ln(W)$ with time up to the third degree using the least squares method. In a subsequent step the derived parameters and the standard errors for the estimates of these parameters were calculated. HUGHES and FREEMAN also suggested that this method would be useful for glasshouse and field experiments as well. Their method was successfully applied in experiments with controlled environment (EAGLES, 1969). The choice of the degree of the polynomials which are used in the method of HUGHES and FREEMAN (1967) remains somewhat arbitrary. HUGHES and COCKSHULL (1969), for instance, used cubic equations in experiments with *Callistephus chinensis* in growth cabinets in which mutual shading was negligible. FUKAI and SILSBURY (1977) could fit their data of subterranean clover, grown in a glasshouse, in most cases with polynomials of the third degree. KOLLER et al. (1970), however, used polynomials up to the seventh degree in analysing the growth of different parts of the soybean crop in the field. NICHOLS and CALDER (1973) suggested an objective method of choosing the degree of the polynomials and they gave a survey of the advantages of a regression analysis in growth studies as done by RADFORD (1967) and HUGHES and FREEMAN (1967). These advantages are:

- estimates of RGR, NAR and LAR can be derived directly from the regression equation without additional assumptions. The only and very important assumption in this respect is that the regression adequately describes the changes of W and A with time;
- all the data collected over the experimental period are utilized for the determination of the growth parameters;
- pairing of plants is not necessary before the first harvest;
- at relatively frequent intervals only small samples are necessary, while a constant number of replicates per sample is not essential.

Quantitative growth analysis of lettuce

The classical growth analysis has also been applied for glass-house crops. CHALLA (1976), for example, used the relationships of dry weight and leaf area with time and the relative growth rate for the description and the definition of his 'standard' cucumber plants. HARSSEMA (1977) used the quantitative analysis of growth for young tomato plants in order to determine the importance of root temperature in relation to other environmental factors. HURD and THORNLEY (1974) analysed growth of young tomato plants.

In the case of lettuce, the relations of W and A versus time (BROUWER and HUYSKES, 1968; DULLFORCE, 1971; NOGUCHI et al., 1978; SMEETS, 1977) or those of $\ln(W)$ and $\ln(A)$ versus time (DENNIS and DULLFORCE, 1974, 1975; DULLFORCE, 1963, 1968, 1971; LEE, 1974) or versus a calculated heat sum (VAN ESCH, 1973; NICHOLS, 1970) or radiation sum (BIERHUIZEN et al., 1973; DULLFORCE, 1968, 1971) is often presented without much application of curve-fitting techniques. In some experiments, the classical growth analysis is applied e.g. to compare various cultivars (SCAIFE, 1973; BROUWER and HUYSKES, 1968; LEE, 1974) and to study the effects of light, temperature, CO_2 , fertilizers or plant density. BROUWER and HUYSKES (1968) also included the GR in their study. The quantitative analysis was used to study the growth during short periods. (DULLFORCE, 1956; SARTI, 1973) as well as during long periods (DENNIS and DULLFORCE, 1974, 1975; DULLFORCE, 1963, 1968, 1971; LEE, 1974; NICHOLS, 1970; NOGUCHI et al., 1978). NICHOLS (1970) fitted a four parameter logistic model to the relationships of the $\ln(W)$ and $\ln(A)$ of lettuce with a calculated heat sum ('environmental time scale'). SCAIFE and JONES (1976) grew lettuce plants in pots in a nearly constant environment. They used logistic expressions according to the suggestions of RICHARDS (1969). Logistic models have, compared with polynomials, the disadvantage that the shape of the curve and the number of parameters are already fixed (e.g. NICHOLS, 1970). Similar problems appeared also in Part I (VAN HOLSTEIJN, 1980), where a logistic model was used for the fit of the soil cover curve, even though in that case the inflexion point was not fixed.

When 100% of the soil surface, available to a plant, is covered, the leaf area index (LAI) can be an important factor for growth. A plant with a high LAI intercepts more light. The LAI is, however, misleading for lettuce. Also it is not correct to use the term 'closed canopy', when lettuce plants are overlapping each other. DULLFORCE (1968) suggested that the LAI underestimates overlapping by 25%. LEE (1974) used the leaf area/ground cover ratio in experiments with solitary plants without noticing the misleading effect of it.

Heading of lettuce and leaf area ratio

The head formation of butterhead lettuce cultivars is extremely important to achieve a good quality of the crop. The first butterhead lettuce cultivar, which formed a head under winter conditions in the glass-house was 'Meikoningin' ('May Queen') (RODENBURG, 1960). BENSINK (1971) analysed head formation of the cultivars 'Meikoningin' and 'Proeftuin's Blackpool'. This process is closely related with leaf morphogenesis. BENSINK studied the arrangement and the

production of the leaves, and the development of the leaf blade and leaf midrib in relation to head formation and he took the leaf length and leaf width as criteria for differences in leaf growth.

For a high amount of light intercepting leaf surface per gram of fresh or dry weight, leaf thickness is important. Thin leaves intercept more light per gram of fresh weight than thick leaves. Leaf thickness is expressed by specific leaf weight (SLW). If only data of the total plant top weight and the total leaf area are known, the calculation of SLW is not useful, since it gives an average thickness for all leaves of the plant. DULLFORCE (e.g. 1963, 1968) used the leaf area ratio (LAR) not in relation with leaf thickness, but as a measure for heading. The process of heading was considered independent of other parameters like RGR and NAR. KvĚT et al. (1971) suggested that in general LAR is a useful measure of the assimilatory apparatus, as influenced by genetic and environmental factors, or cultural practices. Changes in LAR with time also reflect the interaction of ontogenetic factors with environmental conditions. DULLFORCE (1956, 1963, 1968) observed that an unfavourable balance between light and temperature, i.e. a relatively high temperature, and a low light intensity, resulted in a high LAR, while no heading occurred. For the cultivars 'Cheshunt 5-B' and 'Southdown 5-B' head formation was poor at LAR-values above 800 to 900 cm² g⁻¹ with the use of dry weight. No heading at all occurred with LAR-values of 1100 cm² g⁻¹ or higher. For the above mentioned cultivars DULLFORCE checked the usefulness of LAR under various environmental conditions (DENNIS and DULLFORCE, 1974, 1975; DULLFORCE, 1963, 1968). Differences in LAR between cultivars were rather small but in some cases significant (DULLFORCE, 1963). SCAIFE (1973) also found differences in LAR among a number of cultivars, but, since he studied only the early stage of growth, he could not relate LAR to head formation. BROUWER and HUYSKES (1968) did not relate LAR to head formation, but from their published results it can be concluded that at the same fresh weight the cultivar 'Rapide' had a low LAR and formed a head, whereas the F₂ of 'Rapide' × 'Hamadan' had a high LAR, grew faster and did not form a head. EVERAARTS and VAN SLOTEN (1974) concluded that the cultivar 'Noran', grown in late spring, formed a qualitatively good head as soon as LAR decreased below 600 cm² g⁻¹.

Although BENSINK (1971) and DULLFORCE (1968) studied extensively the head formation of lettuce plants, clear definitions of the 'head' of the lettuce plant and of the beginning of heading are not defined in their work. They showed the heading of lettuce plants with the use of photographs and analysed the causes of the heading process. BENSINK studied the shape and the number of the leaves and the leaf curvatures. DULLFORCE studied also the leaf production, stem and midrib elongation and the size of individual leaves and petioles. The use of the term 'head' and the judgement of the quality of the head in this publication is based on their observations and criteria and on my personal observations and experience.

Head formation, studied in relation to LAR, is also described in this publication.

MATERIALS AND METHODS

The growth analysis was carried out with the cultivar 'Noran' in the spring experiment and with cultivar 'Deciso' in the autumn experiment. Both cultivars were grown in three glass-house compartments at different temperature regimes and at three plant densities. Details of the various treatments and the cultivation are given in Growth of Lettuce, Part I (VAN HOLSTEIJN, 1980). Compared with the practice of the growers rather large plants were planted, which could result in a shorter growth period (KLAPWIJK, 1978). The last harvest varied per treatment and was carried out when the fresh weight was at least 150 gram per plant, or when the differences in weight between plants of one plot became exceptionally large.

Destructive harvests were carried out twice a week with intervals of 3 and 4 days. The fresh weight, dry weight and leaf area of four plants per treatment were determined. The dry weights and leaf areas were measured similar to the methods in Part I (VAN HOLSTEIJN, 1980). No data on the root system were obtained. The soil cover data are presented in Part I. Plants were always harvested as much as possible at the same time of day. Data of the environmental parameters during both experiments are presented in Part I.

Fitting procedure of dry weight and leaf area

From the literature survey the conclusion was drawn to use polynomials instead of logistic models for an accurate description of the relationships of dry weight and leaf area with time. From preliminary calculations it had become evident that logarithmic transformation of the primary data did not greatly diminish the variability of the data of both experiments with time. Therefore, the method of the weighted least squares was always used. In this method, as outlined by DRAPER and SMITH (1966) the data of the harvests are weighted according to the reciprocal values of the harvest variance. As to the degree of the polynomials to be fitted, the method of 'lack of fit' was applied (DRAPER and SMITH, 1966; NICHOLS and CALDER, 1973). The method of orthogonal polynomials for fitting the relationships of the weight and the leaf area versus time was used (DRAPER and SMITH, 1966; FOX and MAYERS, 1968) for performing the least squares analysis. In this case especially the polynomials tended to suffer from induced instability (FOX and MAYERS, 1968) as the calculations were done on a desk calculator with a limited accuracy for number storage. The actual calculating program, which incorporated the above mentioned remarks, was made by NILWIK for the desk calculator HP 9518A following the general outlines of FORSYTHE (1957). After data input polynomials of increasing degree were fitted to the data. This procedure was terminated when 'lack of fit' was not significant ($p < 0.001$). The program could continue until the tenth degree. The data and the necessary coefficients for the generation of the orthogonal polynomials were then put on a cassette. A second program was available to calculate the fitted values and the time derivatives of the dry weight ($= dW/dt$) and leaf area ($= dA/dt$) at any chosen time during the growth period.

RESULTS

The results of the curve-fitting procedure are given in Table 1. When the ninth degree still resulted in a significant 'lack of fit' ($p < 0.001$), the degree with the lowest F-value was selected. This occurred with the dry weight fitting for the treatments I-25 and III-35 of 'Noran' and II-35 of 'Deciso' and with the leaf area fitting for the treatments I-25 and II-25 of 'Noran' and II-35, III-20 and III-35 of 'Deciso'. A polynomial of the second degree never gave the best fit and cubic or higher regressions appeared to be necessary. Generally, the longer the growth period, the higher the degree. The number of harvests varied per treatment as well as the number of plants per harvest.

TABLE 1. Results of the curve-fitting procedure of the relationships of dry weight and leaf area with time of plants of 'Noran' and 'Deciso' ($p < 0.001$). a, b, c and d: no harvest data were available at day 36, 44, 48 and 51, resp.. I, II and III represent the three temperature regimes. 20, 25 and 35 represent the plant densities 20×20 , 25×25 and 35×35 cm.

Cultivar	Treatment		Results			
	temperature regime	plant density	dry weight; degree of polynomial	leaf area degree of polynomial	number of harvests	last harvest on day
Noran	I	20	4	4	11	39
	I	25	3	4	11	39
	I	35	3	4	12	43
	II	20	6	7	13	46
	II	25	7	5	12 ^a	46
	II	35	8	6	14	50
	III	20	7	7	11 ^a	48
	III	25	8	8	14 ^a	53
	III	35	8	8	15 ^a	57
	I	20	4	4	12	41
	I	25	6	6	12	41
	I	35	5	5	13	44
Deciso	II	20	3	9	14 ^b	51
	II	25	7	5	14 ^c	51
	II	35	6	5	15	51
	III	20	5	5	15	51
	III	25	5	5	14 ^d	48
	III	35	5	5	16	55

The relationship of dry weight with time

Figure 1 a-d shows examples of relationships of the dry weight with time for 'Noran' and 'Deciso' at the three temperature regimes and the plant density of 25×25 cm, and of the three plant densities at the middle and highest temperature regime for 'Noran' and 'Deciso', resp.. The date of the inflexion point of the

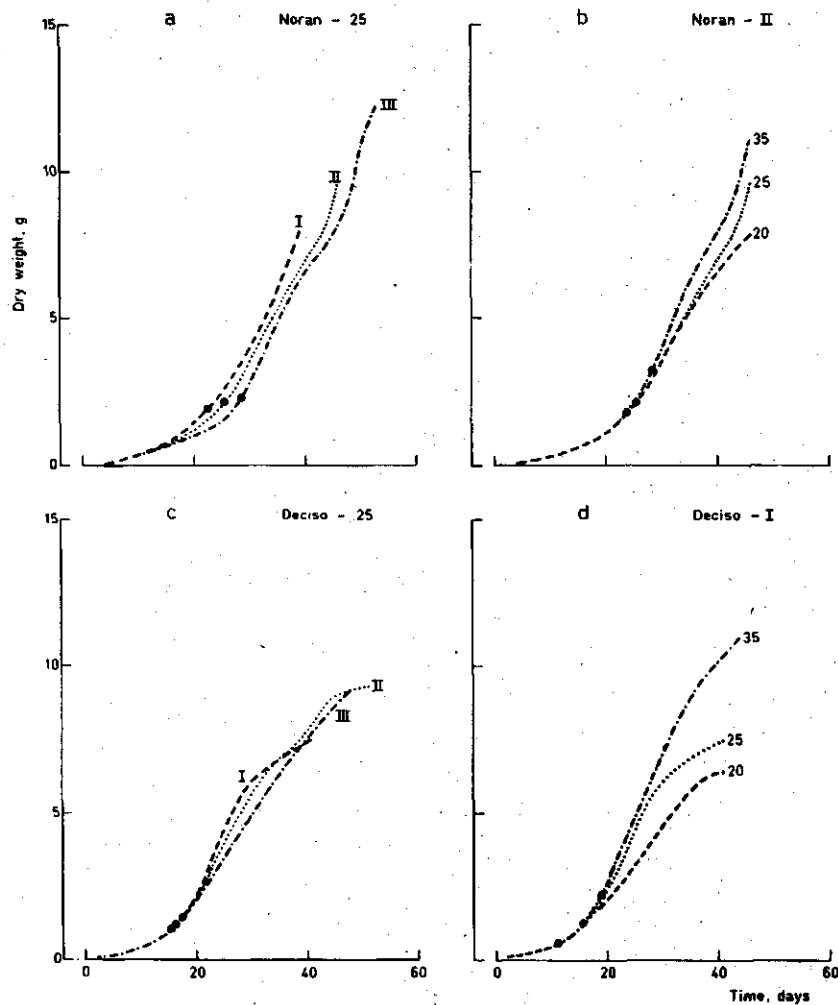


FIG. 1. The calculated dry weight plotted versus time for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b). The calculated dry weight plotted versus time for plants of cultivar 'Deciso' at three temperature regimes and the plant density 25 (c), and at temperature regime I and three plant densities (d). Symbol ● represents the date t_i of the inflexion point of the sigmoid curve of the soil cover (VAN HOLSTEIJN, 1980). I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20×20 , 25×25 and 35×35 cm.

conversion curve (g) is presented as well. Data concerning the relationship of the leaf area with time are not presented. The curves generally show the same patterns of exponential growth during the first weeks. At low temperatures accumulation of dry weight is slower than at higher temperatures (Fig. 1 a, c). At the various plant densities the growth is similar in the beginning, but becomes slower after some time for the plants at the more narrow spacings. The differences in dry

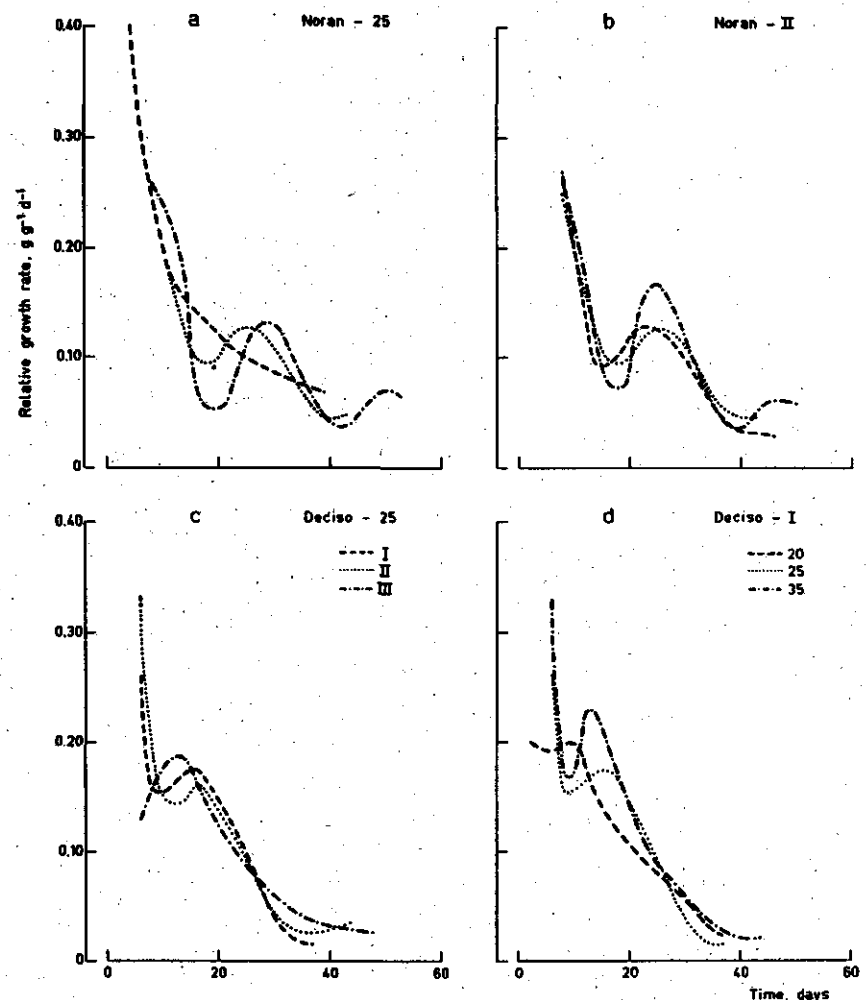


FIG. 2. The relationships of the relative growth rate with time for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of relative growth rate with time for plants of cultivar 'Deciso' at three temperature regimes and the plant density 25 (c), and at temperature regime I and three plant densities (d). I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20×20 , 25×25 and 35×35 cm.

weights between plants at the various plant densities increase with time. The dates, at which the growth curves of the three plant densities become different, are delayed in comparison with the dates of the inflexion point, t_i , of the soil cover curves.

Relative growth rate

The relationships of the relative growth rate (RGR) with time for 'Noran' and 'Deciso' are shown in Figure 2 a-d, while in Figure 3 a-d the relationships of the relative growth rates with the dry weight are given for the same treatments as were used in Figure 1. The irregular pattern of the relationships between RGR and time in the beginning of the growth period occurs for a relatively long period of approximately 2 to 3 weeks. The small plants in this period represent a dry weight range of only 0.1 to 1.5 gram. After this irregular period RGR decreases with time as well as with an increase in plant dry weight for all treatments shown. In this period the dry weight ranges from 1.5 to 6 gram.

The dry weight was used as abscissa, because this parameter presents a better measure of the growth and the ontogenetic phase of the plant as affected by environmental conditions than an arbitrary time scale (EVANS, 1972, p. 319). A higher temperature regime results in a higher RGR at similar dry weights for 'Deciso'. 'Noran' has a lower RGR in the dry weight range between 1.5 and 5 gram at a higher temperature regime, which result is contrary to that of 'Deciso'. Plants with a wider spacing have a higher RGR compared with plants with narrow spacings.

The relationship of growth rate with time

Although RGR and NAR are commonly used in growth analysis studies, the absolute growth rate ($GR = dW/dt$) will present more direct information about the growth process. RICHARDS (1969) mentioned in his introduction of 'Quantitative analysis of growth' that GR could be plotted against A or W in order to give 'rate curves'. Figure 4 a-d (p. 11) shows the relationships of the growth rate with time of 'Noran' and 'Deciso'. Data were obtained from the treatments used in Fig. 1. The data of the inflexion point of the soil cover curve (t_i) is also presented in the Figures. The patterns of the growth rates in the beginning and at the end of the growth period are irregular.

Except for the GR versus time relationship of the treatment 'Noran'-I-25, all curves show an identical pattern. During the first 4 to 5 weeks the growth rates of 'Noran' and 'Deciso' were higher at higher temperatures. Less plants per m^2 resulted in a higher GR per plant. The GR decreased after a certain period for both 'Noran' and 'Deciso' in various conditions of light and temperature. The maximal GR occurred at a later date than that of the inflexion point of the soil cover curve. The maximal GR tends to occur later in time during lower temperature regimes and with wider spacings.

