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GROWTH OF LETTUCE

II. QUANTITATIVE ANALYSIS OF GROWTH

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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 increase of plant material per unit of material present per unit of time' i.e. RGR = (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 polynominal 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 chosing 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 $cm^2 g^{-1}$ with the use of dry weight. No heading at all occurred with LAR-values of 1100 $cm^2 g^{-1}$ 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 F_2 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 $cm^2 g^{-1}$.

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
Deciso	I	20	4	4	12	41
	I	25	6	6	12	41
	I	35	5	5	13	44
	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

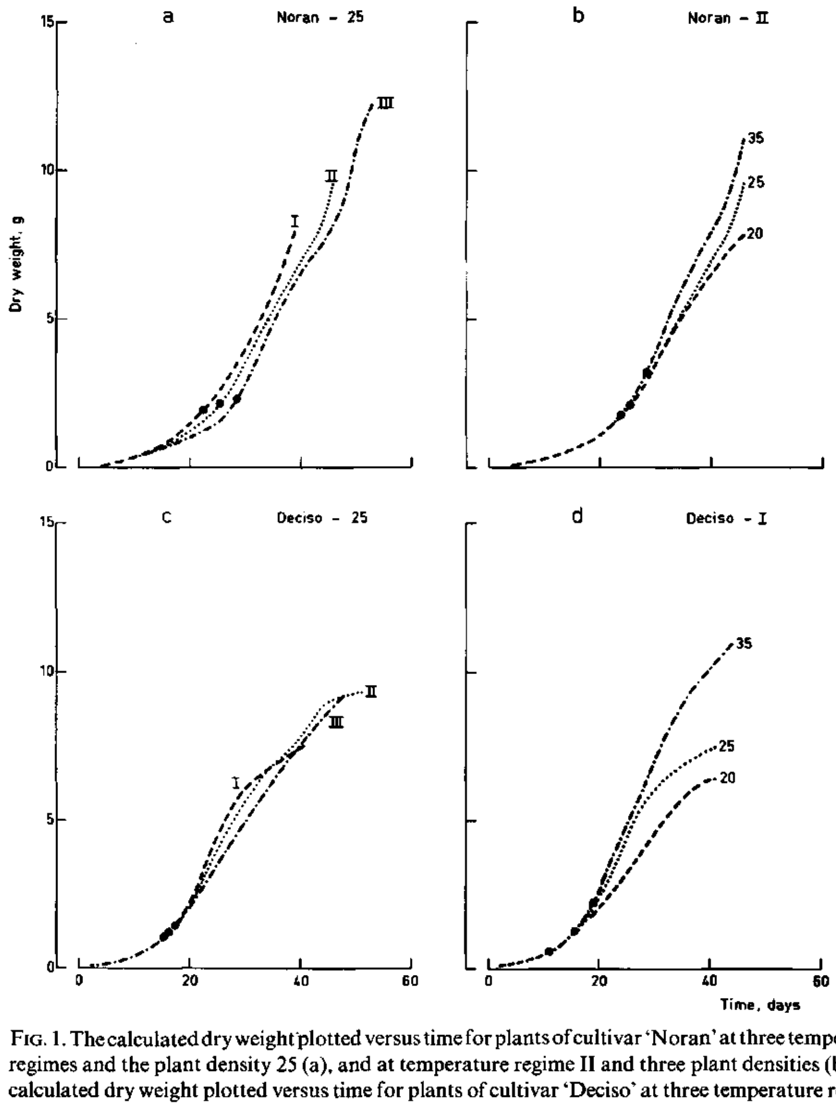


FIG. 1. The calculated dry weight plotted versus time for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b). The calculated dry weight plotted versus time for plants of cultivar 'Deciso' at three temperature 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.

