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GROWTH OF LETTUCE

I. COVERING OF SOIL SURFACE

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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 m^2, 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', 'Deciminor', '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 compact cultivar is that it can be grown 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 × 5 × 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 90–120 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 (MATHIJSSEN, 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 cm^2. 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. CO_2 was not applied. Watering was carried out in the same way as in the spring experiment, but less frequent.

During the first 3 weeks zineb was sprayed; TMTD was applied for 5 weeks. Pirimor was used against aphids and Phosdrin agains 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. Preceeding 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 cm^2.

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

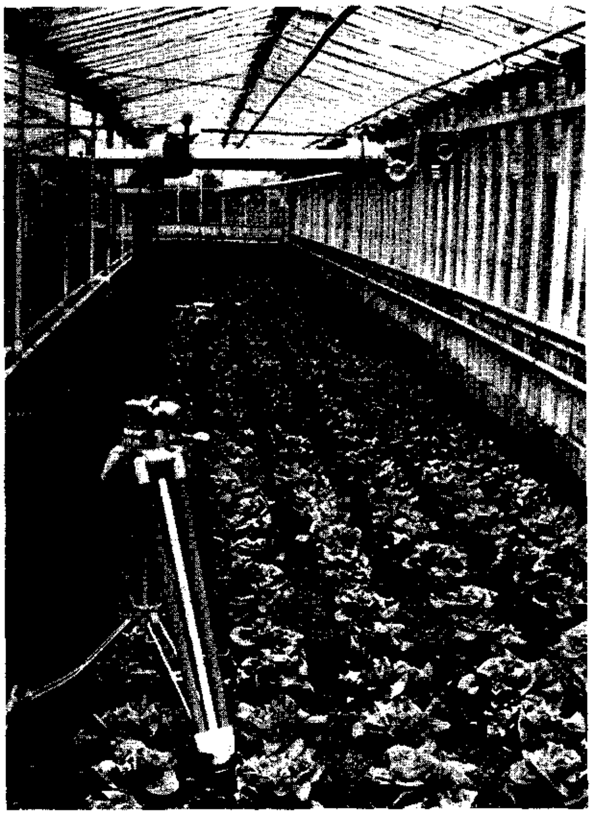


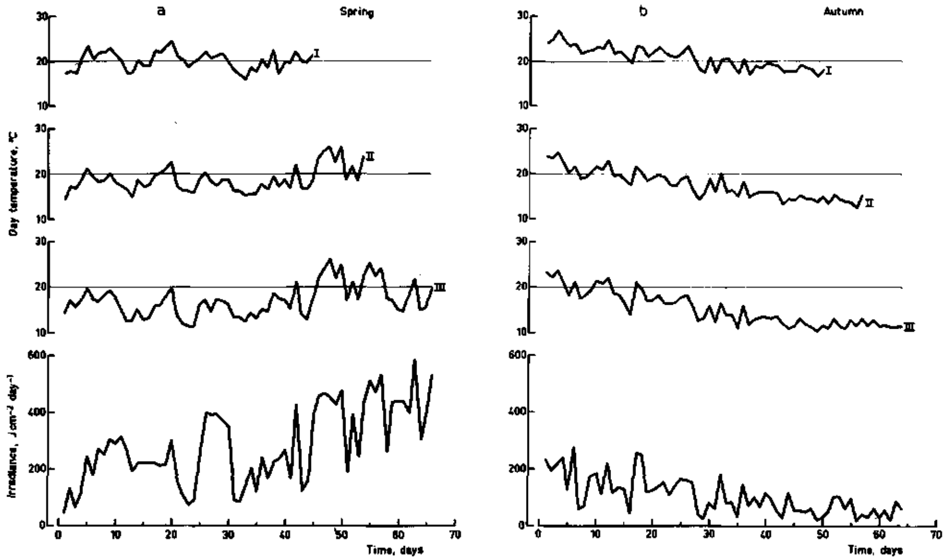
FIG. 1. General view of the set up for soil cover measurements.

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, CO_2-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:

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

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 emperically 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

$$S = S_{max}.\left[1 + p.e.^{-p.r\,(t-t_i)}\right]^{-1/p} \qquad (2)$$

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 $S_{max}.e^{-1} < S_i < S_{max}$, when $0 < p < \infty$. It is obvious that

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

and

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

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.