The relationship of growth rate with dry weight

In Figure 5 a-f (p. 12) dry weight is used instead of time on the abscissa. The data

of all treatments of 'Noran' and 'Deciso' are presented. In these figures both components of RGR are plotted against each other. The pattern of the GR versus W is similar for all treatments, except for 'Noran'-I-25 and -35 in the dry weight range between 1 and 7 gram. GR increases with an increase of weight of the plant. Maximum values of GR are reached when the plants have a dry weight between 2 and 5 gram, in which stage of growth the formation of the head

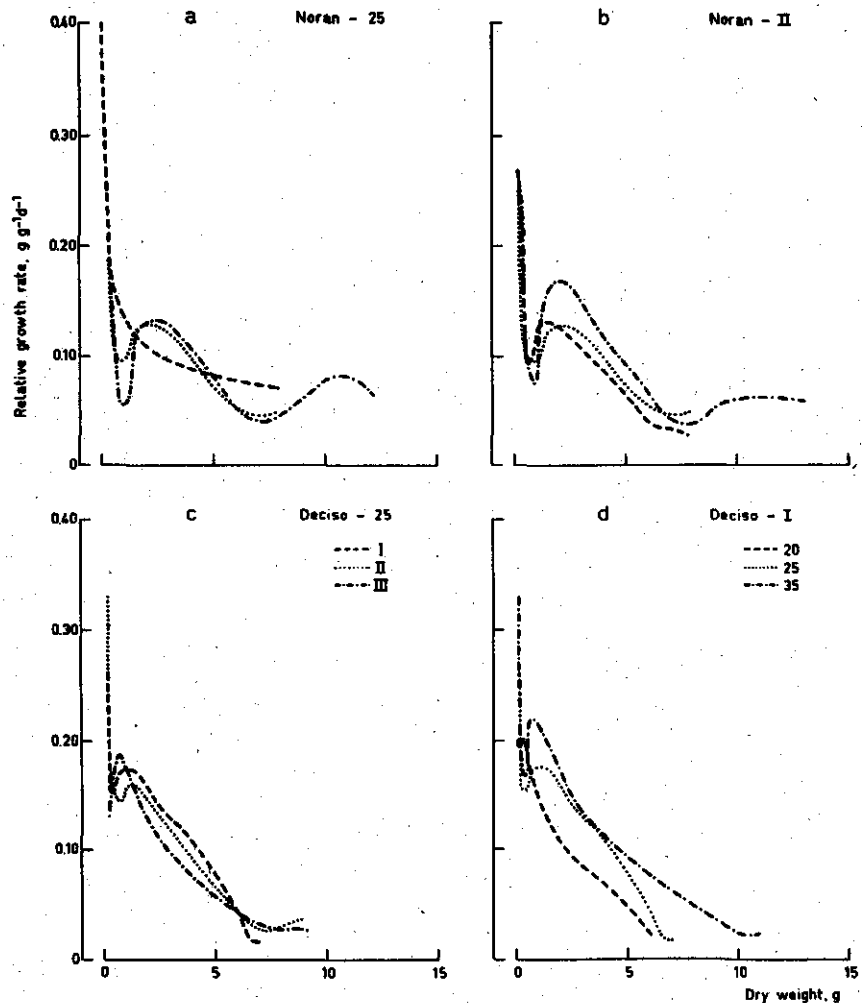


FIG. 3. The relationships of relative growth rate with dry weight for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of the relative growth rate versus time for plants of cultivar 'Deciso' at three temperature regimes and the plant density 25 (c), and at temperature regime I and three plant densities (d). I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20 × 20, 25 × 25 and 35 × 35 cm.

becomes visible. For solitary plants the maximum GR and the decrease of GR occurs at a slightly higher dry weight.

The relationship of the growth rate with soil cover

The parameter NAR includes the leaf area, which is an inaccurate measure of the photosynthetic area of a lettuce plant, because of the bubbled and over-

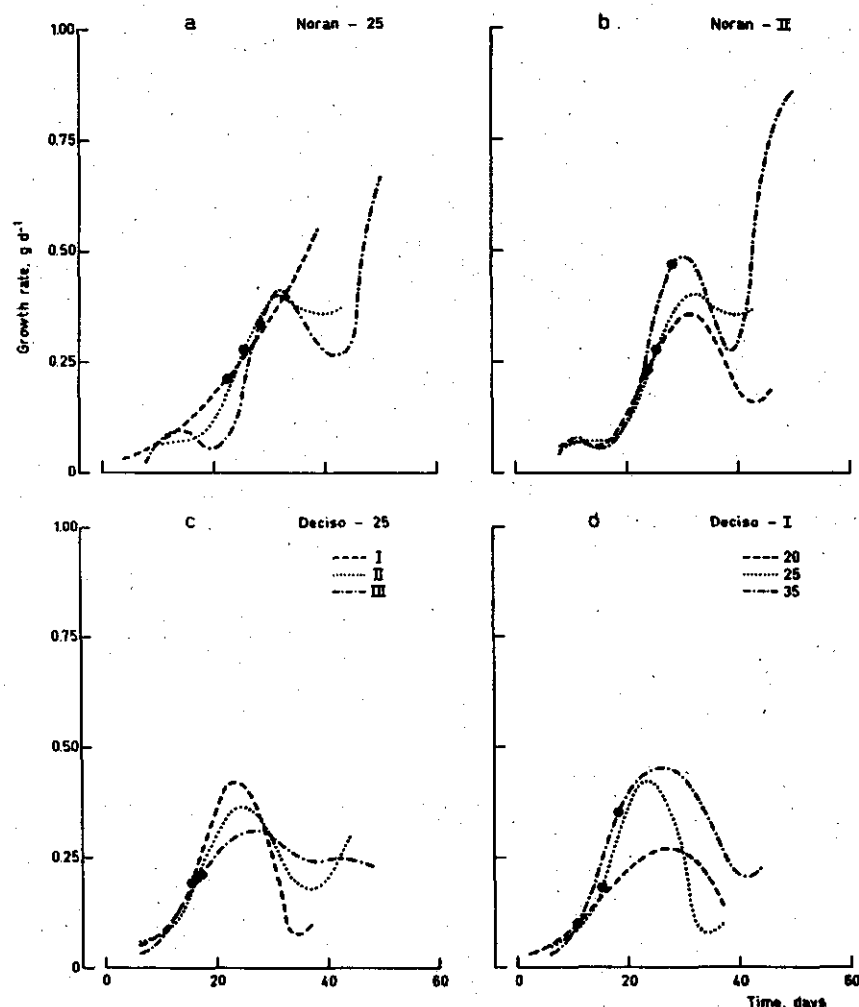


FIG. 4. The relationships of growth rates with time for plants of the cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of growth rates with time for plants of the cultivar 'Deciso' at three temperature regimes and the plant density 25 (c), and at temperature regime I and three plant densities (d). Symbol ● represents the date t_i of the inflexion point of soil cover curve (VAN HOLSTEIJN, 1980). I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20×20 , 25×25 and 35×35 cm.

Figure 6 a-f (p. 13) shows the relationships of GR with soil cover for all treatments of 'Noran' and 'Deciso'. The amount of covered soil (S_i) at the inflexion point of the soil cover curve is presented as well. In the beginning of the growth period the growth rates of plants for all treatments increase almost linear with the soil cover. Different relationships of GR with soil cover exist between the three different temperature regimes and the two cultivars.

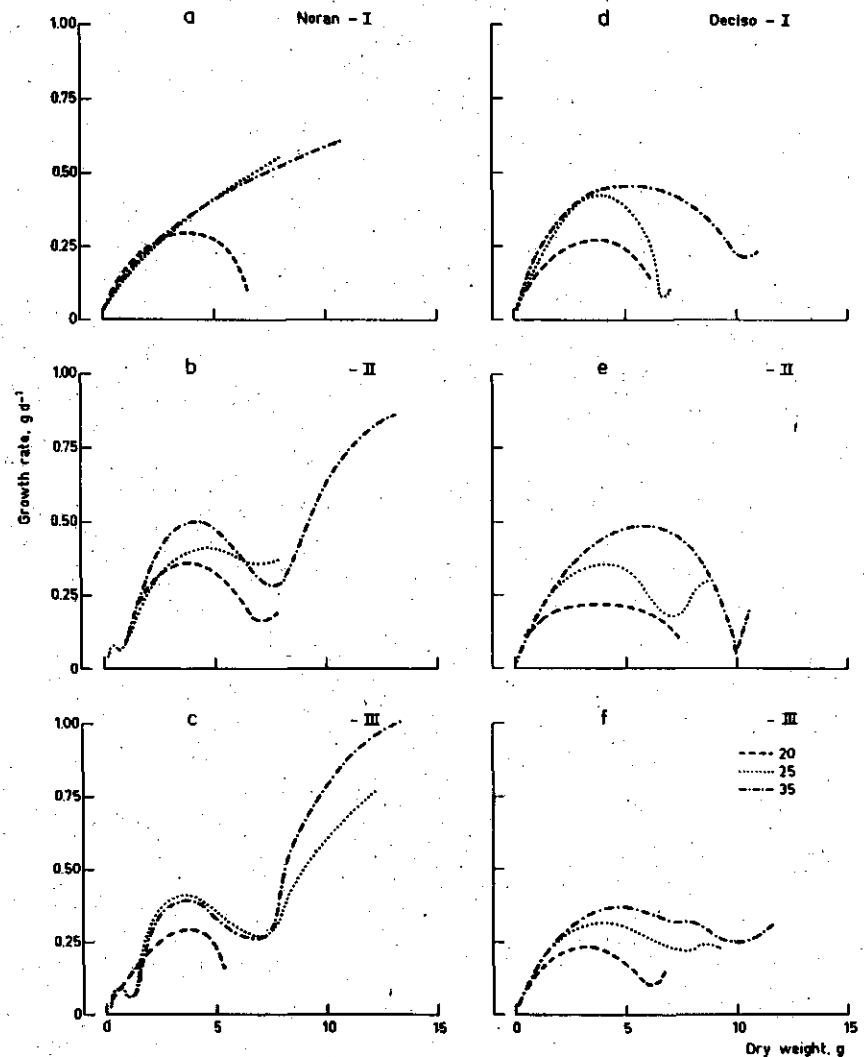


FIG. 5. The relationships of growth rates with dry weight for the plants of all treatments of the cultivars 'Noran' and 'Deciso'. I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20×20 , 25×25 and 35×35 cm.

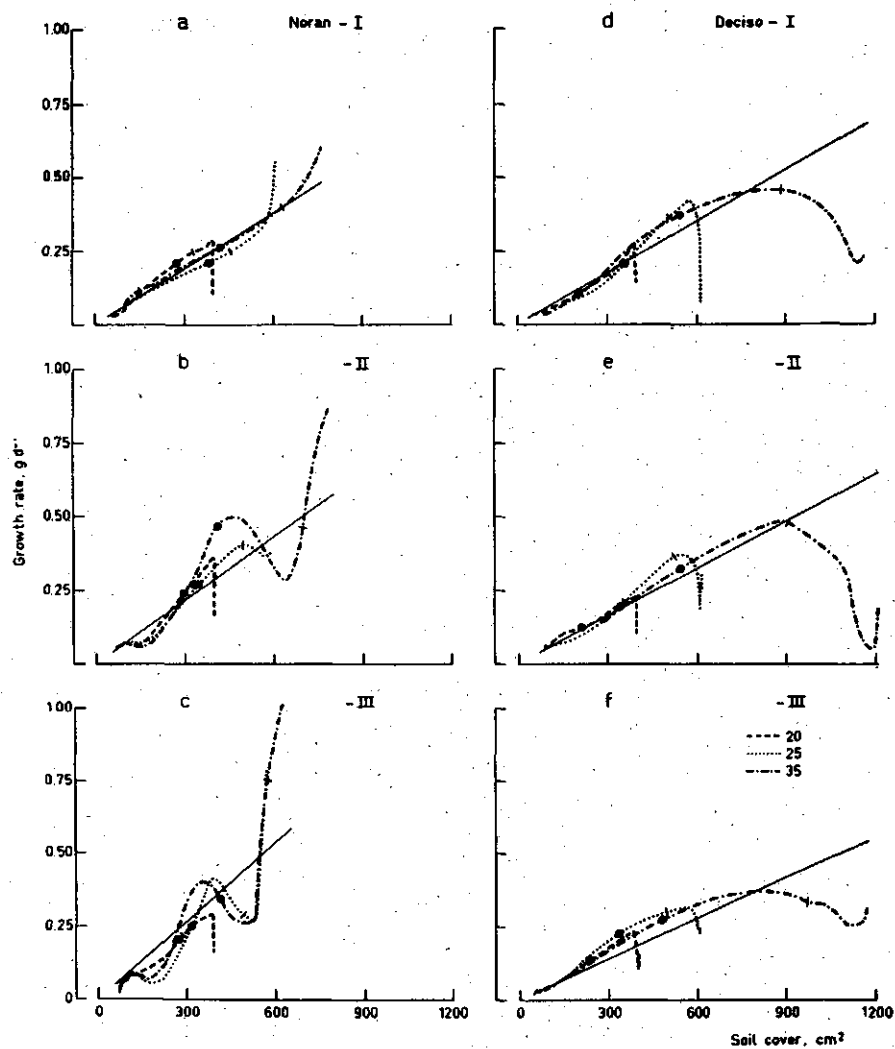


FIG. 6. The relationships of growth rates with soil cover for plants of all treatments of the cultivars 'Noran' (a-c) and 'Deciso' (d-f). The straight lines represent the linear regressions of the soil cover with growth rate. The amount of soil covered in the inflexion point of the soil cover curve is represented in each curve by symbol ●. The data belonging to the period until 80% of the maximum soil cover has been reached are presented on the left of the small vertical lines in the curves. The data after 80% of the soil cover has been reached are presented on the right of these vertical lines. I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities of 20 × 20, 25 × 25 and 35 × 35 cm.

cover was reached, were used for linear regressions of GR with soil cover, leaf area and dry weight resp. and for a multilinear regression of GR with those three parameters. The linear regressions of GR with soil cover are drawn in Fig. 6. At a certain soil cover value the plants of 'Noran', grown at the lowest temperature regime, have a higher GR than plants of the higher temperature regimes, while for 'Deciso' the reversed situation was observed. For 'Noran' in spring a larger increase of the growth rate with increasing soil cover is observed at the low temperatures and for 'Deciso' in autumn at the high temperatures. For a short period, when more than 80% of the soil cover is reached, GR increases more than linear with the soil cover. The maximal value of GR for the non-solitary plants occurs when the maximum soil cover has already been reached. At the end of the growth period the GR for almost all treatments declines. This effect has been observed more clearly for 'Deciso' than for 'Noran'.

Table 2 lists the correlation coefficients of the linear regressions of GR with soil cover, W and A and the coefficients of the multilinear regression model. From the linear regressions it became evident that for all temperature treatments the best fit of GR, over the above mentioned period until 80% of the soil cover was reached, was made with soil cover, except for treatment 'Noran'-III. For this reason soil cover was taken as the first independent variable in the multilinear regression model. The leaf area was taken as the second one. Addition of A and/or W to the multilinear equation results in slightly higher correlation coefficients for most treatments, but the model is not significantly improved by

TABLE 2. The correlation coefficients of the linear regressions of growth rate with resp. soil cover, leaf area and dry weight, and of the multilinear regression of growth rate with soil cover, leaf area and dry weight for the data of 'Noran' and 'Deciso' at the three temperature regimes. The last column indicates whether the addition of another parameter than soil cover for the multilinear regression is significant or not. Data for these regressions are taken over the period until 80% of the maximum soil cover has been reached.

Cultivar	Temperature regime	Correlation coefficients (r^2) of linear regressions of growth rate with			Correlation coefficients (r^2) of multilinear regression	Not significant ($p < 0.01$) is addition of:
		soil cover	leaf area	dry weight		
Noran	I	0.97	0.94	0.95	0.97	Leaf area and dry weight
	II	0.80	0.59	0.65	0.87	Dry weight
	III	0.75	0.74	0.77	0.79	Leaf area and dry weight
Deciso	I	0.96	0.84	0.85	0.97	Leaf area and dry weight
	II	0.98	0.90	0.88	0.99	Leaf area and dry weight
	III	0.89	0.80	0.78	0.98	Dry weight

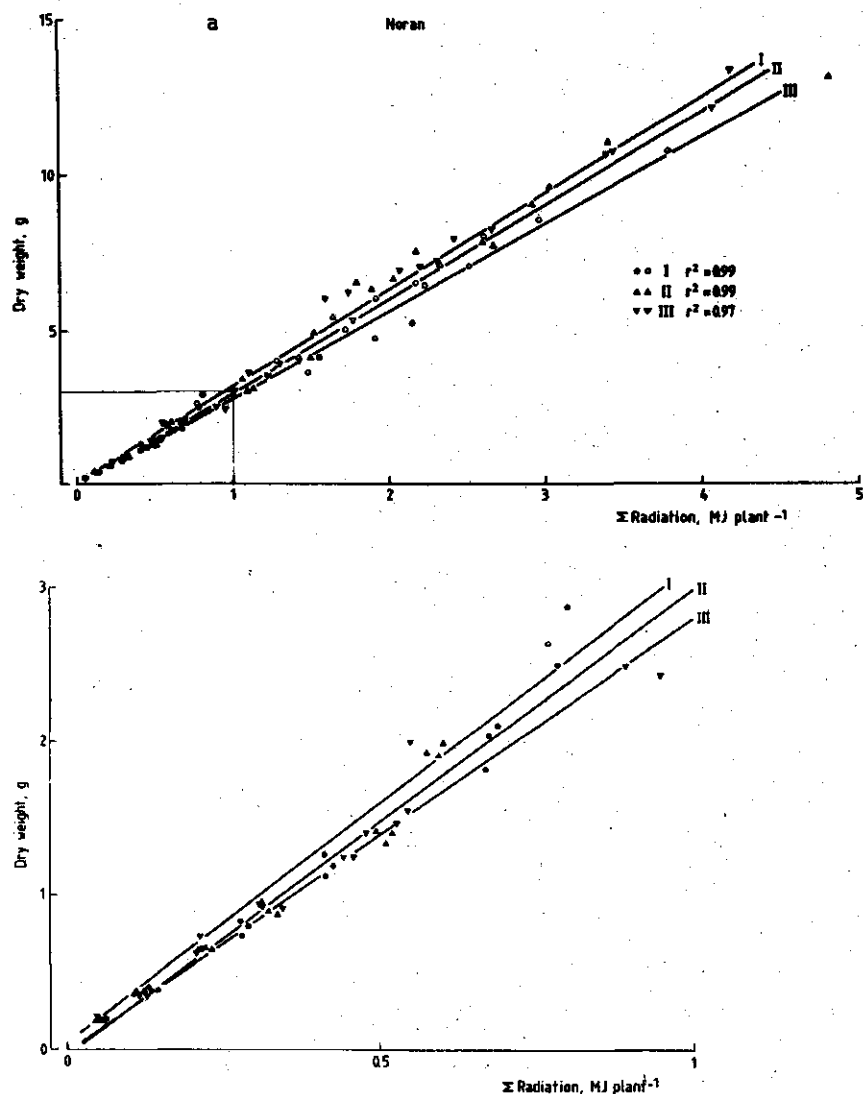


FIG. 7a. The relationship of the total accumulated sum of radiation per plant, with the correction for the amount of intercepted radiation based on the amount of radiation received by the soil surface covered per plant, with the accumulated dry weight per plant of the three temperature treatments of the cultivar 'Noran'. The figure below is an enlargement of the first part of the linear regression of figure 7a. The data of the three plant densities are taken together per temperature regime. The symbols \bullet (= I), \blacktriangle (= II) and \blacktriangledown (= III) represent the temperature regimes. The open symbols are used for the data in the period when more than 80% of the maximum soil cover is reached.