soil cover curve (t_i) 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

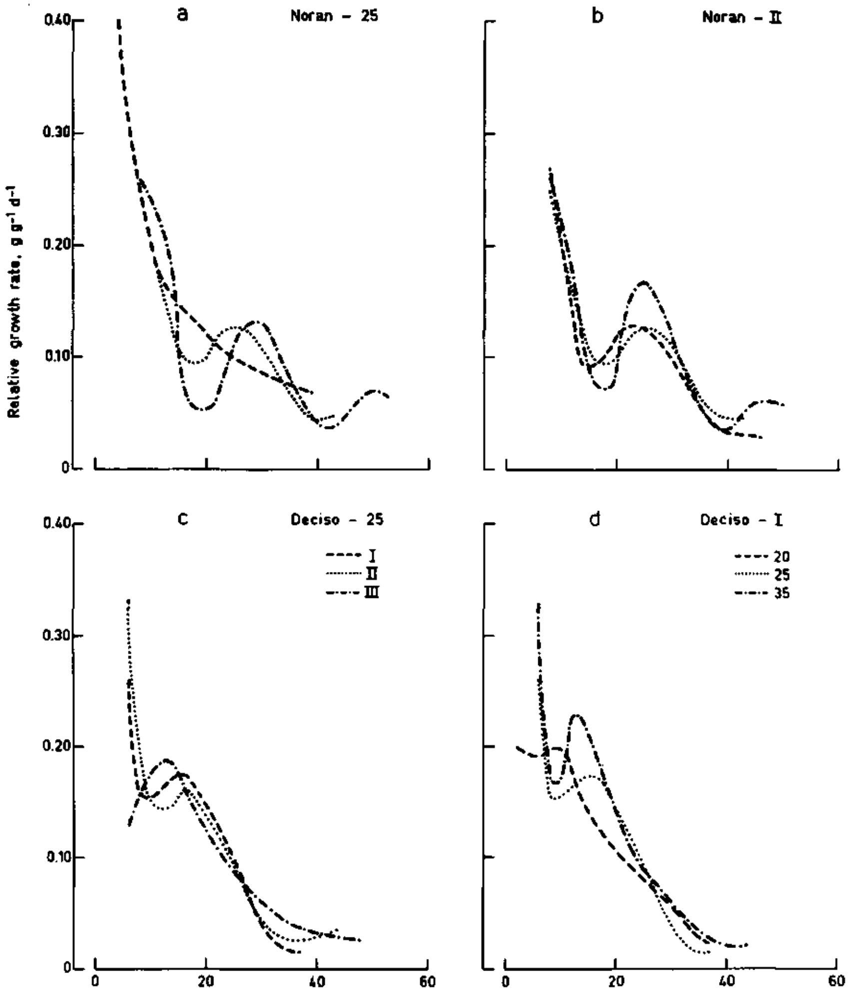


FIG. 2. The relationships of the relative growth rate with time for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of relative growth rate with time for plants of cultivar 'Deciso' 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