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

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 × 20 cm and almost 625 cm^2 at the density of 25 × 25 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. 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:

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

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 NILWIK. 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.

1a. SPRING EXPERIMENT

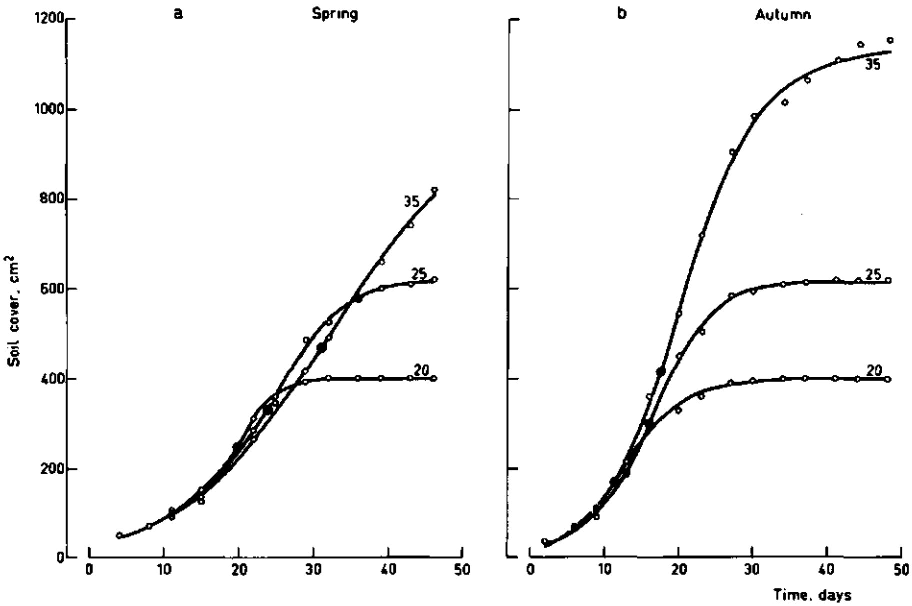
Cultivar	Treatment		Results								
	tempe-rature regime	plant density	t_i (days)	S_i (cm²)	S_{max} (cm²)	r (cm²cm⁻²d⁻¹)	L_i (%)	R_i (cm²d⁻¹)	t_{max} (days)	W_{max} (g)	W_{end} (g)
Amanda Plus	I	20	19.9 *0.9*	284.5 *21.2*	389.4 *7.0*	0.109 *0.008*	71.4 *5.2*	26.3 *1.7*	28	80.3 *3.0*	231.9 *9.4*
	I	25	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*
Deciminor	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								
	temperature 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								
	temperature regime	plant density	t_i (days)	S_i (cm^2)	S_{max} (cm^2)	r ($cm^2cm^{-2}d^{-1}$)	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	27.0 *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*	452.2 *51.0*	1040.2 *43.2*	0.256 *0.154*	43.5 *4.5*	34.6 *5.5*	54		256.4 *9.7*

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*
Deciso	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*
	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*
Ravel	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*

Cultivar	Treatment		Results								
	tempe-rature regime	plant density	t_i (days)	S_i (cm^2)	S_{max} (cm^2)	r ($cm^2cm^{-2}d^{-1}$)	L_i (%)	R_i (cm^2d^{-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