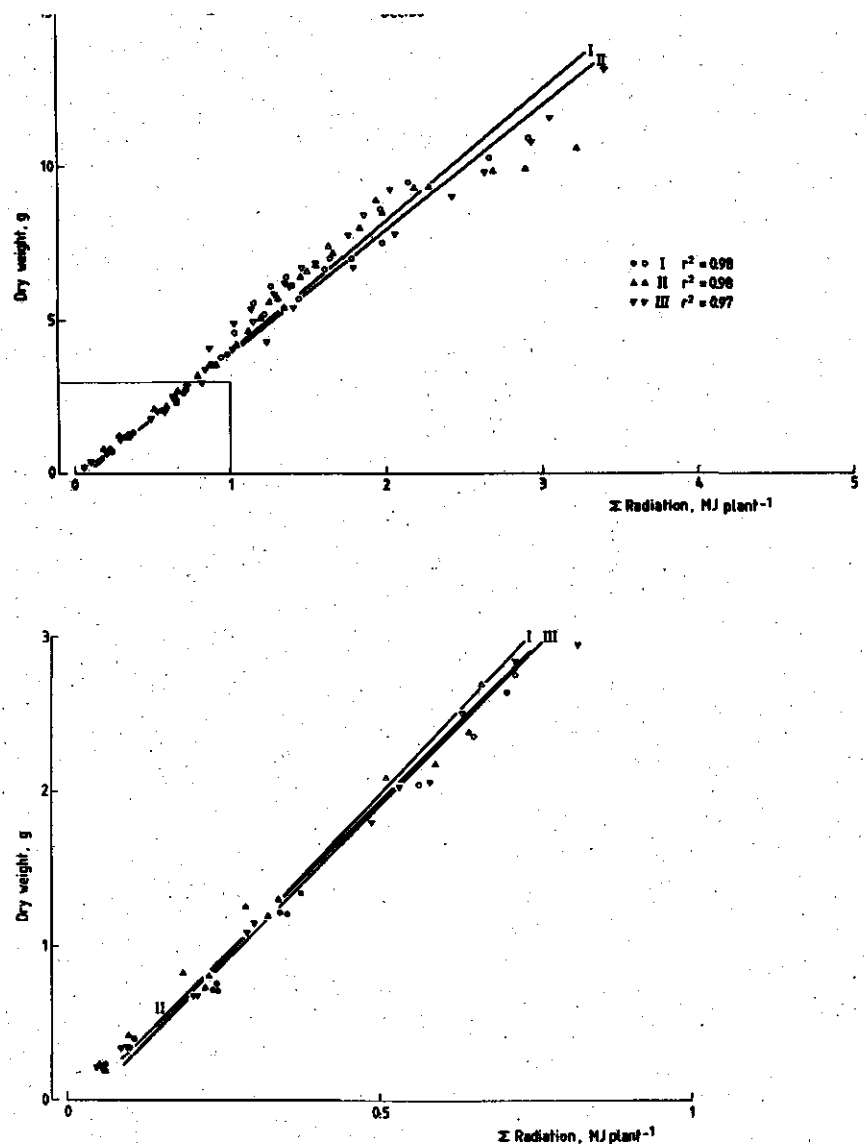


FIG. 7b. The relationship of the total accumulated sum of radiation per plant, with the correction for the amount of intercepted radiation based on the amount of radiation received by the soil surface covered per plant, with the accumulated dry weight per plant of the three temperature treatments of the cultivar 'Deciso'. The figure below is an enlargement of the first part of the linear regression of figure 7b. The data of the three plant densities are taken together per temperature regime. The regressions of II and III are almost identical. The symbols \circ (= I), Δ (= II) and ∇ (= III) represent the temperature regimes. The open symbols are used for the data in the period when more than 80% of the maximum soil cover is reached.

adding these factors except for 'Noran'-II and 'Deciso'-III. In fact, the soil cover in the stage of growth until 80% of the maximum soil cover is reached forms a good measure for the effective light absorbing leaf area of the lettuce plant. GR is almost linear with the soil cover.

The relationship of dry weight with radiation

In Figures 7a and 7b the accumulated dry weight versus the total accumulated short wave radiation per plant with the correction for the amount of intercepted radiation based on the amount of radiation received by the soil surface covered per plant, is presented. The linear regressions, which are calculated with the data of the whole growth period, are shown in these figures. The correlation coefficients of the regressions with the data until 80% of the maximal soil cover was reached were also calculated, but are not presented here, since they were almost identical to the coefficients of the regressions until the end of the growth period. The variation of the data in the regressions is small for both cultivars. The value of the slope of the treatment 'Noran'-I is significantly lower ($p < 0.05$) than the values of the other two treatments of this cultivar. For 'Deciso' the value of 'Deciso'-I is significantly higher than the values of 'Deciso'-II and -III. The low tem-

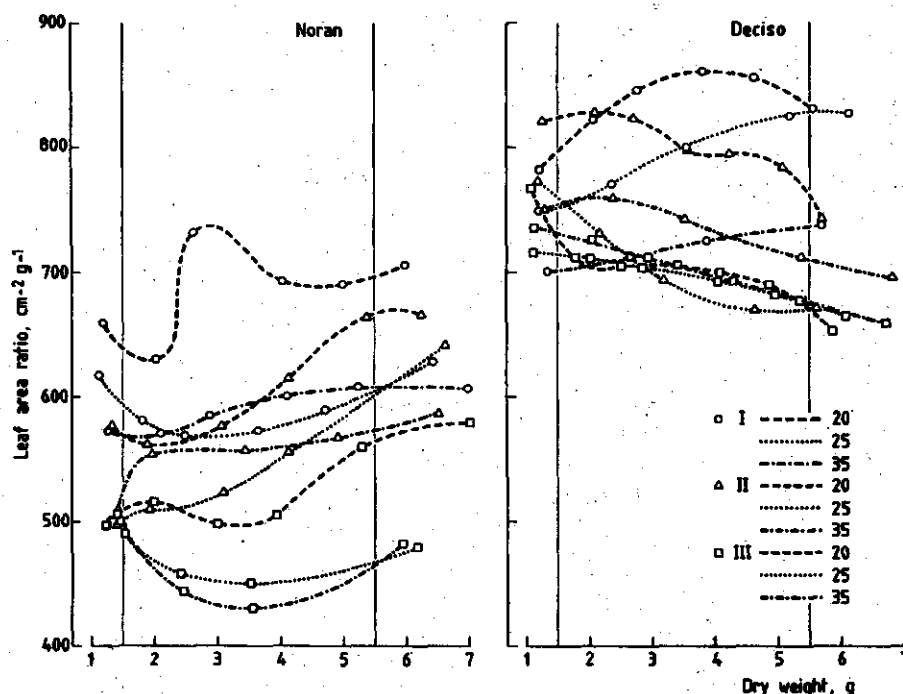


FIG. 8. Relationships between the leaf area ratio and dry weight (between 1.5 and 5.5 grams) of plants of the cultivars 'Noran' and 'Deciso'. Data of all treatments are represented. I, II and III represent the three temperature regimes and 20, 25 and 35 the three plant densities.

so' result in a more efficient interception and/or use of light. Comparing the two experiments the plants of 'Deciso' intercept or convert the light more efficiently than the plants of 'Noran'.

Leaf area ratio and heading

Heading will begin when the plant has achieved a fresh weight of about 35 grams (about 1.5 gram of dry weight). Figure 8 presents the LAR for all treatments of 'Noran' and 'Deciso' between the dry weight of 1.5 and 5.5 gram. In this period plants of 'Noran' demonstrate a minimum value of LAR or an increasing LAR. Plants of 'Deciso' show an irregular pattern of LAR in this period. A good quality has been obtained when LAR is < 550 and $< 710 \text{ cm}^2 \text{ g}^{-1}$ for 'Noran' and 'Deciso', resp. A poor quality occurs when LAR is > 620 and $> 760 \text{ cm}^2 \text{ g}^{-1}$ for 'Noran' and 'Deciso' resp.. Between these values of LAR the quality is also poor, but the product is still marketable. Wider spacing and lower temperatures give a lower LAR, a better head and improve the quality of the marketable product.

DISCUSSION

There were problems during the cultivation, since a long period gives difficulties for an undisturbed and continuous growth. The plants are more liable to get diseases, tipburn, etc. Differences between replicates on plant weight and leaf area increased at the end of the growth period. Especially the measurement of leaf area of older plants caused problems and became less accurate. In more controlled conditions (e.g. BROUWER and HUYSKES, 1968) or during short experiments (e.g. DULLFORCE, 1956; SCAIFE, 1973) these problems are less dominant than in these experiments.

The procedure in these experiments of small, frequent harvests (HUGHES and FREEMAN, 1967) and the use of polynomials (NICHOLS and CALDER, 1973) is correct and useful, but the fitting procedure was not as simple for this glass-house crop as HUGHES and FREEMAN (1967) suggested. For most treatments, however, an accurate fit was possible and the growth analysis gave reliable results. The growth rate ($= dW/dt$) is important as growth characteristic itself and as a factor in the relative growth rate and net assimilation rate (RADFORD, 1967). The calculated values of GR for the beginning and the end of the growth period are not reliable, as the derivatives of the first and last value of W of the polynomial are inaccurate. Apart from this, derivatives of growth curves are sensitive to errors in the primary data (RICHARDS, 1969). The first and last calculated values of RGR are also less reliable.

The high degrees of the polynomials are caused by the long growth period, various ontogenetic stages, self and mutual shading and diseases at the end of the period. The plants were grown under partly controlled conditions. The use of a time scale (in days) which is not corrected for fluctuating environmental con-

ditions, will result in a more complicated analysis than for plants grown in, for instance, growth cabinets (HUGHES and EVANS, 1962). HUGHES and EVANS concluded also that growth analysis becomes more complex when self shading starts, as occurs in the case of lettuce. If only quadratic curves had been applied, the problems with the various parameters of the growth analysis would have been absent, as EAGLES (1969) showed with his results of young plants. NICHOLS and CALDER (1973) explained in their discussion about RGR and NAR that the usefulness of these growth characteristics depends on the degree of the polynomial used. They suggested that a quadratic or higher order of $\ln(W)$ was preferable, but they did not emphasize that a high degree caused serious problems for the physiological interpretation of the growth parameters.

Growth starts exponentially and later the growth rate decreases. DULLFORCE (1963, 1968) and NICHOLS (1970) observed that the growth was exponential for at least half of the growth period. The dry weight increase did not follow the logistic curve as SCAIFE and JONES (1976) suggested in a schematic illustration. They suggested that the harvest time of lettuce occurs in the exponential part of the curve. For the used butterhead lettuce cultivars and the 'commercial plant densities' this does not seem to be true. VAN ESCH (1973) found that, for 'Deciso' and various other cultivars, a higher weight is obtained when the temperature is higher, while in that situation the quality of the head is poor. The results of these experiments confirm his observations of the quality. RGR is decreasing as is observed in other experiments with lettuce (e.g. DENNIS and DULLFORCE, 1975; DULLFORCE, 1968, 1971). Leaf area data are used only in the LAR. No further attention was paid to the NAR. Data of the leaf area were less accurate than those of the dry weight.

Mutual and self shading diminish the growth of lettuce, and their effect becomes evident at a later date for the dry weight increase than for the soil cover rate. This is shown in the relationship between GR and time, since the maximal GR is reached much later than the inflexion point of the soil cover curve.

The relationships of GR with time and with dry weight show the ontogenetic effect of heading, while that effect is not visible in similar relationships of RGR. Maximum values of GR are reached, when the dry weights of the plants are between 2 and 5 gram. In this period of growth heading becomes visible. The process of heading seems to be more or less independent of mutual shading and environmental conditions, since a decrease of GR of both 'Noran' and 'Deciso' starts as soon as a certain dry weight value is reached. Only a strong effect of mutual shading or temperature on GR may become apparent. From the article of BROUWER and HUYSKES (1968) it can be concluded that GR reached a nearly constant level at a fresh weight of about 160 grams and 100 grams, for the F_2 of 'Rapide' \times 'Hamadan' and for 'Rapide', resp.. They explained the constant GR from the constant light conditions and the constant light absorbing area. The plant densities in their experiments were not mentioned, but the plants were probably grown as solitary plants. They did in fact observe a later decrease of GR, but they did not show this in graphs and they explained that decrease as the beginning of the process of bolting. In my opinion the decrease starts already

during the last stage of the process of heading. The exceptional relationships of growth rate with dry weight of the treatments 'Noran'-I-25 and -35 in the spring experiment can be caused by fitting the curve and the absence of the formation of a firm head. An increase of GR during the last week of the growing period of some treatments in both experiments can be a result of bolting.

Attention was paid to the relationship of GR with the soil cover, since the soil cover was considered to be a good measure of the light intercepting surface of a plant. The soil cover gives a good estimate for that surface. However, growth is a result of photosynthetic activity, for which the light intercepting surface is essential, and of respiration, which is more related with the weight of the plant (FUKAI and SILSBURY, 1977). With lettuce the light absorbing surface, estimated with the help of the soil cover, seems to be the most important factor for growth, since the GR is linearly related with the soil cover during a long period of growth. BROUWER and HUYSKES (1968) found an identical relation between GR, expressed in grams of fresh weight per day, and the 'exposed leaf area'.

Different growth rates at similar soil cover values are mainly caused by differences in the amount and intensity of the intercepted light, because a certain soil cover value was not reached at the same day for all treatments in one experiment. In spring the plants of the low temperature treatments and in autumn the plants at high temperatures intercepted more light. The differences between the slopes of the GR-soil cover curves can also be explained by the above mentioned argument, since a certain amount of covered soil is obtained on an earlier or later date. When the soil cover forms a reliable estimate and there should have been no differences in environmental conditions among all the treatments, then the difference between the slopes of 'Noran' and 'Deciso' should have been due to cultivar differences.

The linearity of GR with the soil cover is not in contradiction with the results in the previous publication (VAN HOLSTEIJN, 1980), where the correlation of one or more parameters of the soil cover curve with the end harvest weight was low. In the experiments described in that article the end weight was harvested when the maximal soil cover was reached or even later, while here data are used for the calculations until the date when 80% of the maximal soil cover was reached.

A correct calculation of the radiation sum involves the use of a non-linear photosynthesis-radiation response curve, for the plant temperature in question. The exact amount of light intercepted by the leaves has to be known. The light compensation point, the light saturation level etc. must be taken into account. In Fig. 7 the radiation sum per plant was calculated on the basis of the soil cover, which is a good measure, even though light interception is a three dimensional process. The concept of soil cover as the light intercepting surface is useful and feasible in comparison with the use of other plant characteristics. NICHOLS (1970) used 'environmental time scales', which resulted in a better fit than the fit of the data with the normal time scale. His 'solar radiation scale' was superior to the scale, in which he used the heat sum for the fit of the dry weights. BIERHUIZEN et al. (1973) used fresh weights for their analysis and they found a linear relation for

this weight with the absorbed radiation.

In the same stage of growth, in which the growth rate reaches a maximum value, LAR can be an accurate measure for the head formation and the quality of the head. The results of 'Noran' agree with the results of EVERAARTS and VAN SLOTEN (1974), also done with 'Noran'. They found a good quality when $LAR < 600 \text{ cm}^2 \text{ g}^{-1}$, while some of the plants were grown under controlled conditions and some were transplanted when heading started. DULLFORCE (1963, 1968) found other values for other cultivars. From the differences between the LAR, required for optimal heading, the conclusion can be drawn that the LAR can be used as a criterion for optimal growth and heading within one cultivar, but not as a selection criterion between cultivars or for the selection of new cultivars.

Generally it can be concluded that a quantitative analysis of growth, applied for plants with a long period of growth and with various ontogenetic stages, is complex, but gives valuable information with the applied mathematical approach.

SUMMARY

While many data are available about the growth of lettuce (*Lactuca sativa* L.), fundamental data about the growth process, especially about growth rate, soil cover and the relationship between those parameters, are lacking. In this paper a quantitative analysis of growth has been applied. In the spring experiment the cultivar 'Noran' was used and in the autumn experiment 'Deciso'. Twice a week plant data were collected.

Because of the long period of growth and the partly controlled conditions, a good fit of dry weight and leaf area with time was difficult for some treatments. Polynomials between the third and the ninth degree were needed for an adequate description of the growth curve. The growth rate is the derivative of the polynomial of dry weight with time. It has been used as a growth parameter and for the calculation of RGR and NAR. The relationships of growth rate and RGR with time have been described for representative treatments. Attention has also been paid to the relationships of GR with dry weight and soil cover. The latter relation gives information about the growth stage, during which mutual and self shading becomes visible and heading starts. During the stage of heading GR reaches a maximum value and starts to decrease. The relationship between GR and soil cover is almost linear over the growth period until 80% of the maximal soil cover is reached. The linear fit of GR with soil cover gave better correlation coefficients than the fit with dry weight or leaf area. From a multi-linear regression model it became evident that the soil cover almost sufficiently explains the increase of GR over that period. Low temperatures in spring and high temperatures in autumn resulted in more light interception and/or a better use of light. Narrow spacings gave lower growth rates than wider spacings. The relationship between the accumulated dry weight and the total radiation, in-

absorbed per plant and corrected on soil cover basis, is almost linear. The relation between LAR and heading has also been studied: When LAR is lower than $550 \text{ cm}^2 \text{ g}^{-1}$ and $710 \text{ cm}^2 \text{ g}^{-1}$ for 'Noran' and 'Deciso' resp., the quality of the head is good.

Because of the two different cultivars used and the spring and autumn season not all results of the experiments are comparable. The results of the curve-fitting and the quantitative analysis have been discussed and compared with some data from literature.

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REFERENCES

- 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 PLOEGMAN, C.: Enkele resultaten met CO_2 -dosering bij tomaat, kropsla, andijvie en spinazie. – Meded. Dir. Tuinb. 28: 622–629, 1966.
- BIERHUIZEN, J. F., EBBENS, J. L. and KOOMEN, N. C. A.: Effects of temperature and radiation on lettuce growing. – Neth. J. agric. Sci. 21: 110–116, 1973.
- BLACKMAN, V. H.: The compound interest law and plant growth. – Ann. Bot. 33: 353–360, 1919.
- 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.
- CHALLA, H.: An analysis of the diurnal course of growth, carbon dioxide exchange and carbohydrate reserve content of cucumber. – Verslag landbouwk. Onderz. 861: 1–88, 1976.
- COCKSHULL, K. E. and HUGHES, A. P.: Growth and dry-weight distribution in *Callistephus chinensis* as influenced by lighting treatment. – Ann. Bot. 33: 367–379, 1969.
- DENNIS, D. J. and DULLFORCE, W. M.: Analysis of the subsequent growth and development of winter glasshouse lettuce in response to short periods in growth chambers during propagation. – Acta Hort. 39: 197–218, 1974.
- DENNIS, D. J. and DULLFORCE, W. M.: The response of the heated glasshouse lettuce crop to in situ supplements of low illuminance fluorescent light. – Acta Hort. 51: 185–200, 1975.
- DRAPER, N. R. and SMITH, H.: Applied Regression Analysis. Pp. 267–270. John Wiley & Sons, New York 1966.
- DULLFORCE, W. M.: Growth of lettuce seedlings. – Nature 177: 1244–1245, 1956.
- DULLFORCE, W. M.: Analysis of the growth of winter glasshouse lettuce varieties. – Rep. Univ. Nottingham, Sch. Agric. 1962: 57–64, 1963.
- DULLFORCE, W. M.: Effects of light, temperature and carbon dioxide on the growth of glasshouse lettuce (*Lactuca sativa* L.). – Ph. D. Thesis, Un. of Nottingham: 1–150, 1968.
- DULLFORCE, W. M.: The growth of winter glasshouse lettuce with artificial light. – Acta Hort. 22: 199–210, 1971.