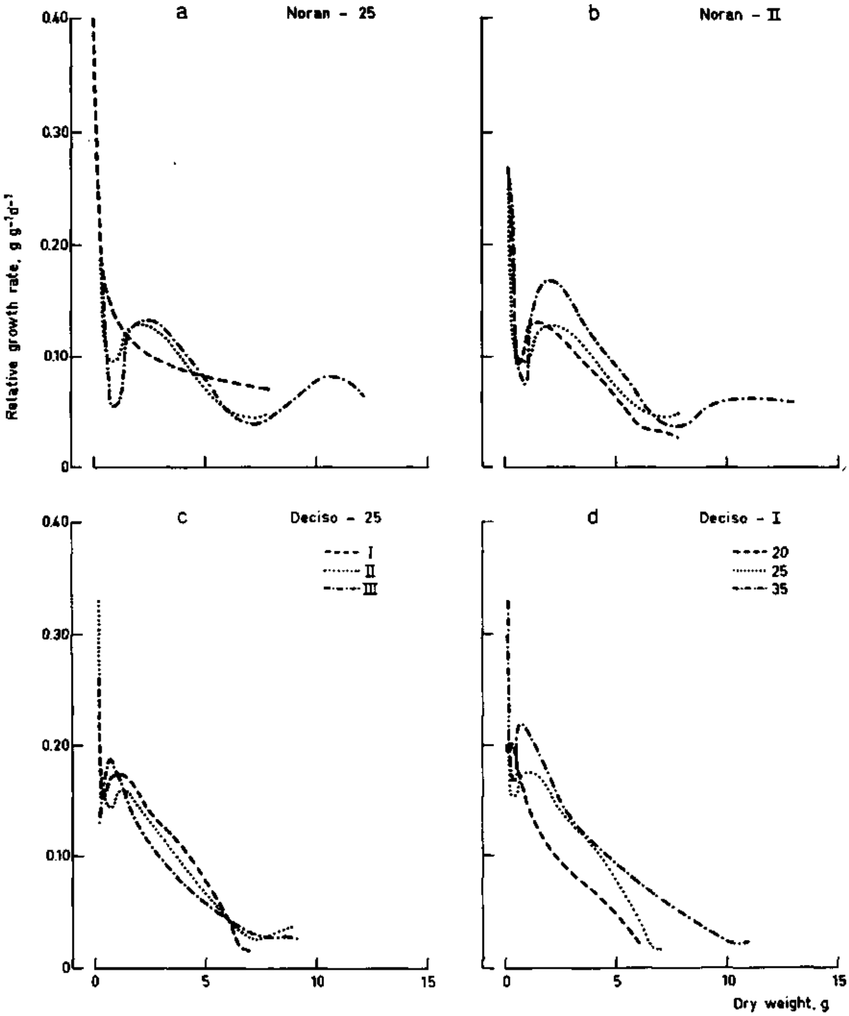


FIG. 3. The relationships of relative growth rate with dry weight for plants of cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of the relative growth rate versus time for plants of cultivar '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-

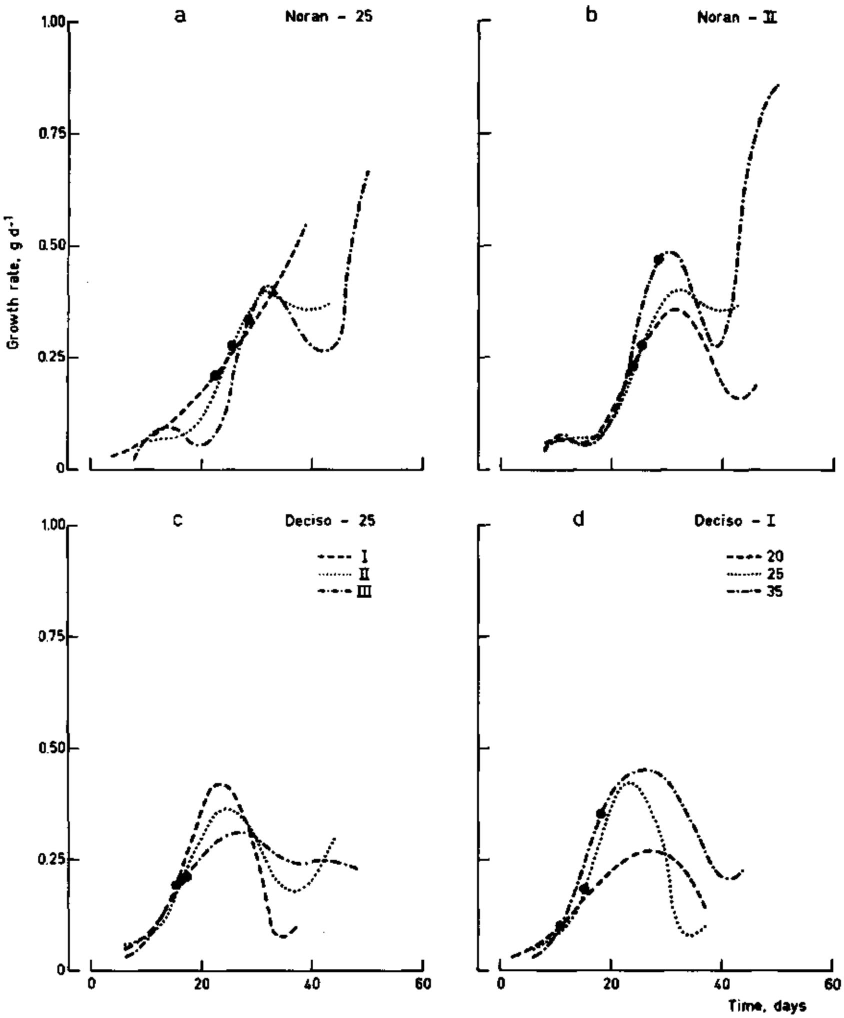


Fig. 4. The relationships of growth rates with time for plants of the cultivar 'Noran' at three temperature regimes and the plant density 25 (a), and at temperature regime II and three plant densities (b), and the relationships of growth rates with time for plants of the cultivar 'Deciso' at three temperature 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 x 20, 25 x 25 and 35 x 35 cm.

lapping leaves. The relationship between GR and soil cover seems more useful. 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.