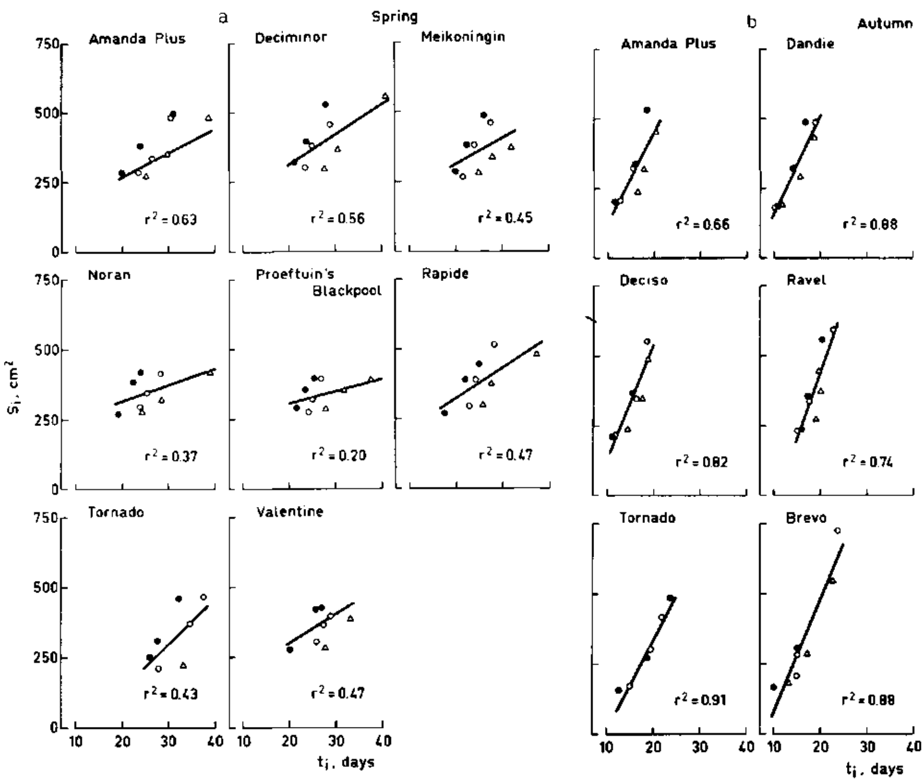
TABLES 2a and 2b. Temperature sums (heat units in degree days) of day temperatures for all treatments and cultivars in spring (a) and in autumn (b) calculated between planting and the inflexion point of the soil cover curve. I, II and III represent the temperature regimes. 20, 25 and 35 represent the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

Cultivar	Treatment								
	I			II			III		
	20	25	35	20	25	35	20	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
Deciminor	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 adventageous 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. 'Deciminor', '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

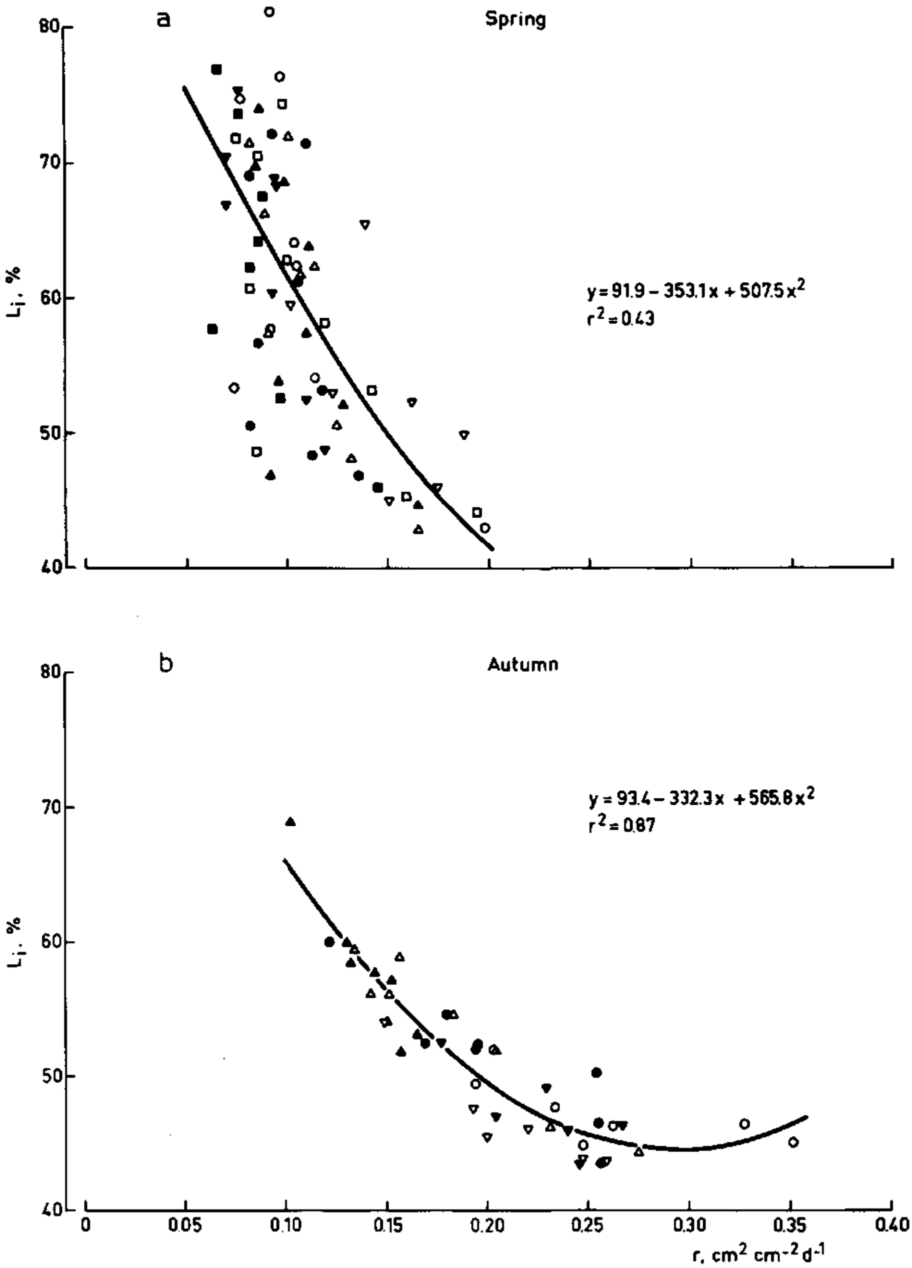
The maximal soil cover for the spacings of 20 and 25 cm is in the order of 400 and 625 cm^2, resp. (vide Tables 1a and 1b). Differences in S_{max} occur mainly for solitary plants. S_{max} tends to be lower at lower temperatures, when the plant forms a more compact head. The cultivar 'Valentine' has 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 cm^2, 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_i for all treatments in spring (a) and in autumn (b).
Spring: ● 'Amanda Plus'; ○ 'Deciminor'; △ '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'.