- EAGLES, C. F.: The effect of temperature on vegetable growth in climatic races of *Dactylis glomerata* in controlled environments. – Ann. Bot. 31: 3–39, 1967.
- EAGLES, C. F.: Time changes of relative growth rate in two natural populations of *Dactylis glomerata* L. – Ann. Bot. 33: 937–946, 1969.
- ESCH, H. G. A. VAN: Invloed van dagtemperatuur in herfst en winter op groei en kwaliteit van sla. – Verslag 619/73. Proefstation voor de Groenten- en Fruitteelt onder Glas, Naaldwijk: 1–17, 1973.
- ESCH, H. G. A. VAN: Plantdichtheidsproeven bij vier slarassen (heteluchtteelt 1976/1977). – Intern verslag 53. Proefstation voor de Groenten- en Fruitteelt onder Glas, Naaldwijk: 1–6, 1977.
- EVANS, G. C.: The quantitative analysis of plant growth. Studies in ecology. I. Pp. 319. Blackwell Scient. Publ., Oxford 1972.
- EVANS, G. C. and HUGHES, A. P.: Plant growth and aerial environment. I. Effect of artificial shading on *Impatiens parviflora*. – New Phytol. 60: 150–180, 1961.
- EVERAARTS, A. P. en SLOTEN, D. H. VAN: De invloed van temperatuur en straling op de groei en ontwikkeling van sla in een late voorjaarsteelt. – Verslag ingenieursproef Tuinbouwplantenteelt: 1–35, 1974.
- FORSYTHE, G. E.: Generation and use of orthogonal polynomials for data-fitting with a digital computer. – J. Soc. indust. appl. Math. 5 (2): 74–88, 1957.
- FOX, L. and MAYERS, D. F.: Computing Methods for Scientists and Engineers. Pp 116–118. Clarendon Press, Oxford 1968.
- FUKAI, S. and SILSBURY, J. H.: Effects of irradiance and solar radiation on dry matter growth and net CO₂ exchange of *Trifolium subterraneum* L. swards at a constant temperature. – Aust. J. Plant Physiol. 4: 485–497, 1977.
- HARSSEMA, H.: Root temperature and growth of young tomato plants. – Meded. Landbouwhogeschool Wageningen 77–19: 1–85, 1977.
- HOLSTEIJN, H. M. C. VAN: Growth of lettuce. I. Covering of soil surface. – Meded. Landbouwhogeschool Wageningen 80–7: 1–27, 1980.
- HUGHES, A. P. and COCKSHULL, K. E.: Effects of carbon dioxide concentration on the growth of *Callistephus chinensis* cultivar Johannistag. – Ann. Bot. 33: 351–365, 1969.
- HUGHES, A. P. and EVANS, G. C.: Plant growth and the aerial environment. II. Effects of light intensity on *Impatiens parviflora*. – New Phytol. 61: 154–174, 1962.
- HUGHES, A. P. and FREEMAN, P. R.: Growth analysis using frequent small harvests. – J. appl. Ecol. 4: 553–560, 1967.
- HURD, R. G. and THORNLEY, J. H. M.: An analysis of the growth of young tomato plants in water culture at different light integrals and CO₂ concentrations. I. Physiological aspects. – Ann. Bot. 38: 375–388, 1974.
- KLAPWIJK, D.: De groeiduur van sla. III. – Tuinderij 18 (24): 24–27, 1978.
- KOLLER, H. R., NYQUIST, W. E. and CHORUSH, I. S.: Growth analysis of the soybean community. – Crop Sci. 10: 407–412, 1970.
- KRIZEK, D. T., BAILEY, W. A., KLÜTER, H. and LIU, R. C.: Maximizing growth of vegetable seedlings in controlled environments at elevated temperature, light and CO₂. – Acta Hort. 39: 89–102, 1974.
- KVĚT, J., ONDOK, J. P., NEČAS, J. and JARVIS, P. G.: Methods of growth analysis. In ŠESTÁK, Z., ČATSKÝ, J., JARVIS, P. G. (ed.): Plant Photosynthetic Production. Manual of Methods. Pp. 343–391. Dr. W. Junk N.V. Publ., The Hague 1971.
- LEE, K. K.: Growth studies with lettuce. – M.Sc. Thesis, Massey Un., New Zealand: 1–137, 1974.
- NICHOLS, A. O. and CALDER, D. M.: Comments on the use of regression analysis for the study of plant growth. – New Phytol. 72: 571–581, 1973.
- NICHOLS, M. A.: Growth studies with lettuce. – Thesis, Massey Un., New Zealand: 1–106, 1970.
- NILWIK, H. J. M.: Personal communication.
- NOGUCHI, M., KIKKAWA, M., HOSHINO, K., IKEDA, S. and KOBAYASHI, K.: Analysis of the factors determining the vegetable crops yield. II. The effect of solar radiation on the growth and dry matter production in lettuce. – Bull. veg. and orn. Crops Res. St., Ishinden-Ogoso, Tsu, A4: 55–76, 1978. (English summary and subtitles).
- RADFORD, P. J.: Growth analysis formulae – Their use and abuse. – Crop Sci. 7: 171–175, 1967.

- Vol. V.A. Academic Press, New York 1969.
- RODENBRUG, C. M.: Varieties of lettuce. An international monograph. W. E. J. Willink, Zwolle, Holland: 1-228, 1960.
- SARTI, A.: Growth and photosynthetic activity of *Lactuca sativa*, c.v. romana, cultivated in three daylight intensities. - Lab. di Radiobiochimica ed Ecofisiologia vegetali CNR, 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.
- SCAIFE, M. A. and JONES, D.: The relationship between crop yield (or mean plant weight) of lettuce and plant density, length of growing period and initial plant weight. - J. agric. Sci. Camb. 86: 83-91, 1976.
- 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.
- THORNLEY, J. H. M. and HURD, R. G.: An analysis of the growth of young tomato plants in water culture at different light integrals and CO₂ concentrations. II. A mathematical model. - Ann. Bot. 38: 389-400, 1974.
- WATSON, D. J.: The physiological basis of variation in yield. - Adv. Agron. 4: 101-145, 1952.
- WILSON, D. and COOPER, J. P.: Assimilation rate and growth of *Lolium* populations in the glasshouse in contrasting light intensities. - Ann. Bot. 33: 951-965, 1969.

4 A CLOSED SYSTEM FOR MEASUREMENT OF PHOTOSYNTHESIS, RESPIRATION AND CO₂-COMPENSATION POINTS

INTRODUCTION

Fundamental data for the production of glass-house crops in relation to temperature, light and CO₂-conc. are greatly needed. Nowadays, advanced equipment is available to control temperature and CO₂-conc. in the glass-house climate. An efficient temperature regulation is now extremely important, because of the amount of energy required to heat the glass-house. In practice the application of artificial light is useful but depends to a large extent on economic factors. Data about the relation between temperature, light and CO₂ on photosynthesis of glass-house crops are scanty.

Many research workers have built open, semi-closed or closed systems or have discussed aspects, which have to be considered in building such a system (ACOCK 1974; JARVIS et al. 1971). At the Agricultural University and Research Institutes in Wageningen, The Netherlands, open systems have been built for measurements of leaves (CHALLA 1976; GAASTRA 1959; PIETERS 1974), whole plants (LOUWERSE and VAN OORSCHOT 1969) or stands (LOUWERSE and EIKHOUDT 1975). VERFAILLIE (1972) constructed a closed system in which the environmental control of the aerial part and the control of the roots was separated. The equipment was used for grains (e.g. rice) and could not be applied to vegetables such as lettuce and sweet pepper. A closed system facilitates the measurement of CO₂-exchange from high external CO₂-conc. to levels as low as the CO₂-compensation point. HEATH and MEIDNER (1967) stated that data obtained in that way give information about possible practical use of CO₂-application. The CO₂-compensation point gives information about the photosynthetic efficiency of plants. For these reasons a relatively simple and cheap apparatus is constructed, based on the principle of a closed system and suitable for glass-house crops.

METHODS AND APPARATUS

General description

Fig. 1 is a diagram of the equipment which consists of the following components: plant chamber and pot chamber, the equipment for light- and temperature control. The infra-red gas-analyser and a 24 channel mV-recorder are not shown in Fig. 1. The closed circuit with the perspex plant chamber (Pl.ch.) and the temperature control equipment is placed on a metal trolley (g; 800 × 880 × 960 mm) with universal wheels (h₁-h₄). This trolley can be pushed under and beside the frame (e). Details of the perspex chamber and temperature control equipment will be given in subsequent paragraphs.

The light equipment consists of 5 Philips high intensity mercury vapour lamps (a₁-a₅; HPLR of 400 W each), arranged at 250 mm from each other,

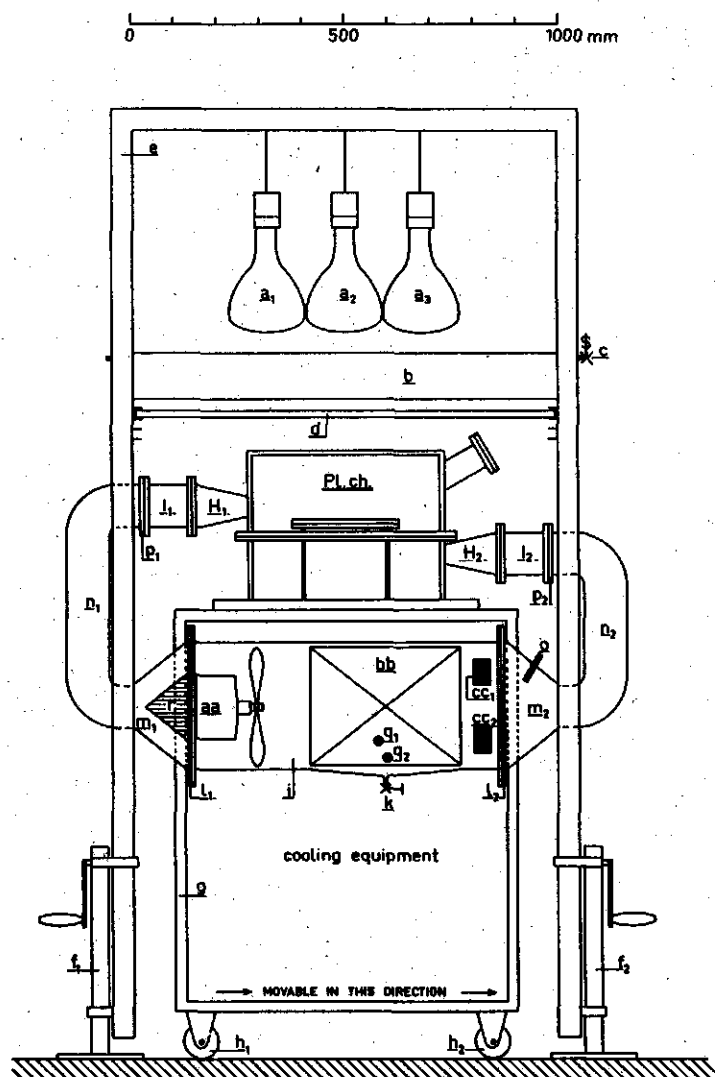


Fig. 1. Diagram of the equipment. All sizes in mm. a_1 - a_3 = lamps, aa = fan and motor, b = water bath, bb = cooling coil, c = valve, cc_1 and cc_2 = air-heating elements, d_1 - d_3 = metal screens, e = metal frame, f_1 - f_4 = screw jacks, g = metal trolley, h_1 - h_4 = universal wheels, i = copper duct, i_1 - i_2 = perspex interunits, k = drain cock, l_1 - l_2 = copper flanges, m_1 - m_2 = copper interunits, n_1 - n_2 = flexible tubes, o = temperature sensor, p_1 - p_2 = perspex flanges, $Pl.ch$ = plant chamber, q_1 - q_2 = places of transits through the copper duct, r = copper cone fixed on aa .

measured from the central lamp. Light intensity is regulated by movable metal screens (d) with a different size and a different number of perforations. A range of irradiance between 0 and 215 W m^{-2} (400-700 nm) at plant level can be realized. The difference in light intensity at the horizontal direction in

the plant chamber is less than 15%. A water bath (b) was installed in order to reduce the long wave radiation. The distance from the water bath to the lamps is 50 mm and from the water bath to the plant chamber 120 mm. The temperature in the water bath is regulated between 12° and 35°C with a thermostat, which operates a valve (c) for the tap-water supply. Lamps, water bath and screens are mounted on a metal frame (e; U-tube, 2250 × 1090 × 1090 mm), the height of which can be increased 400 mm by 4 hand-operated screw jacks (f₁–f₄). More details of the equipment are given in the Appendix.

A copper duct i (700 × 320 × 424 mm) is equipped with a fan (aa), a cooling coil (bb) and 2 air-heating elements (cc₁ and cc₂). A copper cone r is fixed on aa and placed in the airstream. The drain cock (k) is inserted at the lowest point of the duct in order to drain superfluous water. At points q₁ and q₂ 2 copper tubes connect the cooling coil with the cooling equipment at the bottom of the trolley. The copper tubes and 3 transits for electric wires through the copper duct are hermetically sealed with Bucarit-aquarium putty. The duct is connected at both ends to sloping copper units (m₁ and m₂) by means of copper flanges (l₁ and l₂) and bolts and hermetically clothed with foamed cellrubber. The sloping units are connected with flexible tubes (∅ 100 mm) to the inlet (n₂) and to the outlet (n₁) of the plant chamber. The copper part is isolated with Armaflex rubber and the flexible tubes are wrapped in Virginia foam rubber tape. A temperature sensor (o) for the temperature control equipment is placed at unit m₂. The length of tube n₁ can be varied for various heights of the plant chamber. Both tubes (n₁ and n₂) have perspex flanges (p₁ and p₂) which connect the perspex interunits I₁ and I₂ by means of bolts and a quad ring (∅ 113 × 6 mm). The room temperature can be varied between 10° and 34°C with an accuracy of ± 0.8°C by means of thermostatic controlled electric heaters and a cooling battery (s).

Details of the plant chamber

The plant chamber (Fig. 2) consists of a perspex (polymethylmethacrylate) cylinder (A; h = 150 mm) mounted on a solid perspex bottom plate (B; ∅ 620 mm; h = 25 mm) and an upper unit (C) with an internal height of 190 mm. The height of the cylinder can be increased with 2 interunits (D and E) with heights of 100 and 250 mm, resp. (not shown in Fig. 2). The inner diameter of the cylinders (A, C, D, E) is 441 mm and the wall thickness 8 mm. The units are airtight connected with O-rings (∅ 480 × 6 mm) and 6 adjustable metal clips (F). The total volume of the closed circuit with A and C is 180 litres. This volume (b) was calculated from the increase of the CO₂-concentration (ΔCO₂) after injection of a known volume (Δv) of pure CO₂ into the system according to the equation $\Delta v = a + b\Delta\text{CO}_2$. In plotting Δv against ΔCO₂ a straight line was obtained from which the volume was calculated. When there is no leakage, the symbol a is zero in the equation.

Cylinder A is provided with perspex tubes (G₁–G₄) which are used to insert wires for sensor elements, electrical cables and copper tubes conducting the

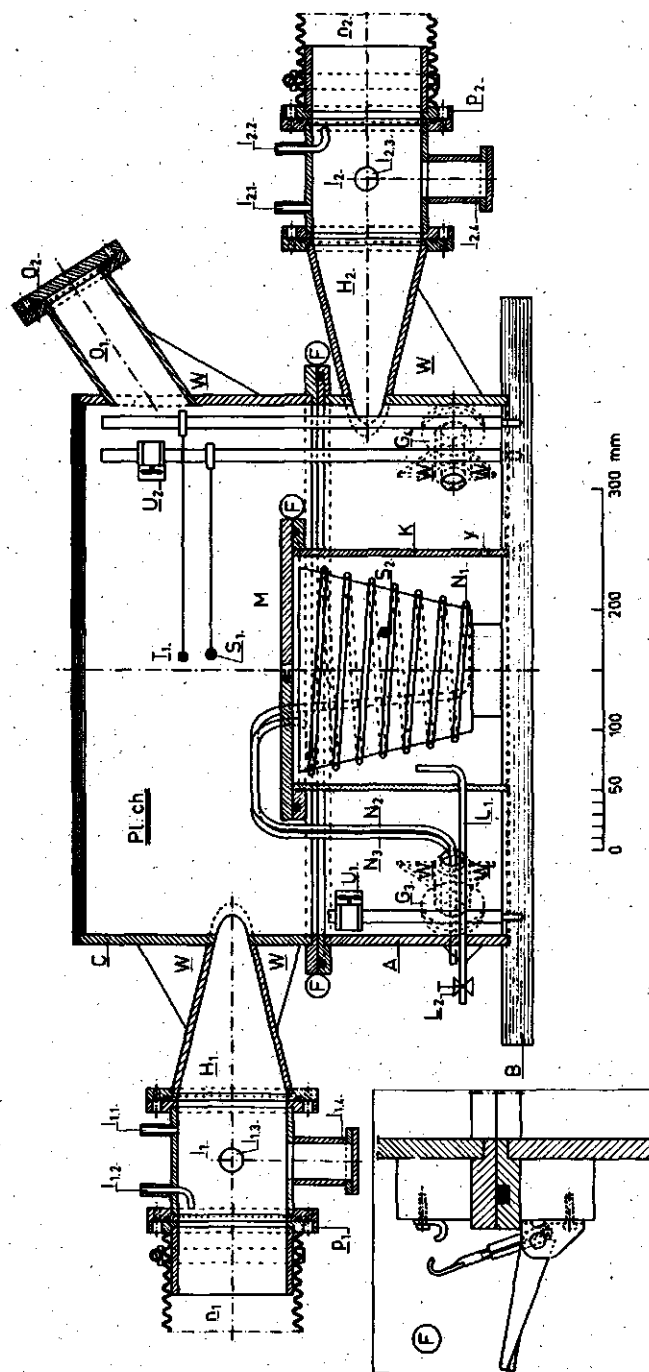


Fig. 2. Diagram of the plant chamber. All sizes in mm. A = perspex basal unit, B = solid perspex bottom plate, C = perspex upper unit, D and E = perspex interunits, F = metal clips (see detail), G = perspex tubes ($\varnothing 40 \times 30$; $l_1 = 32$), H₂ = perspex air inlet (opening with Pl.ch.: 210 wide and maximally 40 high), H₁ = perspex air outlet, I₁ and I₂ = perspex interunits ($\varnothing 110 \times 100$, $l = 100$), I₁, I₁, I₁, I₂, I₂, I₂ and I₂ = perspex tubes ($\varnothing 24 \times 12$; $l = 15$), I₁, I₁ and I₂, I₂ = perspex tubes, similar to G, K = perspex pot chamber ($\varnothing 200 \times 190$; $h = 190$), L₁ = perspex tube ($\varnothing 5 \times 3$ mm; $l = 180$ mm), L₂ = valve, M = perspex disk ($\varnothing 250$; thickness 10), n₁ and n₂ = flexible tubing, N₁ = copper spiral ($\varnothing 6 \times 4$), N₂-N₃ = plastic tubes, O₁ = perspex tube ($\varnothing 60 \times 50$; $l = 75$), O₂ = perspex flange, P₁-P₂ = perspex flanges, Pl.ch. = plant chamber, S₁ and S₂ = thermocouples, T₁ = photocells, U₁ and U₂ = fans, W = perspex supports, Y = place of transit for a thermocouple wire.

thermostat controlled water to achieve any desired temperature of the pot in the chamber. The tubes G_1 - G_4 are filled with perspex stops to prevent CO_2 -pockets in the closed circuit. Air leakage is prevented by use of perspex stop flanges, bolts and airtight foamed cell rubber. The air inlet (H_2) is connected to the interunit I_2 by a flange and a quad ring ($\varnothing 113 \times 6$ mm). In the subscript of Fig. 2 those dimensions of the various parts are given, which have not been mentioned here. The bottom plate is provided with holes with screw thread to insert PVC bars on which sensors can be fitted. A perspex cylinder (K), the pot chamber, is glued onto the bottom plate in which a pot with a soil-volume of almost 2,3 litres can be inserted. The cylinder is provided with a perspex tube (L_1) for supply of water and air via a valve (L_2). W are perspex supports. Point Y is the place for a transit of thermocouple wires.

An airtight seal of the pot chamber with the pot is obtained by means of a flat disk (M) of 2 segments, an O-ring ($\varnothing 226 \times 6$ mm) and metal clips (F). Disks with different slot sizes are used because of various thicknesses of the plant stems. The slot is sealed with aquarium putty after inserting the pot with the plant in the pot chamber. The temperature of the pot can be regulated in a range between 15-35 °C by a copper tube (N_1) bent into a spiral ($l = 225$ or 315 cm) and connected to an isolated water bath (N_4) of 10 litres which contains a portable thermoregulator (N_5) and a cooling unit (N_6). N_2 and N_3 are plastic tubes. N_4 - N_6 are mentioned in the Appendix. The difference in temperature between the pot and the water bath depends mainly on the applied difference in air and soil temperature.

The upper unit C is provided with an air outlet H_1 , constructed in the same way as the air inlet H_2 . Opposite to H_1 a perspex tube (O_1) with a flange (O_2), a perspex stop and an O-ring ($\varnothing 63 \times 4$ mm) are attached. Through this tube the leaf temperature of a plant can be measured with an infra-red thermometer (P; see Appendix) before or after the CO_2 -exchange measurements.

H_1 and H_2 are connected by perspex flanges (p_1 and p_2) with the interunits (I_1 and I_2) and flexible tubes (n_1 and n_2). The interunit I_2 is provided with perspex tubes I_2I_1 and I_2I_2 (both $l = 50$ mm), I_2I_3 and I_2I_4 . I_2I_1 is connected by means of a threeway valve onto a CO_2 -injector and a CO_2 -cylinder. In this way pure CO_2 can be injected in the circulating airstream with an accuracy of 5%. The time needed after injection to achieve a steady mixture is about 4 minutes. I_2I_2 is connected to a U-shaped glass tube (not shown) filled with paraffin oil, which indicates the pressure difference between the closed circuit and the ambient air and prevents damage to the equipment in case of excessive under or over pressure.

Through tube I_2I_3 a humidity sensor (Q; see Appendix) can be inserted in the airstream. I_2I_4 is used for wires. Interunit I_1 has similar tubes (I_1I_1 , I_1I_2 , I_1I_3 , I_1I_4) as I_2 . Tubes I_1I_1 and I_1I_2 are connected via nyloseal tubes to the in- and outlet of the URAS (R_4). The nyloseal tubes are impermeable for CO_2 . Nyloseal flareless tube fittings were used for the connections. The circuit is pro-

Appendix). In tube I_1I_3 a humidity sensor (Q) has been inserted.