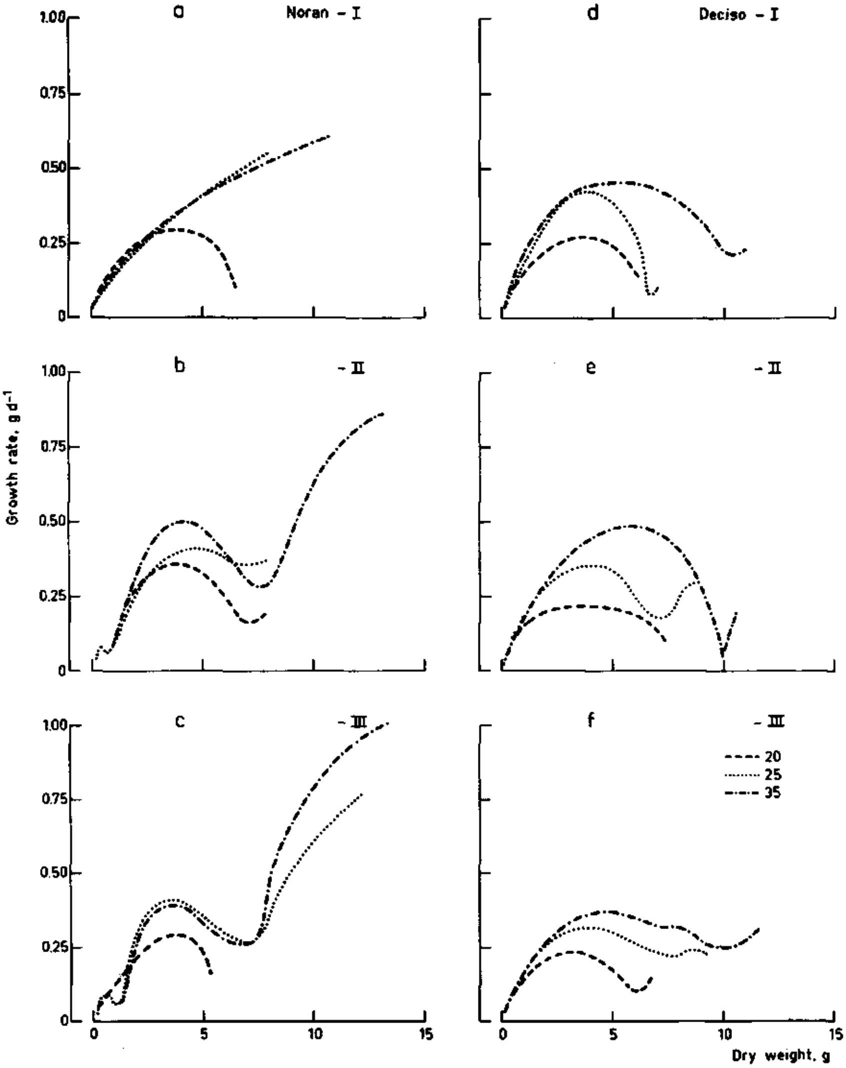


FIG. 5. The relationships of growth rates with dry weight for the plants of all treatments of the cultivars 'Noran' and 'Deciso'. I, II and III represent the three temperature regimes and 20, 25 and 35 the plant densities 20 × 20, 25 × 25 and 35 × 35 cm.