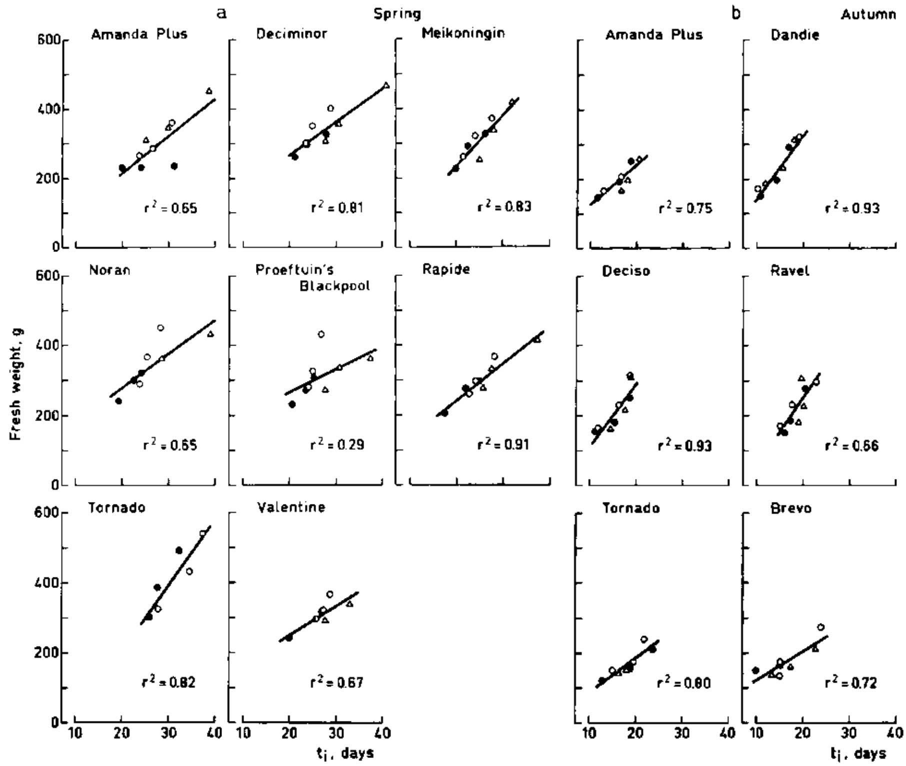
The slope R_i increases at lower plant densities and with higher temperatures. This is more evident in autumn than in spring. The values of R_i are higher in autumn than in spring (see 'Amanda Plus'). 'Deciminor' has in spring slightly higher values than the other cultivars, while 'Proeftuin's Blackpool' 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 values. An explanation of the large differences in the sums between spring and 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 succesful 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.

SUMMARY

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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