Transpiration is determined by measuring in- and outgoing air of the plant chamber by the humidity sensors. The temperatures of the air in cylinder K and in the soil of the pot are measured by copper-constantan thermocouples (S_1 ; 0.5 mm^2). The air and leaf temperature is measured by manganin-constantan thermocouples (S_2 ; 0.2 mm^2) fixed on thin aluminium bars and movable in all directions. The irradiance at various horizontal and vertical positions in the empty plant chamber was measured with a flat photometer for visible light (type TFDL - 65 - 2020) and a Kipp solarimeter (type cc_1). The maximum irradiance at plant level is 215 W m^{-2} . The difference in horizontal distribution was less than 15% and the vertical measurements showed a quadratic relation. During CO_2 -exchange measurements the irradiance is recorded continuously by photocells (T_1) which are fixed on the thin aluminium bars.

To improve the turbulence in the plant chamber 2 small fans (U_1 and U_2) are used. Usually the wind-speed is not recorded during CO_2 -exchange measurements. The wind-speed in the centre of the interunits is about 4.80 m s^{-1} . In the plant chamber without a plant it was $0.60\text{--}0.95 \text{ m s}^{-1}$ with units A and C (in the centre 0.8 m s^{-1}) and $0.50\text{--}1.10 \text{ m s}^{-1}$ with units A, C, D and E. Wind-speed was measured by a heatball anemometer, constructed at the Department of Physics and Meteorology, Agricultural University. Because of the relatively high wind-speed the difference between leaf and ambient air temperature was small, which is in accordance with results obtained by PAPENHAGEN (1974).

The URAS, thermocouples, photocells and humidity sensors are connected to a 24 channel mV-recorder (Philips, type PR 3500) or to a datalogger (Fluke, type 2240 A).

Principle of the temperature control system

A diagram of the temperature control system is given in Fig. 3. The copper-duct i of the closed circuit (see Fig. 1.) is provided with a fan (aa), a cooling coil (bb), 2 air-heating elements (cc_1 and cc_2) and the temperature sensor (o).

Glycol is circulated through the cooling coil. The glycol circuit consists of an expansion vessel (dd) with pressure gauge (ee), a three-way valve with servomotor (ff), a pump (gg) for circulating the glycol through the glycol circuit and a valve (hh). The three-way valve determines the distribution of glycol through the evaporator (ii) and a bypass. In this way the cooling capacity is adapted continuously to the cooling requirement. Temperature is regulated proportionally. The valve hh is used for filling the circuit with glycol.

The freon circuit consists of a freon compressor (kk_1), an air cooled condenser (kk_2), a liquid vessel (kk_3), a filter drier (ll), a sight glass (rr), double tubes evaporator (ii), thermostatic expansion valves (mm_1 and nn_1) with bulb sensors (mm_2 and nn_2), a liquid separator (oo) and a filter drier (pp); qq and ss are pressure valves.

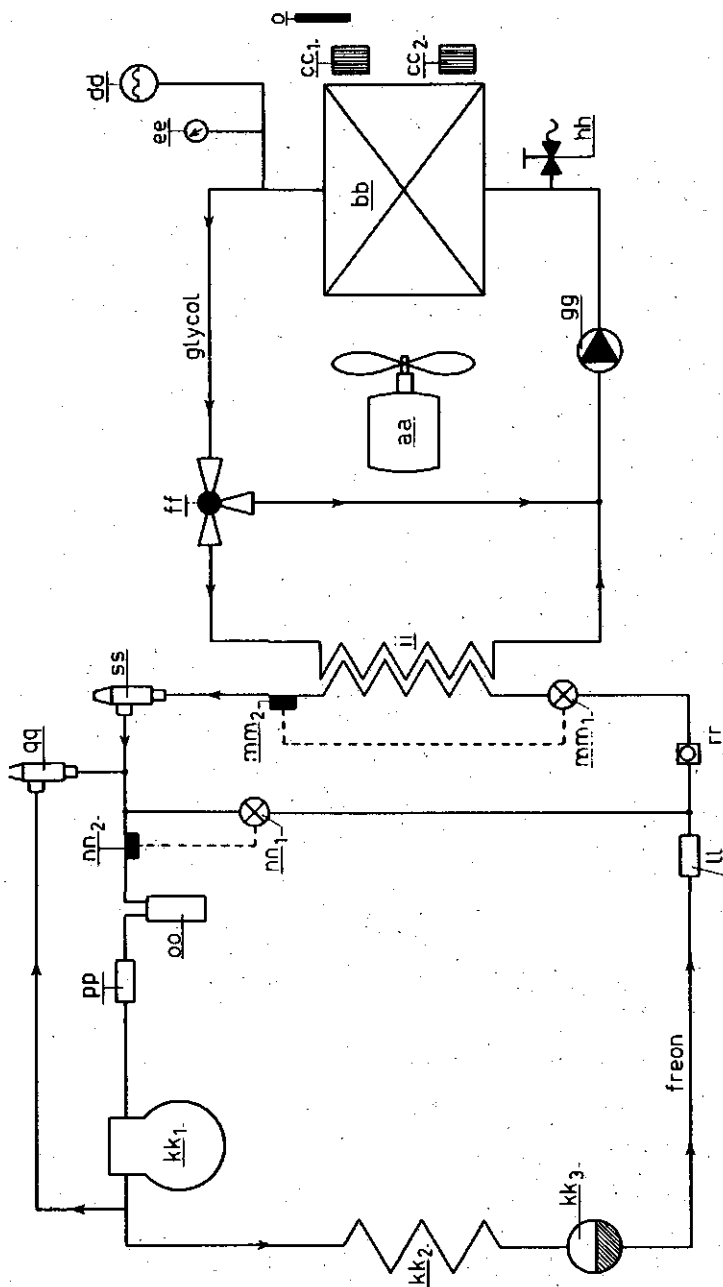


Fig. 3. Diagram of the temperature controlsystem, aa = fan and motor, bb = cooling coil, cc_1 and cc_2 = air-heating elements, dd = expansion vessel, ee = pressure gauge, ff = three-way valve and servo motor, gg = pump, hh = valve, ii = double tubes evaporator (condensor), kk_1 = freon compressor, kk_2 = condensor, kk_3 = cooling vessel, ll = filter drier, mm_1 and mm_2 = thermostatic expansion valves, nn_1 and nn_2 = pressure bulb sensors, oo = temperature sensor, pp = liquid separator, qq = filter drier, rr = pressure valve, ss = constant pressure valve.

A high pressure and high temperature exist in compressor kk_1 . In kk_2 the pressure is still high but the temperature becomes lower, due to the cooling by

... The pressure difference between the high pressure and low pressure part (ii) is provided by mm_1 . A low pressure and low temperature exist at ii. Freon evaporates in ii and takes heat off from the glycol circuit.

The freon system is continuously operating but below full capacity. Pressure valve ss regulates the pressure in ii in such way that the temperature in ii never becomes too low. When ss is closing, an extreme low pressure between ss and kk_1 can exist, because the capacity of kk_1 remains unchanged. For the protection of the compressor the extreme low pressure is taken off via a gas short-circuit, regulated by qq. Expansion valve nn_1 is necessary to prevent high temperatures in the short-circuit in a period of prolonged low cooling capacity at ii. Temperature sensor bulb nn_2 regulates nn_1 in such way that the temperature in the shortcircuit never becomes too high and the compressor is protected against burning. The evaporation of freon after nn_1 in the low pressure part cools the short-circuit.

Since the room temperature can be controlled in a range between 10 and 34°C, the temperature in the plant chamber can be chosen between 5 and 32°C. Usually the room temperature was kept a few degrees above the plant chamber temperature in order to prevent condensation on the plant chamber wall. The temperature of the plant chamber could be kept constant with an accuracy of $\pm 0.5^\circ\text{C}$. With rapid changes in irradiance manual control of the temperature can be applied in order to achieve more quickly the desired temperature.

In case the equipment fails, a safety fuse will cut the current in order to prevent damage.

SOME PRELIMINARY RESULTS ON PHOTOSYNTHESIS AND TRANSPIRATION

During preliminary experiments it appeared that the humidity sensors were accurate and sufficiently sensitive. The difficulty of exactly calibrating the sensors at the high air humidity and of the high wind-speed applied in the plant chamber, which gives a small difference in water vapour between the in- and outgoing air, resulted in a less accurate recording of transpiration than desired. At present data on transpiration can be obtained only under steady conditions (ACOCK et al. 1977; KING et al. 1977) by measuring the amount of water condensed at point k (see Fig. 1.). Measurement of transpiration by humidity sensors would have been cheap. In the near future we hope to use a URAS for continuous recording of transpiration.

The rates of photosynthesis and respiration are determined in a closed system by measuring the CO_2 -content of the circulating air by infra-red gas-analysis. The rate of photosynthesis (Pn) depends on the decline in CO_2 -concentration (ΔCO_2) per unit time (Δt) and the volume (b) of the closed circuit according to $Pn = b \cdot \Delta\text{CO}_2 / \Delta t \cdot c$. Symbol c contains a factor for the calibration of the URAS and the density of CO_2 at the measured temperature. Analogue to the measurements of HEATH and MEIDNER (1967) with lettuce leaves

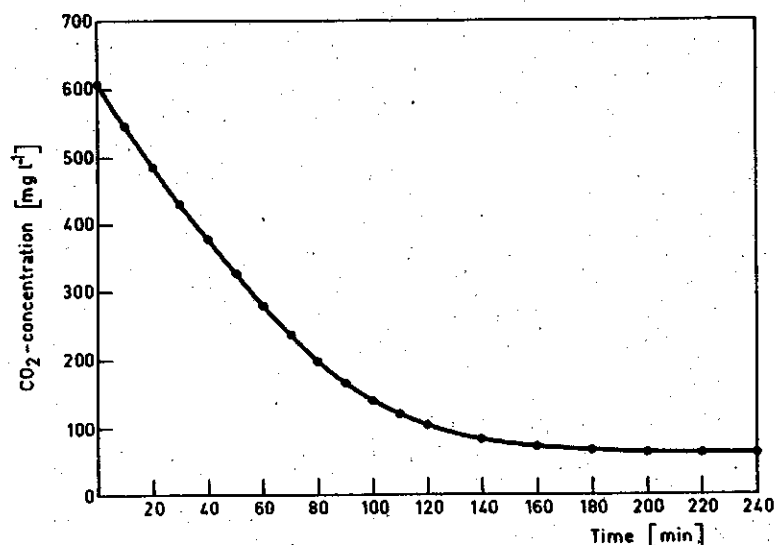


Fig. 4. Decrease of CO₂-concentration during 4 hours in a closed circuit with a sweet pepper plant cv. Bruinsma Wonder at irradiance of 61 W m⁻² at plant level. The injected CO₂-conc. was about 620 mg l⁻¹. Plant chamber and pot chamber temperature was 25.5 °C ± 0.5 °C during the measurement. The plant was grown at day-night temperatures of 26–21 °C in a glass-house in April-May 1977. The leaf area was 23.3 dm² and the plant had 3 small fruits.

or VERFAILLIE (1972) with rice plants, the CO₂-exchange can be measured at any external CO₂-concentration. Fig. 4 shows the decrease in CO₂-concentration against time for a sweet pepper plant cv. Bruinsma Wonder. It is evident from Fig. 4 that below a concentration of 300 mg l⁻¹ the rate of photosynthesis declines until a steady condition is achieved and the net CO₂-exchange is zero. The CO₂-concentration at the compensation point, which was 62 mg l⁻¹ in this particular case, can be read directly from the chart. Leakage in a short period is neglectable. If there was some leakage of CO₂, the CO₂-compensation point would actually be lower than on the chart.

When knowledge regarding photosynthesis at only one CO₂-concentration is required, a calculated amount of CO₂ can be injected each time to obtain the desired CO₂-concentration. Fig. 5a shows an example with lettuce cv. Amanda Plus at various light intensities. The figure shows that within a few minutes after injection a gradual decline in CO₂-concentration set in and ΔCO₂ can be measured. The data of Fig. 5a were used to calculate the CO₂-exchange rates, which are presented in Fig. 5b, showing the photosynthesis-light response curve.

It should be mentioned that the volume of the plant chamber can be varied depending on the height of the plant. With the smallest volume, plants should have a leaf area of at least 5 dm² in order to obtain accurate data.

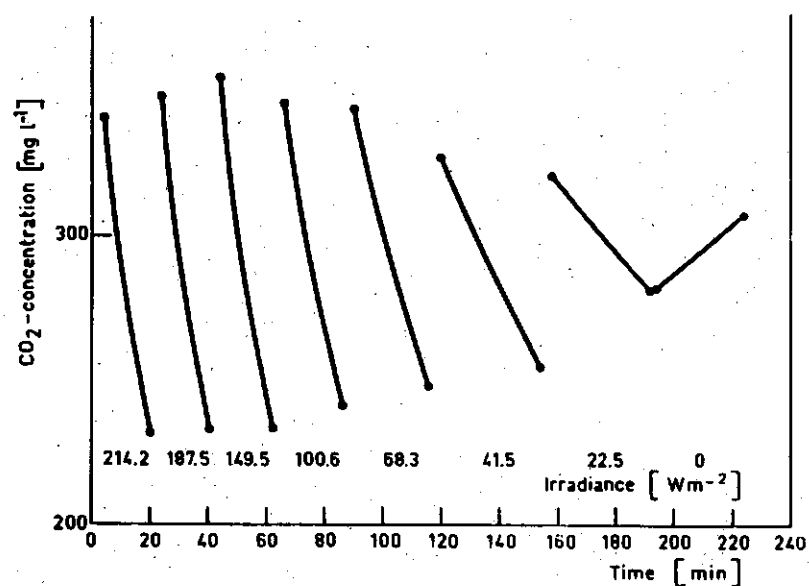


Fig. 5a. Decrease of CO_2 -concentration in a closed circuit with a lettuce plant cv. Amanda Plus during short periods at various irradiance levels. The CO_2 -conc. was between 350 and 250 mg l^{-1} . Plant chamber and pot chamber temperature was 14 ± 0.5 C during the measurement. The plant was grown at day-night temperatures of 16–11 C in a glass-house in Februari-March 1977 with 30 W m^{-2} (400–700 nm) artificial illumination and the last two weeks before the measurement 65 W m^{-2} . The fresh weight was 52.4 g and the leaf area 18.0 dm^2 .

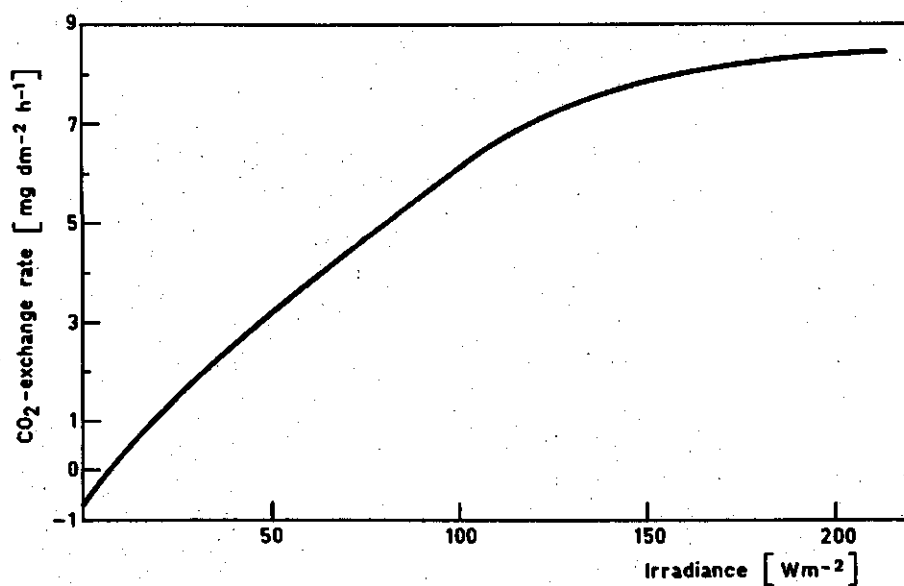


Fig. 5b. CO_2 -exchange rate ($\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) of a lettuce plant cv. Amanda Plus at various irradiance levels.

SUMMARY

A closed system for determination of photosynthesis, respiration and CO_2 -compensation points is described. The internal gaseous volume of the closed circuit is 180 litres. It consists of a plant chamber, a copper duct with built-in fan, cooling coil and air-heating elements and connecting flexible tubes. The cylindrical perspex plant chamber has an internal diameter of 441 mm and a height of 340 mm, which can be enlarged to 690 mm. The cylindrical perspex pot chamber has an internal diameter of 190 mm and a height of 190 mm.

Temperature in the plant chamber can be kept constant in the range between 5 and 32°C and in the pot chamber between 15 and 35°C with an accuracy of $\pm 0.5^\circ\text{C}$. Temperatures are measured by thermocouples. The maximum irradiance on plant level is 215 W m^{-2} (400–700 nm). Irradiance is measured by selenium photocells and air humidity with thin film humidity sensors. Wind-speed in the centre of the plant chamber is about 0.8 m s^{-1} . The rate of CO_2 -exchange is determined by an infra-red gas-analyser. Injection of pure CO_2 or a gas mixture facilitates continuous monitoring of photosynthesis and respiration. During short periods leakage can be neglected.

All measurements are recorded on a 24 channel mV-recorder or a data-logger. The equipment has been used in a controlled environment room but can be transferred to the field. Since 1976 this closed system has been used for CO_2 -exchange measurements with lettuce and sweet pepper plants.

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REFERENCES

- ACOCK, B.: The design and use of growth chambers for investigating the effects of environmental factors on plant growth. – *Acta Hort.* 39: 15–38, 1974.
- ACOCK, B., CHARLES – EDWARDS, D. A., HEARN, A. R.: Growth response of a Chrysanthemum crop to the environment. I. Experimental techniques – *Ann. Bot.* 41: 41–48, 1977.
- CHALLA, H.: An analysis of the diurnal course of growth, carbon dioxide exchange and carbohydrate reserve content of cucumber. – *Agri. Res. Rep.* 861: 1–88, 1976.
- 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.

- LESTER, G. F. G., HEDDERLEY, H.: Compensation points and carbon dioxide enrichment for lettuce grown under glass in winter. - J. exp. Bot. 18: 746-751, 1967.
- JARVIS, P. G., ČÁTSKÝ, J. et al.: General principles of gasometric methods and the main aspects of installation design. In ŠESTÁK, Z., ČÁTSKÝ, J., JARVIS, P. G. (ed.): Plant Photosynthetic Production. Manual of Methods. Pp. 49-110. Dr. W. JUNK N.V. Publ., The Hague 1971.
- KRUG, H., WIEBE, H. J., ROSE, H. B.: Gasmessanlage mit CO₂-kompensationsverfahren. - Gartenbauwiss. 42: 105-108, 1977.
- LOUWERSE, W., EIKHOUDT, J. W.: A mobile laboratory for measuring photosynthesis, respiration and transpiration of field crops. - Photosynthetica 9: 31-34, 1975.
- LOUWERSE, W., 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.
- PAPENHAGEN, A.: Apparatus for plant gas exchange measurements with microchambers and its suitability for physiological studies. - Acta Hort. 39: 49-58, 1974.
- PIETERS, G. A.: The growth of sun and shade leaves of *Populus Euramericana* 'Robusta' in relation to age, light intensity and temperature. - Meded. Landbouwhogeschool, Wageningen 74(11): 1-107, 1974.
- SUATOLA, T., ANTON, J.: A thin film humidity sensor. - Vaisala News 59: 1-7, 1973.
- VERFAILLIE, G. R. M.: A method to study the kinetics of photosynthesis at constant rate of transpiration. Results obtained with rice plants. (*Oriza sativa* Maratelli). - J. exp. Bot. 23: 1106-1119, 1972.