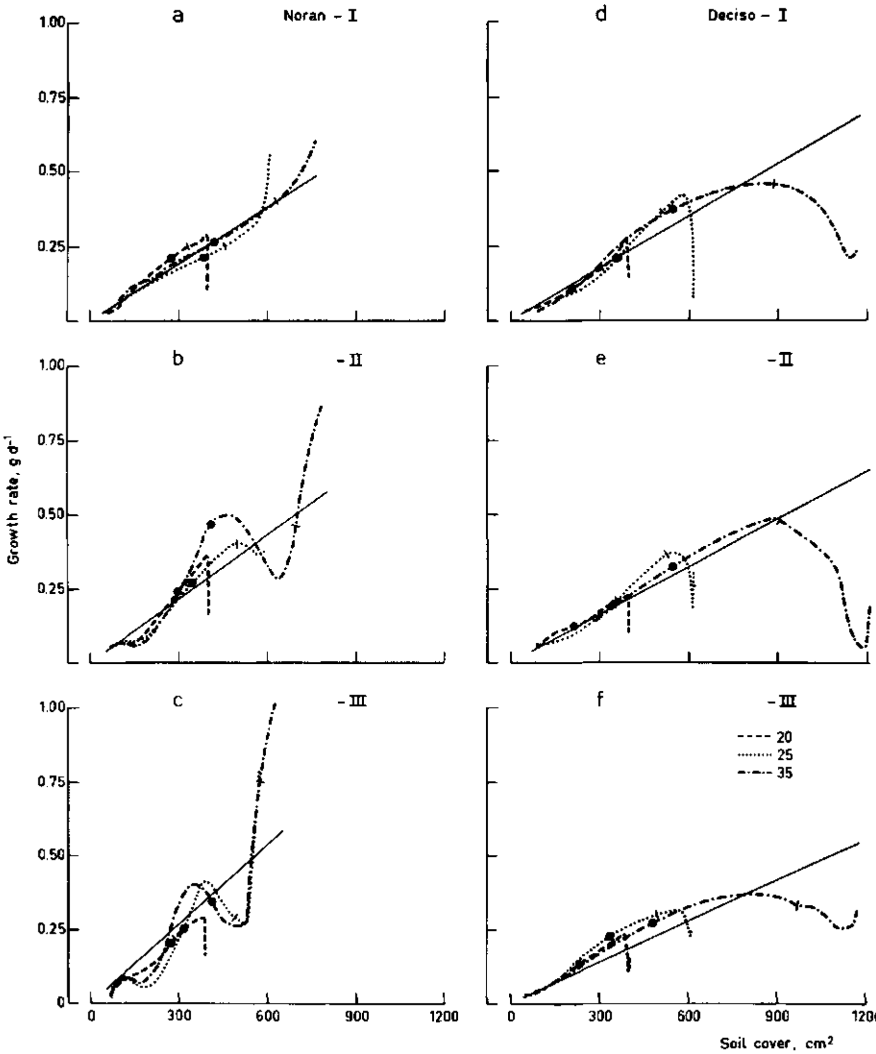


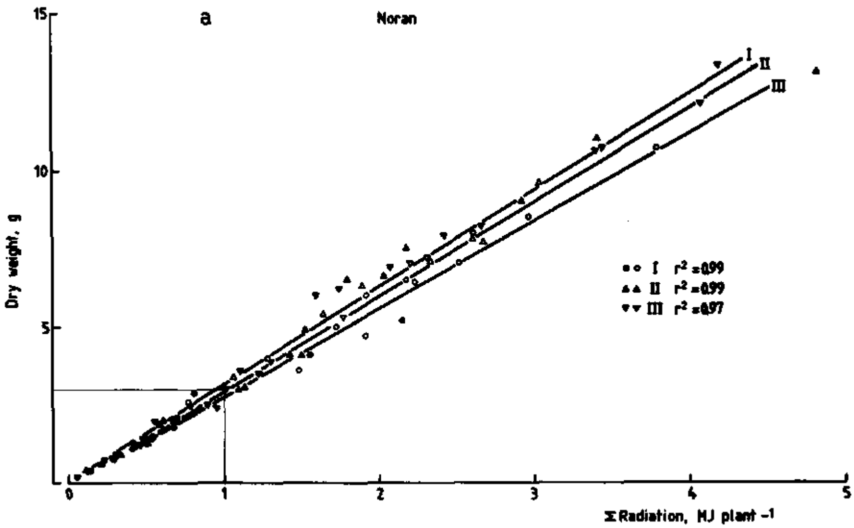
FIG. 6. The relationships of growth rates with soil cover for plants of all treatments of the cultivars 'Noran' (a–c) and 'Deciso' (d–f). The straight lines represent the linear regressions of the soil cover with growth rate. The amount of soil covered in the inflexion point of the soil cover curve is 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.

Data of GR for all treatments, taken until about 80% of the maximum soil 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



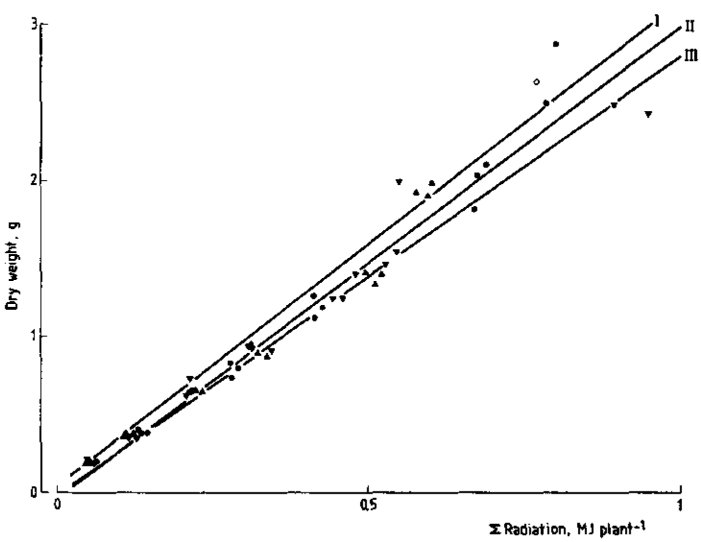


FIG. 7a. The relationship of the total accumulated sum of radiation per plant, with the correction for the amount of intercepted radiation based on the amount of radiation received by the soil surface covered per plant, with the accumulated dry weight per plant of the three temperature treatments of 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 ● (= I), ▲ (= 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.