APPENDIX

aa	Ventilator motor. Küba, type EA-24, with Küba-wings 300KS 15/12 and stepless revolution regulator, type VRH-502.
b	Water bath of aluminium plate ($h = 110$ mm) with a glass plate ($d = 10$ mm) on the bottom.
bb	Cooling coil Küba, type 6×7 (0.3) B6. Total cooling area is 10 m ² . At a temperature difference of 10°C the capacity with forced cooling is about 5040 kJ h ⁻¹ .
c	Water bath thermostat. Danfoss solenoid valve, type EVJD 15.
cc ₁ and cc ₂	Air-heating elements. Küba, type HR300. Power 315 W.
dd	Expansion vessel. Flexon, type 2/0.5.
ee	Flexon pressure gauge with a range of 0.1 – 0.4 g m ⁻² .
f ₁ –f ₄	Old screw jacks, used for cars.
ff	Servomotor. Zentra, type VM-13P and a threeway valve, Zentra type DRK-15.
F	Metal clips. Camloc, type 5 IL 7-IBF.
gg	Pump. SMC, Commander 'S', with a maximal working pressure of $6 \cdot 10^5$ Pa.
ii	Double tubes evaporator (condensor). Küba, type G3. Capacity at a temperature difference of 10°C is 7350 kJ h ⁻¹ .
kk ₁ –kk ₃	Compressor unit L'unité hermétique, type TAH4518/AHR. This fan-cooled condensing unit consists out of the freon compressor kk ₁ , condensor kk ₂ and cooling unit kk ₃ . Airflow of $23 \cdot 10^5$ l h ⁻¹ .
ll	Filter drier. Danfoss, type DC-0833.
mm ₁	Thermostatic expansion valve, Danfoss, type TF2-0.5 with pressure sensor mm ₂ . Capacity max. 6300 kJ h ⁻¹ .
n ₁ –n ₂	Flexible tubes Flexofit, type NG2M ($\varnothing 100$ mm).
nn ₁	Thermostatic expansion valve, Danfoss, type TF2-0.2 with pressure sensor nn ₂ . Capacity: max. 3780 kJ h ⁻¹ .
N ₅	Portable thermoregulator. Braun, type Thermomix II. Capacity: 800 l h ⁻¹ . Temperature range 0 – 40°C .
N ₆	Cooling unit. Grant, type CC15. Cooling power of 295 kJ h ⁻¹ at 0°C and of 590 kJ h ⁻¹ at 25°C .
o	Temperature sensor. Zentra, type GF-11 with selector, type FG-2. The temperature in the closed circuit is regulated proportionally by the Zentra thermostat type 2G13/TE3/TK, (ES) with above mentioned sensor and selector by switching the cooling coil bb and air-heating elements cc ₁ and cc ₂ simultaneously.
oo	Liquid separator (a suction line accumulator), Virginia, type VA32-55.
pp	Lo-side filter drier, Virginia, type AL 24-5SV.
p	Infra-red thermometer, Heimann, type KT with objective A. Temperature range 0 – 60°C .
qq	Capacity regulator/receiver pressure valve. Danfoss, type CPC-15.

Q	The Vaisala humidity sensor has been described by SUATOLA and ANTON (1973). The electronical circuit is changed by Hoogendoorn B.V. 's-Gravenzande, The Netherlands.
rr	Sight glass. Danfoss, type SGI-10S.
R ₂	Membrane pump. Hartmann und Braun, type 2-Wisa.
R ₃	Flowmeter. Brooks, type E/C, model 1550-V. Capacity: 0–115 l h ⁻¹ .
R ₄	Infra-red gas-analyser, Hartmann und Braun, URAS-2. The URAS has a measuring cuvette of 21 cm with an optical H ₂ O-filter in order to reduce interference with the water vapour content of the air sample. Applied flow rate is about 40 l h ⁻¹ . The URAS is weekly calibrated with gas mixtures mixed by 2 mixing pumps (R ₅ and R ₆), set in series. Variations in sensitivity of the URAS are always less than 3%.
R ₅ and R ₆	Gas mixing pumps. Wöstoff, type SA 27/2a and SA 27/3a.
s	Searle-Bush refrigerators, type SR-240.
ss	Constant pressure valve. Danfoss, type CPP-15.
T ₂ –T ₆	Small selenium cells. Megatron, type B (ø 7 mm). The photocells are calibrated with a flat photometer and the Kipp solarimeter, mentioned in the text.
U ₁ –U ₂	Fans. Micronell, type V361 M. Maximal capacity 50.10 ⁴ l h ⁻¹ .

5 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 :

$$P_g = \frac{\alpha I \tau C}{\alpha I + \tau C}$$

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 $\tau C (I = \infty)$ or $\alpha I (C = \infty)$. 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_p) 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 $\alpha_g (I = 0)$ and the net initial slope $\alpha_n (I = I_c)$. 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 $\tau_g (C = 0)$ and the net initial slope $\tau_n (C = C_c)$. 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 C_3 -plants. However, this potential value ($\alpha_{g,con}$) is never obtained due to limitations of external CO_2 -concentration, conductance for CO_2 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 ($m^2 Pl^{-1}$), 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 ($mg CO_2 Pl^{-1} s^{-1}$), expressed on the basis of effective leaf area, is now described by: $P_{cor} = P \cdot EL^{-1}$ ($mg CO_2 m^{-2} s^{-1}$) and I_{cor} by $I \cdot EL$.

The efficiency $\alpha_{g,con}$ ($mg CO_2 J^{-1}$) is defined by:

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

with α_g ($mg CO_2 m^2 Pl^{-1} J^{-1}$) calculated from the obtained plant data. The conclusion from (7) is that $EL = \alpha_g / \alpha_{g,con}$ ($m^2 Pl^{-1}$). The photosynthetic rate per effective leaf area ($P \cdot EL^{-1}$) is $P_{pl} \cdot \alpha_{g,con} \cdot \alpha_g^{-1}$. The effective leaf area is equal to $k \cdot A$ or $k' \cdot S$, 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 $P_l \cdot \alpha_{g,con} \cdot \alpha_{g,l}^{-1}$ or $P_s \cdot \alpha_{g,con} \cdot \alpha_{g,s}^{-1}$ with $\alpha_{g,l}$ 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 $I_c \cdot EL = I_c \cdot \alpha_g \cdot \alpha_{g,con}^{-1}$.

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 dm² 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 dm² and between 1.70 and 3.90 g and for age C between 31.0 and 43.5 dm² 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 × 5 × 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	
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

... again selected and transplanted into the 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 W m^{-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 W m^{-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_n decrease with an increase of age. The values of α_g and α_n 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

treatments (I, II, III and IV) of the groups A, B and C of experiment I. Measurements were carried out at 14° and 26°C and at an external CO₂-concentration of about 560 (14°C) and 545 (26°C) mg m⁻³. α_s and α_s^1 : photochemical efficiencies (in I = 0) expressed per plant (mg CO₂ m² Pl⁻¹ J⁻¹) and per unit leaf area (mg CO₂ J⁻¹); P_{m,g} and P_{m,g}¹: maximum P_g at saturating I expressed per plant (mg CO₂ Pl⁻¹ h⁻¹) and per unit leaf area (mg CO₂ dm⁻² h⁻¹); R_d: dark respiration per unit leaf weight (mg CO₂ g⁻¹ 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						
	(°C)	$10^3 \alpha_s$	$10^3 \alpha_s^1$	$P_{m,s}$	$P_{m,s}^1$	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}¹-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

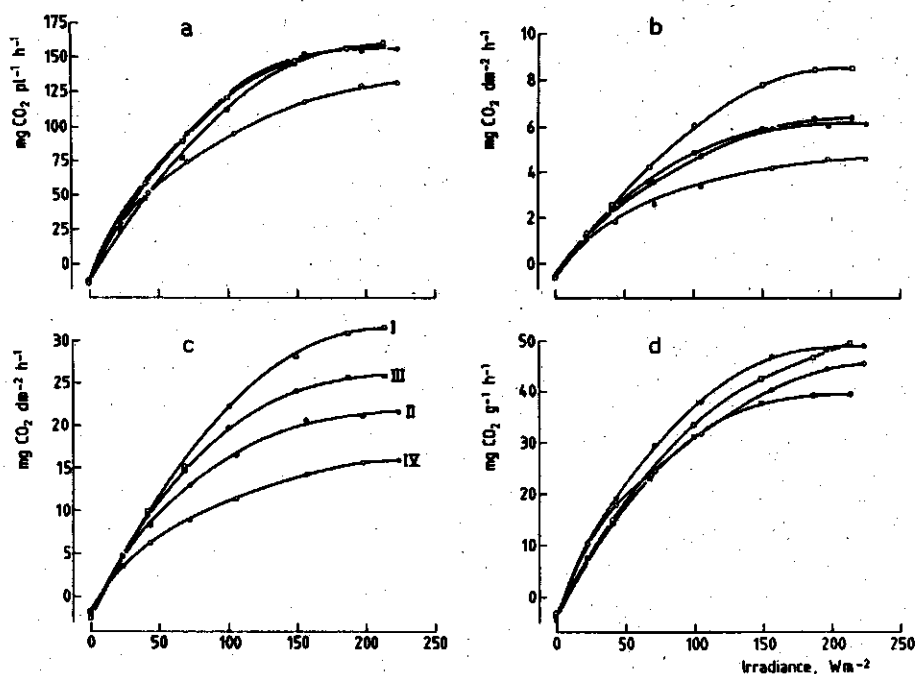


FIG. 1. Curves through measured data describing the response of net photosynthesis to irradiance of the 4 treatments (I, II, III and IV) of experiment 1, age B. The photosynthetic rates ($\text{mg CO}_2 \text{ h}^{-1}$) are expressed per plant (a), per unit leaf area (b), per unit soil cover (c) and per unit dry weight (d). The measurements were carried out at 14°C and an external CO_2 -concentration of about 560 mg m^{-3} . \square = I; \bullet = II; \blacksquare = III; \circ = 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: $EL = \alpha_g \cdot \alpha_{g, \text{con}}^{-1} = k \cdot A$ 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 Wm^{-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 ($= \alpha_g \alpha_{g, \text{con}}^{-1}$) only the factor α_g has been used, since $\alpha_{g, \text{con}}$ 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 Wm^{-2}) the temperature during measurements did not affect the net photosynthetic rates. The corrected light compensation point ($I_{c, \text{cor}}$) 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_g and α_g^1 : gross photochemical efficiencies (in $l = 0$) expressed per plant ($mg\ CO_2\ m^{-1}\ J^{-1}$) and per unit leaf area ($mg\ CO_2\ J^{-1}$); $P_{m,\alpha_g^{-1}}$, $P_{m,\alpha_g^{-1}}$ and $P_{m,100\alpha_g^{-1}}$ (Wm^{-2}) are the net photosynthetic rates at saturated irradiance level and at 35 and 100 Wm^{-2} expressed on basis of α_g ; $P_{m,s}^1$: maximum gross photosynthesis per unit leaf area ($mg\ CO_2\ dm^{-2}\ h^{-1}$); I_c and I_{c,α_g} : light compensation point (Wm^{-2}) and corrected light compensation point ($mg\ CO_2\ Pl^{-1}\ s^{-1}$); ** = 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 ($p < 0.01$).

Factor	Degrees of freedom	Results									
		$10^3\alpha_g$	$10^3\alpha_g^1$	$P_{m,\alpha_g^{-1}}$	$P_{m,35\alpha_g^{-1}}$	$P_{m,100\alpha_g^{-1}}$	$P_{m,s}^1$	I_c	$10^3I_{c,\alpha_g}$		
age	2	**	**	**	**	**	**	ns	**		
A		0.342 ^a	4.50 ^c	115.3 ^a	13.2 ^a	40.6 ^a	20.3 ^c	15.5 ^a	4.5 ^a		
B		0.563 ^b	2.93 ^b	158.2 ^b	16.4 ^b	47.4 ^b	17.4 ^b	12.5 ^a	6.4 ^b		
C		0.746 ^c	2.02 ^a	143.4 ^{ab}	15.9 ^b	46.3 ^b	11.1 ^a	12.9 ^a	9.1 ^c		
treatment	3	**	ns	**	ns	**	**	ns	ns		
I		0.492 ^a	3.18 ^{ab}	189.6 ^b	14.3 ^a	48.9 ^b	21.5 ^c	16.0 ^b	7.3 ^a		
II		0.600 ^b	3.53 ^b	109.8 ^a	15.0 ^a	41.9 ^a	14.8 ^b	13.2 ^{ab}	6.8 ^a		
III		0.547 ^{ab}	3.04 ^{ab}	157.5 ^b	15.1 ^a	47.0 ^b	18.0 ^b	14.2 ^{ab}	6.6 ^a		
IV		0.562 ^b	2.85 ^a	98.9 ^a	16.2 ^a	41.3 ^a	10.8 ^a	11.2 ^a	7.0 ^a		
temperature	1	**	ns	**	**	ns	**	**	**		
14		0.613 ^b	3.00 ^a	99.7 ^a	19.1 ^b	44.1 ^a	11.6 ^a	7.5 ^a	4.3 ^a		
26		0.487 ^a	3.30 ^a	178.2 ^b	11.2 ^a	45.5 ^a	21.0 ^b	19.8 ^b	10.0 ^b		
interaction	6	**	ns	**	ns	**	**	ns	**		
age-treatment interaction	2	ns	ns	**	ns	**	ns	ns	**		
age-temperature interaction	3	**	**	**	ns	ns	ns	**	ns		
treatment-temperature overall interaction	6	ns	ns	**	ns	ns	**	ns	ns		
mean	1	0.550	3.15	139.0	15.3	44.8	16.3	13.6	6.7		
error	24										
total	48										

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^I are conductances for CO₂ (in C = C_c) expressed per plant (m³Pl⁻¹s⁻¹) and per unit leaf area (m s⁻¹); P_{m,n} and P_{m,n}^I: maximum P_n at saturating C expressed per plant (mgCO₂Pl⁻¹h⁻¹) and per unit leaf area (mgCO₂dm⁻²h⁻¹); C_c: CO₂ compensation concentration (mgCO₂m⁻³). Specific leaf weight is expressed in gm⁻². THSD: Tukey's Honest Significant Difference (p < 0.01).

Treatment	Temperatuur (°C)	Results					
		10 ³ τ _n	10 ³ τ _n ^I	P _{m,n}	P _{m,n} ^I	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^I . Temperature affects maximum P_n, resulting in higher values for P_{m,n} and P_{m,n}^I 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^l -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 (NILWIK, 1980a). Moreover, young lettuce plants have a more open structure, which can result in a higher photochemical efficiency as shown by NILWIK (1980a) for sweet pepper plants. Typical sun and shade-effects on α_g^l or α_n^l 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. NILWIK (1980a) observed differences in α_n^l .

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 VAN DE ZWEEERDE (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 Wm^{-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 scm^{-1} , but the applied level of irradiance (14.4 Wm^{-2}) was below saturation for lettuce leaves. The average total conductance on leaf basis (from $P_{m,g}^I$) 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 NILWIK (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; NILWIK, 1980b). The correlation coefficients (r) between τ_n^I 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 I, 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; WITTWER 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^l), the maximal gross and net photosynthesis ($P_{m,g}$ and $P_{m,n}$) per plant and per unit leaf area ($P_{m,g}^l$), 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 ($= I_c \alpha_g$) were analysed. The values of α_g^l and $P_{m,g}^l$ decreased with increasing age. The α_g^l -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

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 CO_2 per plant (τ_n) and per unit leaf area (τ_n^l), the $P_{m,n}$ and $P_{m,n}^l$, and the CO_2 compensation concentration (C_c) were calculated. An increase in measurement temperature decreased τ_n and τ_n^l , 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.

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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.
- 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 CO₂ 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.
- 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.
- 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 C₃ species. - *Ann. Bot.* **38**: 921-930, 1974.

- ... 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 CO_2 exchange of a C_3 plant in relation to light, CO_2 -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 CO_2 -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 CO_2 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 CO_2 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 ZWIERDE, 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 BISCOE, 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. Radiobiologica ed Ecolofisiologia 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*. – Phytotron 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. A8: 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. A9: 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.

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

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 'Decimnor', '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 phytotro 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 Ostinata Hilde	Sept. 19 " "	Oct. 10 " "	Nov. 3-5 " "	22.0/14.7 " "	21.0/13.0 " "
2 G	Amanda Plus Ostinata Hilde	Sept. 19 " "	Oct. 10 " "	Nov. 5-7 " "	22.0/14.7 " "	19.4/14.1 " "
3 G	Amanda Plus Ostinata Hilde	Jan. 12 " "	Febr. 24 " "	March 22-26 " "	15.3/9.6 " "	19.3/14.0 16.3/9.6 "
	Ostinata Hilde	" "	" "	" "	" "	" 16.4/9.6 "
	Decimor Meikoningin Rapide Valentine	" " " "	" " " "	" " " "	" " " "	" " " "
4 G	Cynthia Noran Profos Ravel Tornado Sucrine Plucos C-5 Y-6	Febr. 9 " " " " Febr. 7 Febr. 9 Febr. 7 " May 19	March 17 " " " " " " " " June 7	April 13-22 " " " " " " " " June 23-24	16.1/9.8 " " " " " " " " 23.2/17.0	16.7/ 9.9 16.5/ 9.9 17.7/10.0 16.7/ 9.9 " 17.7/10.0 16.5/ 9.9 16.7/ 9.9 17.7/10.0 26.5/18.3 26.6/18.4 26.5/18.3 20.5/15.1
5 G	Amanda Plus Ostinata Hilde	" " "	" " "	" " "	" " "	" " "
6 O	Amanda Plus Ostinata Hilde	May 19 " "	June 7 " "	June 22-23 " "	23.2/17.0 " "	148.2 " "
		" "	" "	" "	" "	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^l) are inaccurate, since only a part of the leaf area contributes to photosynthesis. The differences between α_g^l are smaller between 'Amanda Plus', 'Ostinata' and 'Hilde'

TABLE 2. Parameters describing the response of net photosynthesis (α_g) 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 (W m^{-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	Decimnor	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
	Y-6	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 $P_{m,n}$, 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 0.76 and the coefficients with r_m were 0.93, 0.86, 0.01 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_g : photochemical efficiencies (mol^{-1}) per plant ($\text{mg CO}_2 \text{ m}^{-2} \text{ Pl}^{-1} \text{ J}^{-1}$) and per unit leaf area ($\text{mg CO}_2 \text{ J}^{-1}$); $P_{m,a} \alpha_g^{-1}$, $P_{m,a} \alpha_g^{-1}$, $P_{n,50} \alpha_g^{-1}$, $P_{n,100} \alpha_g^{-1}$ and $P_{n,150} \alpha_g^{-1}$ (W m^{-2}): net photosynthetic rates at saturated level of irradiance and at respectively 30, 50, 70, 100 and 150 W m^{-2} , expressed on basis of α_g ; $P_{m,a} S^{-1}$: 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 (W m^{-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										
		$10^3 \alpha_g$	$10^3 \alpha_g^{-1}$	$P_{m,a} \alpha_g^{-1}$	$P_{n,30} \alpha_g^{-1}$	$P_{n,50} \alpha_g^{-1}$	$P_{n,70} \alpha_g^{-1}$	$P_{n,100} \alpha_g^{-1}$	$P_{n,150} \alpha_g^{-1}$	$P_{m,a} S^{-1}$	I_c	$10^3 I_c \alpha_g$
a. cultivar												
Amanda Plus	2	ns	**	ns	ns	**	-	ns	ns	ns	ns	ns
Ostinata		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
Hilde		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
experiment	4	0.455 ^a	2.47 ^a	144.7 ^a	12.6 ^a	23.2 ^b	-	42.3 ^a	55.6 ^a	37.7 ^a	10.3 ^a	4.21 ^a
1		**	**	**	**	**		**	**	**	**	**
2		0.714 ^d	2.91 ^c	66.8 ^a	13.9 ^d	21.7 ^a		34.0 ^a	41.0 ^a	26.7 ^a	6.2 ^a	4.43 ^{bc}
3		0.457 ^c	3.84 ^d	63.0 ^a	14.1 ^d	21.9 ^a		33.4 ^a	39.6 ^a	20.7 ^a	5.5 ^a	2.52 ^a
5		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
6		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
interaction	8	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}
cultivar-experiment		**	**	ns	**	ns	-	ns	ns	ns	ns	ns
error	45											
mean	1	0.439	2.73	137.8	12.5	22.9	-	41.9	55.1	42.8	10.5	4.09
total	60											
b. cultivar												
Amanda plus	6	**	**	**	-	ns	-	-	-	ns	ns	ns
Ostinata		0.406 ^{ab}	2.92 ^b	137.0 ^a	27.1 ^a	27.1 ^a				42.1 ^a	10.7 ^{ab}	4.35 ^a
Hilde		0.339 ^a	2.82 ^b	170.0 ^{bc}	28.9 ^b	28.9 ^b				47.0 ^a	10.7 ^{ab}	3.65 ^a
Decimor		0.436 ^b	2.93 ^b	147.1 ^{abc}	27.9 ^{ab}	27.9 ^{ab}				44.6 ^a	10.7 ^{ab}	4.65 ^a
Meikoningin		0.377 ^{ab}	2.63 ^b	145.2 ^{ab}	28.0 ^{ab}	28.0 ^{ab}				45.8 ^a	10.4 ^b	3.92 ^a
Rapide		0.335 ^a	2.74 ^b	179.6 ^c	28.4 ^{ab}	28.4 ^{ab}				53.3 ^a	12.3 ^b	4.14 ^a
		0.406 ^{ab}	2.56 ^{ab}	136.6 ^a	27.6 ^{ab}	27.6 ^{ab}				44.3 ^a	10.1 ^a	4.10 ^a

Valentine	0.33d ^a	2.10 ^a	150.8 ^{abc}	26.7 ^a	44.3 ^a	12.4 ^b	4.14 ^a
error	21						
mean	1	0.376	2.67	27.8	45.9	11.0	4.14
total	28						
c. cultivar	8	**	**	-	ns	**	**
Cynthia		0.616 ^{cd}	2.12 ^{ab}			12.8 ^a	7.89 ^{abc}
Noran		0.585 ^{bcd}	2.16 ^{ab}	38.2 ^a	51.3 ^{ab}	12.9 ^{ab}	7.55 ^{abc}
Profos		0.403 ^a	1.73 ^a	38.6 ^a	52.5 ^b	13.8 ^{abc}	5.56 ^a
Ravel		0.610 ^{bcd}	2.13 ^{ab}	39.4 ^a	52.2 ^{ab}	15.1 ^{abcd}	9.21 ^c
Tornado		0.813 ^c	3.38 ^c	39.2 ^a	55.1 ^b	11.6 ^a	9.43 ^c
Sucrine		0.358 ^a	1.94 ^{ab}	38.3 ^a	54.5 ^b	17.8 ^d	6.37 ^{ab}
Plucos		0.732 ^{de}	3.07 ^c	40.0 ^b	52.5 ^{ab}	13.0 ^{ab}	9.55 ^c
C-5		0.494 ^{abc}	2.32 ^b	38.1 ^a	37.2 ^a	16.6 ^{bcd}	8.20 ^{bc}
Y-6		0.444 ^{ab}	2.08 ^{ab}	39.3 ^a	59.0 ^b	17.4 ^{cd}	7.73 ^{abc}
error	27						
mean	1	0.561	2.33	38.9	52.5	14.5	7.94
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 (BJÖRKMAN 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 .