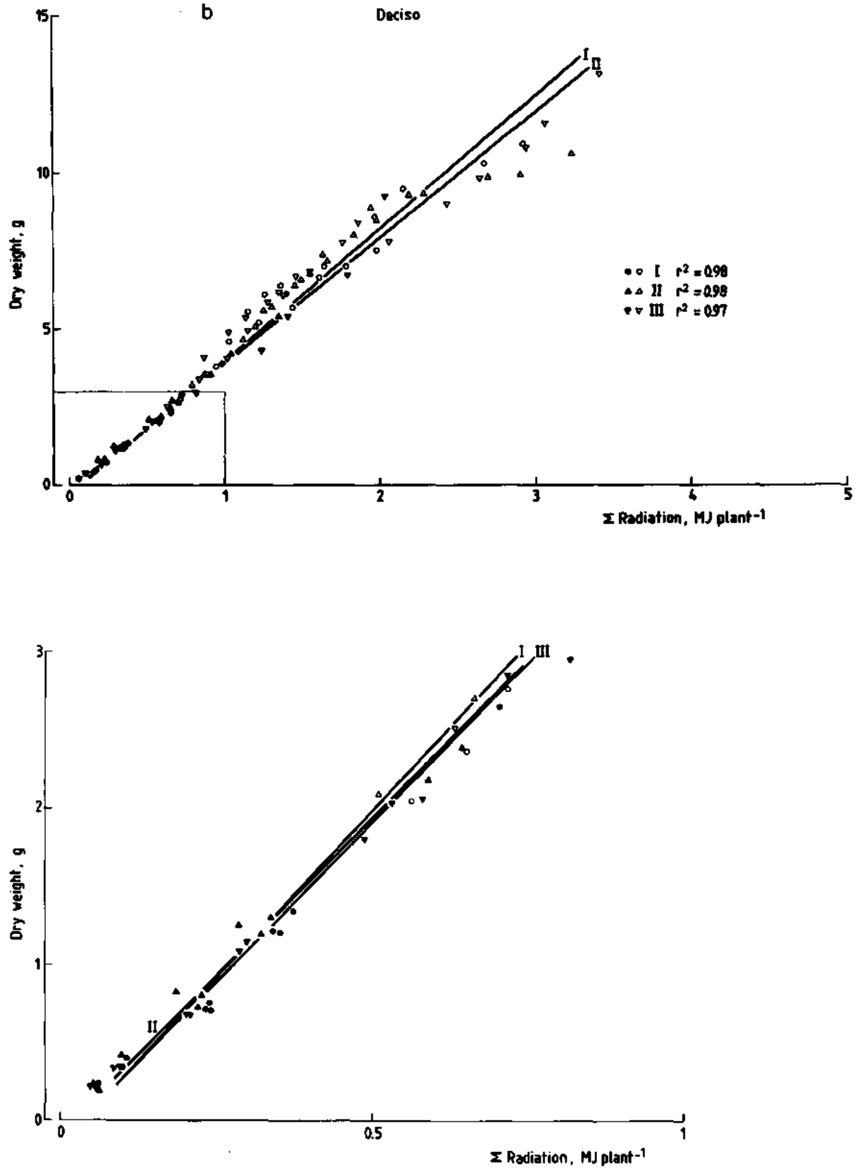


FIG. 7b. The relationship of the total accumulated sum of radiation per plant, with the correction for the amount of intercepted radiation based on the amount of radiation received by the soil surface covered per plant, with the accumulated dry weight per plant of the three temperature treatments of 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 ● (= I), ▲ (= 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-

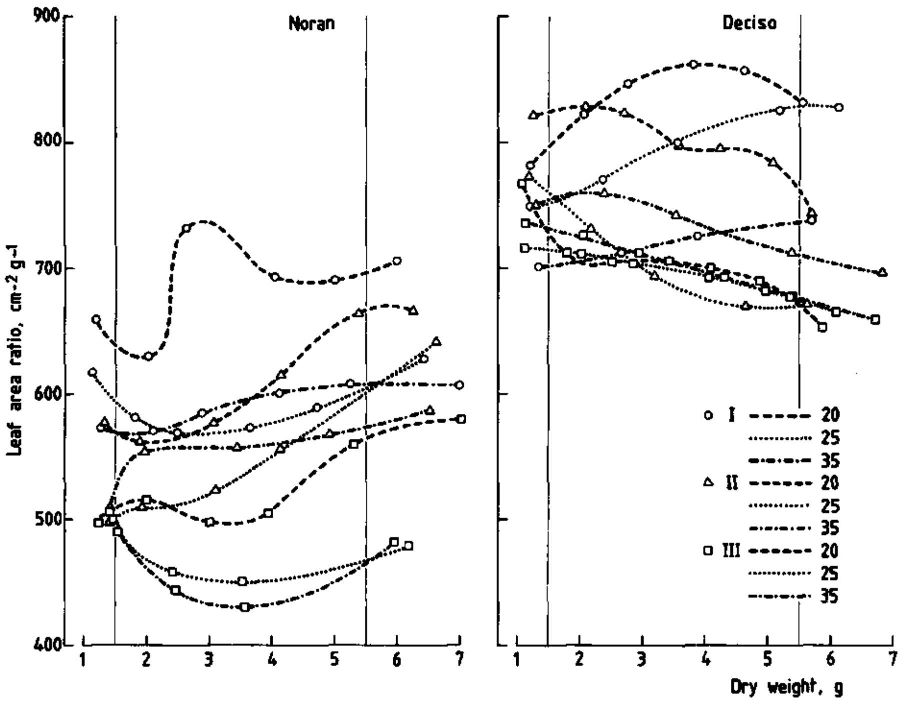


FIG. 8. Relationships between the leaf area ratio and dry weight (between 1.5 and 5.5 grams) of plants of the cultivars 'Noran' and 'Deciso'. Data of all treatments are represented. I, II and III represent the three temperature regimes and 20, 25 and 35 the three plant densities.

perature regime for 'Noran' in the beginning and the high temperatures for 'Deciso' 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 $< 710\ cm^2\ g^{-1}$ for 'Noran' and 'Deciso', resp. A poor quality occurs when LAR is > 620 and $> 760\ cm^2\ g^{-1}$ 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 glasshouse 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 conditions, 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' × '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 $cm^2\ g^{-1}$, 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-

tercepted 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 $cm^2 g^{-1}$ and 710 $cm^2 g^{-1}$ 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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