CO₂-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 α_g , α_g^1 , P_n at 30, 50, 100 and 150 Wm⁻² and at saturating level, expressed on basis of α_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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- 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 Sommergerste. - 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.
- BJÖRKMAN, 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.
- DORNHOF, 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. – *Zaadbelen* 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 ZWEEDE, 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).

- 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.

Summary

Butterhead lettuce is an important glass-house crop in the poor light period in The Netherlands. Fundamental data about the influence of temperature, light and CO_2 on growth and photosynthesis are important e.g. to facilitate selection criteria for new cultivars. In this study on lettuce emphasis has been given to light interception in the poor light period, the relationship of growth rate and relative growth rate with time, dry weight and soil cover, and to photosynthesis properties of the cultivar 'Amanda Plus' and other cultivars.

The soil area which is covered by a lettuce plant determines to a certain extent the light interception and growth of a plant. Therefore, the process of soil covering was studied in two experiments, the first one in spring with 8 cultivars and the second one in autumn with lettuce cultivars and one endive cultivar (*chapter 2*). The cultivar 'Amanda Plus' was used in both experiments. Three plant densities (10 cm x 20 cm; 25 cm x 25 cm; 35 cm x 35 cm) and 3 day/night temperatures were applied. The soil cover was determined according to the dot counting method. The process of soil covering related with time was described by a four parameter sigmoid curve with the parameters t (time in days from planting), S (amount of soil cover at time t), S_{\max} (maximal covered area) and p (the position of the inflexion point, S_1) of the curve). Derived parameters are r (the initial soil cover rate), $L_1 (= S_1/S_{\max})$ and R_1 (the soil cover rate in the inflexion point). W_{\max} is the fresh weight of the head at t_{\max} (time from transplanting until no visible increase in soil cover occurred), and W_{end} the fresh weight at the end of the experiment.

Sigmoid curves fitted from the obtained data were all asymmetrical. Problems with curve-fitting occurred for the data of the treatments

with long growing periods (low temperatures, 35 cm x 35 cm spacing). The data of the endive cultivar also could be fitted according to the similar sigmoid curve. The standard errors for the parameters r and p were high and these parameters were less useful for further analysis. At higher temperatures t_{\max} is lower. Mutual shading shortens the period until t_1 . At lower temperatures t_1 became higher. Wider spacing resulted in higher t_1 - and S_1 -values. The soil covering process of 'Amanda Plus' is more rapid in autumn than in spring. For the 35 cm x 35 cm plant density S_{\max} tended to decrease at lower temperatures. For the other two densities the maximum available soil cover was reached almost all treatments. When t_{\max} is low and the growth period is short or the plant density high, L_1 becomes high. Differences between the parameters of the S-curves of the cultivars existed in spring as well as in autumn.

A favourable combination between some parameters e.g. low t_1 with high S_1 , or high r with high L_1 , is present for some treatments and cultivars; but no cultivar showed the optimal combination of all parameters (high r , high L_1 , low t_1 combined with a high S_1 , high R_1 and low t_{\max}) for a fast soil covering process. The correlations of some of the soil cover parameters (t_1 , L_1 or W_{\max}) with W_{end} were low, especially of L_1 with W_{end} , and of t_1 with W_{end} for a number of cultivars in spring. The low correlation was partly due to the late harvest dates in the experiments. High correlations, however, are not to be expected and indirect selection of a high W_{end} based on parameters of the soil cover curve is doubtful.

In chapter 3 a quantitative growth analysis for the butterhead cultivar 'Noran' grown in spring and 'Deciso' in autumn has been described. The plants were cultivated at similar day/night temperatures and plant densities as those described in chapter 2. For the quantitative analysis a good fit of the growth curves is essential. Polynomials between the third and ninth degree were needed for an adequate description of dry weight (W) and leaf area (A) versus time (t). The

ing growth period and the partly controlled conditions of the glass-
house complicated a good fit of some data.

The growth rate ($GR = dW/dt$), being the derivative of the polynomial of dry weight with time, was also used for the calculation of other parameters. The relative growth rate ($RGR = dW/dt \cdot 1/W$) decreases with time as well as with an increase in dry weight for all treatments presented. Plants grown at wider spacings have a higher RGR than plants at narrow spacings.

Attention was paid to the relationship of GR with soil cover. These S-curves indicate the growth stage during which mutual and self shading occur and heading becomes visible. When head formation occurs (between 2 and 5 gram dry weight) GR reaches a maximum value and starts to decrease. Plants at 35 cm x 35 cm have higher maximal growth rates, whereas the decrease of GR starts at a higher dry weight. The relationship between GR and S for the growth period until 80% of S_{max} is almost linear. After this period the rise of GR is larger and then followed by a decline of GR at maximal or increasing S. Except one situation, the linear relation of GR with S gave higher correlation coefficients than those with A and W. Multilinear regression showed that mainly S is related to the increase of GR over that period until 80% of S_{max} .

The plants grown at lower temperatures in spring had a lower GR. They reached a certain soil cover at a later date in this season than plants grown at higher temperatures, which resulted in a higher interception of irradiance and/or better use of the intercepted irradiance. In the autumn experiment the plants grown at higher temperatures intercepted more irradiance than those grown at lower temperatures, because a high S was reached earlier during that period with a high level of irradiance and a longer day-length (Fig. 6). The growth rates of the plants of the narrow spacings were lower than those of the plants of wider spacings. The relationship between accumulated dry weight, total irradiance, intercepted per plant after correction for the sward area, is almost linear.

The relationship between leaf area ratio ($LAR = A/W$) and heading

has also been studied. When LAR is lower than 500 cm g² resp. 710 cm g⁻¹ for 'Noran' and 'Deciso' the quality of the head is good.

Since equipment for photosynthesis measurements and determination of CO₂ compensation concentrations was not available at the Department of Horticulture of the Agricultural University of Wageningen, a closed system was built suitable for whole plants of lettuce and of other crops (sweet pepper, tomato). The system is described in *chapter 4*. The internal gaseous volume of the closed circuit as used for the lettuce measurements is 180 litres. The circuit consists of a cylindrical perspex plant chamber, a copper duct with a built-in fan, cooling and air-heating elements and connecting flexible tubes. The internal diameter of the chamber is 441 mm and the height is 340 mm, which can be enlarged to 690 mm. A cylindrical perspex pot chamber which has an internal diameter of 190 mm and a height of 190 mm is placed in the plant chamber.

The equipment is placed on a metal trolley in a room, in which temperature can be regulated between 10 and 34°C ± 1°C. The temperature in the plant chamber can be kept constant between 5 and 32°C ± 0.5°C and in the pot chamber between 15 and 35°C ± 0.5°C. Temperatures are measured by thermocouples. The light equipment consists of 5 Philips high mercury vapour lamps (400 W) arranged above a waterbath with running water, which is constructed above the plant chamber. The maximum irradiance on plant level is 215 W m⁻². Irradiance is measured by selenium photocells and the air humidity with thin film humidity sensors. Windspeed in the centre of the plant chamber is about 0.8 ms⁻¹. An infra-red gas-analyser determines the rate of CO₂ exchange. Injection of pure CO₂ or a mixture of air with CO₂ admits continuous monitoring of this exchange. During the relatively short periods of measurements leakage can be neglected. All measurements are recorded by a 24 channel mV-recorder or a data logger.

Photosynthesis rates of whole lettuce shoots of butterhead

tivar 'Amanda Plus' were measured with this closed system (chapter
 In a first experiment the response of photosynthesis (P) to
 adiance (I) was measured for plants of 3 different ages at 14°C
 26°C and in the second experiment the response to CO₂-concentration
 was measured at 15°C and 25°C, and the CO₂ compensation concen-
 tion was determined. In both experiments plants were cultivated
 2 different levels of irradiance and 2 different day/night tempera-
 es.

The photosynthesis data per plant were fitted with the use of a
 tangular hyperbola, which related photosynthesis to both irradiance
 and CO₂-concentration (C), in which α represents the initial slope
 the P-I-curve, i.e. the photochemical efficiency, and τ the initial
 e of the P-C-curve, i.e. the plant conductance for CO₂ transfer.
 carboxylation efficiency is included in this conductance. In the
 it series τ determines to a great extent the gross maximal photo-
 thesis ($P_{m,g} = \tau C$).

Attention was paid to the basis of expression for the photosyn-
 tic rates, obtained per plant. Since those rates expressed per unit
 area, weight (or soil cover) were not adequate for comparison
 other results, another basis, the effective leaf area (EL) was
 oduced. $EL = \alpha_g \alpha_{g,con}^{-1} (m^2 Pl^{-1})$, with α_g as the gross photochemical
 .ciency per plant and $\alpha_{g,con}$ as the constant value of α_g when all
 it quanta should be absorbed. For the calculations of the photo-
 thesis rates on EL-basis only α_g -values have been used.

A multilinear regression model of α_g with S, A and W (in this
 or) gave high correlation coefficients, while addition of the
 ght of the plant, as included in the profile area, did not improve
 model significantly. The linear relation of α_g with the covered
 by the plant gave higher correlation coefficients than of α_g
 leaf area or weight, except for the group of younger plants.

In experiment 1 the gross photochemical efficiency per plant
 and per unit leaf area (α_g^1), the maximal gross photosynthesis
 plant ($P_{m,g}$) and per unit leaf area ($P_{m,g}^1$), the dark respiration

per unit dry weight (α_g) and the light compensation point (I_c) were calculated and listed. The values of α_g and α_g^1 , the net photosynthetic rates at 35 and 100 Wm^{-2} and at saturated level of irradiance, expressed on the basis of α_g , the $P_{m,g}^1$, I_c and the corrected light compensation point ($I_{c\alpha}$) were used in a 3 way analysis of variance.

The values of α_g^1 and $P_{m,g}^1$ decreased with ageing, but α_g^1 was also not affected by the temperatures of the treatment and of the measurement. The net photosynthetic rates on α_g -basis gave lower values for the group of young plants and similar values for the other age-groups. At a low irradiance level (35 Wm^{-2}) the effect of the various cultivation treatments on net photosynthesis diminished, but at 100 Wm^{-2} the influence of the treatments on net photosynthesis increased, and this influence became much more distinct on the maximal net photosynthetic rates. At 35 Wm^{-2} the net photosynthesis on α_g -basis is higher at 14°C than at 26°C. At saturated level of irradiance the opposite situation occurred while at 100 Wm^{-2} this difference is absent. The light compensation point is strongly influenced by temperature during measurements and much less by treatment and age. The corrected I_c was affected by age and measurement temperature and not by cultivation. The correlation coefficients (r) between specific leaf weight (SLW = W/A), as an average of the leaf area and leaf weight of the plant, and $P_{m,n}$ on α_g -basis at 14°C is 0. and at 26°C 0.55.

In experiment 2 the net conductance for CO_2 transfer per plant (τ_n) and per unit leaf area (τ_n^1), the maximal net photosynthesis per plant and per unit leaf area ($P_{m,n}$ and $P_{m,n}^1$) and the CO_2 compensation concentration (C_c) were calculated. The values of τ_n and τ_n^1 decreased and the $P_{m,n}$ increased with a rise in measurement temperature. C_c is strongly influenced by temperature during measurement but not by temperature during cultivation.

The use of the rectangular hyperbola and of α and τ was discussed in relation with the light interception and CO_2 transport of whole lettuce shoots. It was suggested that the boundary air layer resistance for CO_2 transport of the whole plant, which is considered to be low for

t plants or crops in optimal conditions, can play a more important role for plants with a dense leaf orientation, such as lettuce. The use of α_g as basis of expression did not completely solve the interpretation problems of photosynthesis data obtained per plant.

In chapter 6 six experiments have been described in which the response of photosynthesis to irradiance of whole lettuce shoots of various cultivars was measured in an open system at 22°C. The butterhead lettuce cultivars 'Amanda Plus', 'Ostinata' and 'Hilde' were cultivated in 3 experiments (nrs. 2, 3, 5) in the glass-house, one in the phytotron (nr. 1) and one outdoor (nr. 6). Besides those 3 cultivars 4 other butterhead cultivars were used in the first spring experiment (nr. 3). Five butterhead, 2 cos- and 2 iceberg cultivars were used in the second spring experiment (nr. 4).

According to a similar procedure as described in chapter 5 the gross photochemical efficiency per plant (α_g) and per unit leaf area (α_g^1), the maximal net photosynthetic rates per plant ($P_{m,n}$) and per unit leaf area ($P_{m,n}^1$), the dark respiration per unit dry weight (R_d) and the light compensation point (I_c) were calculated. The SLW, stomatal (r_g) and residual (r_m) resistances were also calculated. The values were used as basis of expression for photosynthetic rates according to the theory outlined in chapter 5. A multilinear regression of α_g with S, A and W was carried out and the best fit of α_g was obtained with S.

In a two way analysis of variance α_g , α_g^1 , the net photosynthetic rates at 30, 50, 100 and 150 Wm^{-2} and at saturated level of irradiance (I_{sat}) on basis of α_g , the $P_{m,n}$ per unit S, the I_c and corrected I_c ($I_{c,corr}$) were analysed for the 3 cultivars in the 5 experiments. For the results of experiments 3 and 4 a one way analysis of variance for the parameters except the net photosynthetic rates at 30, 100 and 150 Wm^{-2} was carried out. For 'Amanda Plus', 'Ostinata' and 'Hilde' 'Hilde' is more influenced by treatment (thus experiments 1, 2, 3, 5 and 6) than by cultivar. The α_g^1 of 'Hilde' differs from those of 'Amanda Plus'

and *Ostinata*. A lower irradiance during growth resulted in a high α_g and α_g^1 . In experiments 3 and 4 varietal differences for α_g^1 appeared to be higher. $P_{m,n}$ increased after a higher irradiance during growth. Differences between the values of P_n (and also other parameters involved in photosynthesis) increased when differences between the cultivars regarding habitus, growth and genetical background were more pronounced (exp. 4). Results of the analysis of variance of $P_{m,n}$ per unit soil cover were identical to those of $P_{m,n}$ per unit α_g for 'Amanda Plus', 'Ostinata' and 'Hilde'. When the photosynthesis measurements are carried out at a level of irradiance close to that during growth, no significant differences between the photosynthetic rates of the cultivars on α_g -basis occur (exp. 3 and 4).

For butterhead lettuce the influence of cultivar on the light compensation point is less pronounced than that of treatment. In two experiments the r_m of 'Hilde' was larger than those of 'Amanda Plus' and 'Ostinata'. In the two spring experiments different r_m -values between the cultivars were also present. A period of low irradiance resulted in a high r_m for the plant. Differences between the r_s -values existed only in experiments 3 and 4. The correlation coefficient (r) between the total plant resistance for CO_2 transfer ($1/\tau_n^1$) and $r_s + r_m$ for all data is 0.81.

For butterhead cultivars the specific leaf weight is more influenced by cultivation conditions than by genetic differences. However, significant differences between cultivars existed. A high negative correlation existed between SLW and r_m , when the differences were caused by the various cultivation conditions. The two cos-lettuce cultivars, one selected for glass-house cultivation and one for outdoor growing, gave different results, while the two iceberg genotypes, both selected as glass-house crops, always gave similar results. The used cos- and iceberg lettuce cultivars were less adapted for growth during the winter season in The Netherlands.

No clear criteria for indirect selection on higher yield have been found between the parameters, which describe the photosynthetic

process. Success with indirect selection on higher yield based on parameters of the soil cover curve was also expected to be doubtful. When photosynthesis will be measured at irradiance and temperature conditions close to that during growth, no differences between the photosynthetic rates on a _g-basis of the various genotypes can be expected. It is felt desirable that more research is carried out on the morphology of the lettuce plant in relation to growth, light interception and CO₂ transport and diffusion from the external air to the carboxylation sites. The introduction and use of non-heading cultivars would make the study of lettuce easier and facilitate cultivation of lettuce during the poor light period.

Kropsla is één van de belangrijkste kasgroenten die in de lichtarme periode in Nederland worden geteeld. Het verkrijgen van fundamentele gegevens over de invloed van de temperatuur, de lichtintensiteit en het koolzuurgehalte op de groei en fotosynthese van sla is belangrijk om bijvoorbeeld gemakkelijker tot goede selectiecriteria voor nieuwe rassen te komen. In dit onderzoek is de nadruk gelegd op de lichtopvang door individuele slaplanten in de lichtarme periode, en op de relatie van de groeisnelheid en van de relatieve groeisnelheid met de tijd, het drooggewicht en de door de plant bedekte hoeveelheid grond. Daarnaast is van het kropslaras Amanda Plus en enkele andere slarassen een aantal fotosynthesekarakteristieken bepaald.

Omdat de door de plant bedekte grond mede de lichtopvang en groei bepaalt, werd in twee proeven het proces van de grondbedekking bekeken. De eerste proef werd uitgevoerd in het voorjaar met 8 slarassen en de tweede in het najaar met 5 slarassen en één andijvieras (*hoofdstuk 2*). Amanda Plus werd geplant in beide proeven. De slaplanten werden uitgeplant op 3 plantafstanden (20 cm x 20 cm; 25 cm x 25 cm; 35 cm x 35 cm) en geteeld bij 3 combinaties van dag- en nachttemperaturen.

De bedekte hoeveelheid grond werd bepaald volgens een methode waarbij puntjes op een raster werden geteld. Elk puntje kwam overeen met een bepaald aantal cm^2 . De relatie tussen de bedekte grond en de tijd werd beschreven met een sigmoïde curve met 4 variabelen. Deze zijn: de tijd t in aantal dagen vanaf uitplanten; de bedekte grond S op tijdstip t ; de maximale hoeveelheid bedekte grond S_{max} ; en de positie van het buigpunt (t_1, S_1) welke weergegeven wordt met de variabele p . Andere, afgeleide parameters zijn de aanvangsgrondbedekkingsnelheid r ; de variabele $L_1 (= S_1/S_{\text{max}})$ en de grondbedekkingsnelheid R_1 in het buig-

punt van de curve. W_{\max} is het versgewicht van de krop op het tijdstip waarop er geen zichtbare toename van de grondbedekking meer plaats vindt (t_{\max}). W_{end} is het versgewicht van de krop aan het einde van de proef.

Alle berekende sigmoïde curves voor de grondbedekking waren asymmetrisch. Voor de curves van de planten met een lange teeltduur ontstonden enige berekeningsproblemen. De gegevens van de grondbedekking van het andijvieras konden verwerkt worden met gebruik van dezelfde sigmoïde curve als bij de sla. Omdat de standaardafwijkingen van r en p in de meeste gevallen hoog waren, bleken deze parameters minder bruikbaar voor een uitgebreide analyse. Bij hogere temperaturen wordt het buigpunt eerder bereikt (t_i korter), evenals het tijdstip t_{\max} . Ook onderlinge beschaduwning vervroegt het afbuigen van de curve. Bij lagere temperaturen wordt t_i langer. Bij ruimere plantafstanden zijn de waarden van t_i en S_i hoger. Het grondbedekkingsproces van Amanda Plus verloopt sneller in het najaar dan in het voorjaar.

S_{\max} leek voor planten van de ruimste plantafstand af te nemen met lagere temperaturen. Bij de twee nauwere plantafstanden werd de maximale hoeveelheid beschikbare grond (400 en 625 cm^2) voor bijna alle behandelingen bereikt. De L_i is hoog als de periode tot t_{\max} of de teeltduur kort is of als de planten nauw geplant worden.

Rasverschillen voor de diverse parameters van de sigmoïde bedekkingscurven kwamen zowel in het voor- als het najaar voor. Een gunstige combinatie van enige van deze parameters, bijvoorbeeld een korte t_i met een hoge S_i of een hoge r met een hoge L_i , kwam voor bij enkele rassen en behandelingen. De optimale combinatie van alle parameters, dwz. een hoge r , hoge L_i , korte t_i samen met een hoge S_i , hoge R_i en een korte t_{\max} , werd echter bij geen enkel ras gevonden. De correlaties van t_i , L_i en W_{\max} met W_{end} waren laag, vooral tussen L_i en W_{end} en, bij een aantal rassen in het voorjaar, tussen t_i en W_{end} . Deze lage correlaties waren deels te wijten aan de late oogsttijdstippen in de beide proeven. Hoge correlaties zijn echter in andere gevallen ook niet altijd te verwachten. Succes van indirecte

selectie op een hoog eindgewicht via parameters van de grondbedekkingscurve is daarom twijfelachtig.

In *hoofdstuk 3* is de kwantitatieve groeianalyse van het kropslaras Noran, dat in het voorjaar werd geteeld, en Deciso, geteeld in het najaar, beschreven. De dag- en nachttemperaturen en plantafstanden zijn gelijk aan die gegeven in hoofdstuk 2. Een goede berekening van de groeicurven is van wezenlijk belang voor de kwantitatieve groeianalyse. Gebruik van polynomen van de derde tot en met de negende graad was daarom nodig om de juiste relatie te beschrijven tussen het drooggewicht (W) en het bladoppervlak (A) van de plant met de tijd (t). De lange teeltduur en het slechts gedeeltelijk te beheersen kasklimaat werkten een hoge graad van de polynomen in de hand.

De groeisnelheid ($GR = dW/dt$) is de afgeleide van de polynome groeicurve van het drooggewicht met de tijd. Deze groeisnelheid werd tevens gebruikt bij de berekening van andere parameters die de groei beschrijven, zoals de relatieve groeisnelheid ($RGR = dW/dt \cdot 1/W$). Deze RGR neemt zowel in de tijd als met een toename van het drooggewicht van de krop af bij planten van elke behandeling. Bij een ruimere plantafstand hebben planten een gemiddeld grotere RGR dan bij een nauwere plantafstand.

Aandacht werd besteed aan de relatie tussen de groeisnelheid GR en de bedekte grond S . Deze $GR-S$ -grafiek geeft namelijk het groeistadium aan waarin beschaduwing binnen de plant of beschaduwing door buurplanten optreedt en het proces van kropvorming zichtbaar wordt. De groeisnelheid bereikt een maximum waarde tijdens het kropvormingsproces (tussen 2 en 5 gram drooggewicht) en neemt daarna weer af. Sla, geplant op 35 cm, bereikt een grotere maximale groeisnelheid dan nauw geplante sla en de afname van de GR begint bij de ruim geplante sla bij een hoger drooggewicht. Er bestaat een bijna lineaire relatie tussen GR en S tijdens de periode vanaf het uitplanten tot het tijdstip waarop 80% van S_{max} is bereikt. Na deze periode is de

toename van GR eerst groter geworden en daarna begint GR af te nemen bij een nog toenemende of reeds maximale S. Op één geval na waren de correlatiecoëfficiënten van GR met S hoger dan van GR met W of A. Een multilineaire regressie van GR met S, A en W liet zien dat de toename van GR in de periode vanaf uitplanten tot 80% van S_{max} hoofdzakelijk gerelateerd is aan S.

In het voorjaar hadden de planten bij de lagere temperaturen een kleinere GR en zij bereikten een bepaalde grondbedekking later dan de planten bij hogere temperaturen. Dit resulteerde in een hogere lichtopvang bij een bepaalde bereikte S en/of in een beter gebruik van de opgevangen straling. In de najaarsproef daarentegen kregen de planten die geteeld werden bij hogere temperaturen meer licht dan de planten van de lagere temperaturen, omdat een hoge S juist vroeg in het najaar, wanneer de daglengte nog langer en het stralingsniveau nog hoger is dan later in het seizoen, werd bereikt (fig. 6). De groeisnelheid per plant van de nauw geplante sla was kleiner dan die van de ruim geplante sla. De relatie tussen het totale drooggewicht van de krop en de totale hoeveelheid opgevangen straling door de plant, berekend op basis van het bedekt grondoppervlak, is bijna lineair. De relatie bladoppervlak/gewicht van de plant ($LAR = A/W$) en de kropvorming is eveneens bestudeerd. Een goede kwaliteit slakrop kan voor Noran verkregen worden wanneer de LAR kleiner is dan $550 \text{ cm}^2 \text{ g}^{-1}$ en voor Deciso wanneer de LAR kleiner is dan $710 \text{ cm}^2 \text{ g}^{-1}$.

Omdat er geen apparatuur voor fotosynthesemetingen en het bepalen van het CO_2 compensatiepunt beschikbaar was op de vakgroep Tuinbouwplantenteelt van de Landbouwhogeschool in Wageningen, werd er een zogenaamd 'gesloten systeem' gebouwd dat geschikt is voor fotosynthesemetingen aan intacte planten van sla en van andere gewassen, zoals paprika en tomaat. Dit gesloten systeem is beschreven in *hoofdstuk 4*. De inhoud van het gesloten circuit is 180 liter. Dit circuit bestaat uit een cilindervormige plantkamer van perspex, een koperen kanaal waar een ventilator en de koelings- en verwarmingselementen zijn inge-

nenzijde van de plantkamer is 441 mm en de hoogte is 340 mm, welke verhoogd kan worden tot 690 mm. Een cilindervormige potkamer van perspex (diameter 190 mm en hoogte 190 mm) is in de plantkamer geplaatst.

De apparatuur staat gemonteerd op een metalen wagentje en is in een aparte ruimte gezet, waar de temperatuur tussen de 10 en 34°C (+ 1°C) geregeld kan worden. De temperatuur in de plantkamer kan konstant gehouden worden tussen 5 en 32°C (+ 0,5°C) en die in de potkamer tussen 15 en 35°C (+ 0,5°C). De temperatuur wordt gemeten met thermokoppels. De lichtbron wordt gevormd door 5 Philips hogedrukkwiklampen (400 W) die boven een boven de plantkamer gebouwd waterbad met stromend water hangen. De maximale lichtintensiteit op plantniveau is 215 Wm⁻². De lichtintensiteit wordt gemeten met behulp van selenium fotocellen. De luchtvochtigheid wordt gemeten met Vaisalavoelers. De gemeten windsnelheid in het midden van de plantkamer is ongeveer 0,8 ms⁻¹. Met een infrarood-gasanalysator wordt de CO₂-uitwisseling gemeten. Injectie met zuivere CO₂ of een mengsel van lucht en CO₂ maakt continue registratie van de CO₂ concentratie mogelijk. Gedurende de betreffende korte meetperioden kan de lekkage van CO₂ in of uit het systeem verwaarloosd worden. Alle metingen worden geregistreerd met een 24 punts mV-recorder of een datalogger.

De fotosynthesesnelheden van intacte slapplanten van het kropsalaras Amada Plus werden gemeten in dit gesloten systeem (hoofdstuk 5). De respons van de fotosynthesesnelheid (P) op de lichtintensiteit (I) werd in een eerste proef gemeten bij 14°C en 26°C bij planten van 3 verschillende leeftijden. In een tweede proef werd de respons van P op de CO₂ concentratie (C) gemeten en tevens het CO₂ compensatiepunt bepaald bij 15°C en 25°C. Zowel in de eerste als de tweede fotosyntheseproef werden de planten opgekweekt bij twee lichtintensiteiten twee combinaties van dag- en nachttemperaturen.

De relatie van de fotosynthesesnelheid P met zowel de lichtintensiteit I als de CO₂ concentratie C werd beschreven met een recht-

hoekige hyperbool. In de formule van deze hyperbool is α de helling in het beginpunt van de P-I-curve, d.w.z. de fotochemische efficiëntie, en τ is de helling in het beginpunt van de P-C-curve, d.w.z. het geleidingsvermogen van de plant voor het CO_2 -transport. De carboxylatie-efficiëntie behoort eveneens tot τ . In de fotosynthese-lichtseries bepaalt τ in grote mate de maximale bruto fotosynthesesnelheid ($P_{m,g} = \tau C$).

Aan de manier waarop de fotosynthesesnelheid, gemeten per plant, wordt uitgedrukt is speciale aandacht besteed, omdat de fotosynthesesnelheden uitgedrukt per eenheid bladoppervlak, gewicht (of, in mindere mate, bedekte grond) niet nauwkeurig genoeg waren om met andere resultaten te vergelijken. Daarom is een andere basis, het effectieve bladoppervlak (EL), geïntroduceerd. $EL = \alpha_g \cdot \alpha_{g,con}^{-1} (m^2 Pl^{-1})$, waarin α_g de bruto fotochemische efficiëntie per plant is en $\alpha_{g,con}$ de konstante waarde van α_g in het geval dat alle lichtquanta zouden worden opgenomen door de plant. Bij de berekeningen van de fotosynthesesnelheden op EL-basis is voor EL niet $\alpha_g \alpha_{g,con}^{-1}$ gebruikt, maar alléén α_g omdat de $\alpha_{g,con}$ een constante waarde heeft.

Multilineaire regressie van de bruto fotochemische efficiëntie met de bedekte grond, het bladoppervlak en het drooggewicht (in deze volgorde) gaf hoge correlaties tussen α_g en deze drie plantkarakteristieken. Uitgezonderd voor de jongste planten waren de correlatiecoëfficiënten van α_g met de bedekte grond hoger dan van α_g met het bladoppervlak of het gewicht. De toevoeging van de factor hoogte van de plant, zoals verwerkt in het profieloppervlak, gaf géén significant betere multilineaire regressie.

De bruto fotochemische efficiëntie per plant (α_g) en per eenheid bladoppervlak (α_g^1), de maximale bruto fotosynthese per plant ($P_{m,g}$) en per eenheid bladoppervlak ($P_{m,g}^1$), de donkerademhaling per eenheid drooggewicht (R_d) en het lichtcompensatiepunt (I_c) van de planten in de eerste fotosyntheseproef werden berekend en in een tabel weergegeven. Bovendien werden voor een variantieanalyse met een indeling in drie klassen de gegevens van bovengenoemde α_g en α_g^1 , de netto foto-

... op basis van α_g), de $P_{m,g}^1$, I_c en het gecorrigeerde lichtcompensatiepunt ($I_{c,g}$) gebruikt.

De waarden van α_g^1 en $P_{m,g}^1$ nemen af met een toename van de plantleeftijd. De α_g^1 werd bijna niet beïnvloed door de temperatuur tijdens de voorbehandeling of de meting. De netto fotosynthesesnelheden op α_g -basis waren het laagst bij de groep met de jongste planten, terwijl de planten van de twee andere groepen dezelfde netto fotosynthesesnelheden hadden. Bij lage lichtintensiteiten (35 Wm^{-2}) verdween het effect van de verschillende opkweekbehandelingen op de netto fotosynthese. De invloed van de behandelingen nam weer toe bij 100 Wm^{-2} en werd nog duidelijker zichtbaar bij de maximum netto fotosynthese. Bij 35 Wm^{-2} is de netto fotosynthese op α_g -basis hoger bij de metingen 14° dan bij die van 26°C . Bij 100 Wm^{-2} waren er geen verschillen meer waarneembaar, terwijl bij lichtverzadiging de netto fotosynthese op de α_g -basis juist hoger is bij 26°C in vergelijking met de metingen bij 14°C . Het lichtcompensatiepunt wordt in sterke mate beïnvloed door de temperatuur tijdens de fotosynthesemetingen en veel minder sterk door de temperatuur tijdens opkweek of de leeftijd. Het gecorrigeerde lichtcompensatiepunt is afhankelijk van de leeftijd van de plant en de temperatuur tijdens de meting, maar niet van de opkweek. De correlatiecoëfficiënt van het specifiek bladgewicht ($\text{SLW} = W/A$), gebaseerd op W en A van alle bladeren van de plant, met de maximale netto fotosynthese op α_g -basis is 0,73 bij de metingen van 14°C en 0,55 bij 26°C .

In de tweede fotosyntheseproef werden het netto geleidingsvermogen voor het CO_2 transport per plant (τ_n) en per eenheid bladoppervlak (τ_n^1), de maximum netto fotosynthese per plant en per eenheid bladoppervlak ($P_{m,n}$ en $P_{m,n}^1$) en het CO_2 compensatiepunt (C_c) berekend. De waarden van τ_n en τ_n^1 namen af en die van $P_{m,n}$ namen toe bij een stijging van de meettemperatuur. C_c wordt sterk beïnvloed door de temperatuur tijdens de meting, maar niet door de temperatuur tijdens opkweek.

De toepassing van de rechthoekige hyperbool en het gebruik van α en τ is besproken in betrekking tot de lichtopvang van de plant en het

CO₂ transport in de slapplanten. De suggestie werd gedaan dat de grenslaagweerstand van de plant voor het CO₂ transport, welke weerstand bij de bladeren van de meeste planten en gewassen onder optimale omstandigheden als laag gezien wordt, een belangrijker rol kan spelen bij planten met een dichte opeenhoping van bladeren, zoals bij slapplanten. Het gebruik van de bruto fotochemische efficiëntie α_g als basis waarop de fotosynthesesnelheden worden uitgedrukt loste niet volledig de problemen op die er bestaan omtrent de interpretatie van fotosynthesegegevens die per plant verkregen zijn.

In hoofdstuk 6 zijn zes proeven beschreven waarin de respons van de fotosynthese op de lichtintensiteit bij slapplanten van diverse rassen werd gemeten bij 22°C in een 'open systeem'. In drie proeven (nrs. 2, 3 en 5) werden de kropslarassen Amanda Plus, Ostinata en Hilde opgekweekt in de kas, in één proef (nr. 1) in het fytotron en in een laatste in de vollegrond (nr. 6). In een eerste voorjaarsproef (nr. 3) werden behalve deze drie rassen nog vier kropslarassen opgekweekt. In de tweede voorjaarsproef (nr. 4) werden 5 kropslarassen, twee bindslarassen en twee ijsslaselecties gebruikt.

De bruto fotochemische efficiëntie per plant (α_g) en per eenheid bladoppervlak (α_g^1), de maximale netto fotosynthese per plant ($P_{m,n}$) en per eenheid bladoppervlak ($P_{m,n}^1$), de donkerademhaling per eenheid drooggewicht (R_d) en het lichtcompensatiepunt (I_c) werden op dezelfde wijze berekend als in hoofdstuk 5. De SLW, de huidmondjesweerstand (r_s) en de restweerstand (r_m , mesofylweerstand) werden eveneens berekend. Ook bij deze proeven werden de fotosynthesesnelheden uitgedrukt op basis van α_g .

De multilinaire regressie van de bruto fotochemische efficiëntie met de bedekte grond, het bladoppervlak en het drooggewicht gaf hoge correlatiecoëfficiënten tussen α_g en de drie plantkarakteristieken, waarbij die van α_g met de bedekte grond de hoogste waren.

In een variantieanalyse met een indeling in twee klassen werden de α_g , α_g^1 , de netto fotosynthesesnelheden bij 30, 50, 100 en 150 Wm⁻²

en bij lichtverzadiging, alle op basis van α_g , de $r_{m,n}$ per eenheid α_g , het lichtcompensatiepunt en het gecorrigeerde lichtcompensatiepunt ($I_c \alpha_g$) van Amanda Plus, Ostinata en Hilde in de 5 proeven nader bestudeerd. Met de resultaten van de proeven 3 en 4 werden variantieanalyses met een indeling in één klasse uitgevoerd. Dezelfde parameters als in de andere analyses werden daarbij gebruikt, behalve de netto fotosynthesesnelheden bij 30, 100 en 150 Wm^{-2} .

De α_g^1 van Amanda Plus, Ostinata en Hilde wordt in grotere mate beïnvloed door de voorbehandeling (dus door de proefomstandigheden van de proeven 1, 2, 3, 5 en 6) dan door het gebruikte ras. De α_g^1 van Hilde verschilt van die van Amanda Plus en Ostinata. Een lage lichtintensiteit tijdens opkweek heeft een hoge α_g en α_g^1 tot gevolg. In de beide voorjaarsproeven (nrs. 3 en 4) waren de rasverschillen voor α_g^1 groter dan tussen Amanda Plus, Ostinata en Hilde in de proeven 1, 2, 3, 5 en 6. Slapplanten hadden een hogere $P_{m,n}$ als de lichtintensiteit tijdens de opkweek hoger was. De rasverschillen met betrekking tot P_n (en ook de andere fotosyntheseparameters) namen toe wanneer de verschillen tussen de rassen wat betreft habitus, groeiwijze en genetische afkomst groter waren (proef 4). Voor Amanda Plus, Ostinata en Hilde waren de resultaten van de variantieanalyses van $P_{m,n}$ per eenheid bedekte grond gelijk aan die van $P_{m,n}$ per eenheid α_g . Er waren geen significante rasverschillen voor de fotosynthesesnelheden op α_g -basis, wanneer de fotosynthese gemeten werd bij een lichtintensiteit die dicht lag bij die tijdens de opkweek van de planten (proeven 3 en 4).

Bij kropsla is de invloed van de voorbehandeling op het lichtcompensatiepunt sterker dan de invloed van de rassen. De r_m van Hilde is in twee proeven groter dan die van Amanda Plus en Ostinata. In de beide voorjaarsproeven kwamen ook rasverschillen met betrekking tot r_m voor. Na een periode met een lage lichtintensiteit was de r_m hoog. Rasverschillen voor de huidmondjesweerstand kwamen alléén in de beide voorjaarsproeven voor. De correlatiecoëfficiënt tussen de totale weerstand van de plant voor het CO_2 transport ($1/\tau_n^1$) en de som van r_s en r_m

is, over alle gegevens van de proeven 1 - 6 samen, 0,81.

Bij kropslarassen wordt het specifiek bladgewicht meer bepaald door de opkweekomstandigheden dan door het genotype, hoewel significante rasverschillen voorkomen. Wanneer de grote verschillen in SLW- en r_m -waarden een gevolg zijn van de opkweekomstandigheden, dan zijn SLW en r_m sterk negatief gecorreleerd. De beide bindslarassen, waarvan er één geselecteerd is voor de kasteelt en de ander voor de teelt in de vollegrond, gaven verschillende resultaten. De twee ijsslatypen waren beide geselecteerd voor de kasteelt en gaven ook identieke resultaten bij de fotosynthesemetingen. De in proef 4 gebruikte bind- en ijsslatypen leken minder geschikt voor de teelt in de winter in Nederland.

Bij de parameters, die het fotosyntheseprocess beschrijven, zijn er géén gevonden die als duidelijk criterium kunnen dienen bij indirecte selectie op een hogere opbrengst. Bij de parameters die het proces van grondbedekking beschrijven konden evenmin criteria gevonden worden die als zodanig voor indirecte selectie bruikbaar zouden zijn. Er kunnen géén rasverschillen voor de fotosynthesesnelheden op α_g -basis verwacht worden, wanneer de fotosynthese gemeten wordt onder omstandigheden die dicht liggen bij die tijdens de opkweek. Méér onderzoek naar de morfologie van de slaplant in relatie tot de groei, de lichtopvang en het CO_2 transport en de CO_2 diffusie van de omringende lucht naar de carboxylatieplaatsen is wenselijk. De introductie en het gebruik van slarassen die niet kroppen zouden de studie van sla vergemakkelijken en in de toekomst de teelt van sla in de lichtarme periode vereenvoudigen.

Curriculum vitae

Hein van Holsteijn werd geboren op 12 december 1949 te Delft en groeide op te Kwintsheul. Hij volgde de gymnasium b opleiding aan het Xaverius College te Vught en begon in september 1968 met zijn studie aan de Landbouwhogeschool in Wageningen. In januari 1975 slaagde hij met lof voor het doctoraal examen in de richting Tuinbouwplantenteelt. Plantenveredeling was als verzwaard bijvak en erfelijkheidsleer als bijvak in de studie opgenomen. Van december 1974 tot december 1977 was hij promotie-assistent bij de vakgroep Tuinbouwplantenteelt van de Landbouwhogeschool en de 9 daarop volgende maanden gastmedewerker, mogelijk gemaakt door een promotiebeurs. Van november 1978 tot juni 1980 deed hij vervangende dienst op het hoofdkantoor van de International Fellowship of Reconciliation te Alkmaar. Hierna is hij actief gebleven in de vredesbeweging.