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Effect of nitrogen dressings on growth and development of sugar-beet

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Abstract

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The growth and development of sugar-beet with different nitrogen dressings was studied by measurement of leaf area and of dry weight and chemical composition (inorganic cations and anions) of several plant parts during the growth season.

For a correct interpretation of the data, the losses in dry weight, leaf area and minerals due to leaf fall could not be ignored and were therefore estimated. The losses were calculated to be 4–5 tons dry matter $\cdot$ ha^{-1} and 3–4 m^2 leaf area $\cdot$ m^{-2} soil area depending on the amount of nitrogen dressed. The losses of N, H_2PO_4 and K were 90–140, 5–13 and 80–105 kg $\cdot$ ha^{-1}, respectively.

When the losses were included in the harvest data, other growth and uptake figures were obtained than when these losses were ignored. With no deficiency, instead of three growth stages, only two stages appeared in the distribution curve.

Furthermore a hypothesis was developed which could explain the differences in dry weight, chemical composition and leaf area of the succeeding laminae of a sugar-beet plant. It was suggested that the laminae formed first stayed small due to competition for the produced minerals within the plant. Maximum leaf area and weight was found for the 10th to 15th leaf. Later formed laminae stayed small due to the shortage of light, minerals, water and time.

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The author graduated on 9 May 1973 as Doctor in de Landbouwwetenschappen at the Agricultural University, Wageningen, the Netherlands, on a thesis with the same title and contents.

Voorwoord

Zeer velen hebben in meerdere of mindere mate geholpen dit proefschrift tot een goed einde te brengen.

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Curriculum vitae

Na het behalen van het diploma HBS-B aan het Jacob Roelands college te Boxtel begon de auteur in 1956 zijn studie aan de Landbouwhogeschool te Wageningen. Hij specialiseerde zich in de bodemkunde en bemestingsleer. In 1961 en 1962 was hij in militaire dienst. Na zijn afstuderen werd hij in 1966 aangesteld als medewerker op de afdeling Landbouwscheikunde. Vanaf 1970 was hij verbonden aan de internationale bodemkundige cursus en vanaf 1971 aan de MSc-opleiding bodem-water.

Samenvatting

In een veldproef werd de invloed van stikstofbemesting op groei en ontwikkeling en op de chemische samenstelling van een gewas suikerbieten bestudeerd. De groei en ontwikkeling werd gemeten aan droge-stofopbrengsten en aan het bladoppervlak. De chemische samenstelling werd bepaald van verschillende onderdelen van het gewas, zoals bladschijven en bladstelen van onderscheiden ouderdom en van de wortel.

Gedurende het groeiseizoen bleek dat voor een juiste interpretatie van groei, ontwikkeling en opname van mineralen, de verliezen door bladval niet konden worden verwaarloosd. In een aantal veldjes kon nog worden nagegaan dat vanaf ongeveer half juli tot het eind van het groeiseizoen, gemiddeld 3 bladeren per 14 dagen verloren gingen. Door het afsterven van 21 bladeren gedurende het groeiseizoen ging bij lage stikstofbemesting 4100 kg droge stof per ha verloren en 3,2 m^2 bladoppervlak per m^2 grondoppervlak. Bij hoge stikstofbemesting waren deze getallen 4600 kg droge stof per ha en 3.9 m^2 bladoppervlak per m^2. De verliezen aan mineralen door bladafval waren vooral hoog voor die elementen die geaccumuleerd worden of achterblijven in de oudste bladeren. Verliezen van 90–140 kg stikstof per ha, 80–105 kg kalium per ha en 5–13 kg fosfaat (H_2PO_4) per ha werden berekend. Daar deze verliezen weer in de grond terugkeren, hebben zij voor de bodemvruchtbaarheid weinig consequenties. Wel moeten deze verliezen in een studie over groei, ontwikkeling en de chemische samenstelling van een gewas betrokken worden.

Door deze verliezen op te tellen bij de gemeten produktie en opname werd een produktiepatroon gevonden dat afwijkt van wat men in de literatuur vermeld vindt. Met voldoende stikstof bemeste bieten doorliepen in dit experiment slechts twee fasen van ontwikkeling. In de eerste fase werd het merendeel van de geproduceerde droge stof gebruikt voor uitbreiding van het bovengrondse materiaal. In de tweede fase werd het meest geïnvesteerd in uitbreiding en vulling van de biet. In een gewas dat stikstoftekort had, werd relatief meer droge stof geïnvesteerd in de biet vergeleken met een goed met stikstof voorzien gewas. Bovendien kon hier nog een derde fase worden onderscheiden. Het tijdstip waarop deze derde fase begint is vermoedelijk afhankelijk van het tijdstip van stikstofgebrek. In deze derde fase werd geen toename van suikervrije droge stof in de biet meer gevonden, wel een toename in hoeveelheid suiker. Van de droge stof, die gebruikt werd voor instandhouding en uitbreiding van het bovengrondse materiaal, was de verdeling over bladschijven en bladstelen binnen de fasen onafhankelijk van de stikstofbemesting. Ook de opname van kationen en anionen en de produktie van organische stikstof en organische zouten $(C-A)$ per eenheid geproduceerde droge stof was constant binnen een fase. Wel werden verschillen gevonden tussen de hoog en laag met stikstof bemeste objecten.

In deze proef werd de grootste toename in droge stof en suiker per tijdseenheid gevonden in augustus. Daarentegen was de drogestoftoename per eenheid bladoppervlak per tijdseenheid het grootst in het begin van het groeiseizoen. De eerst gevormde bladeren, die zeer actief zijn in deze periode, konden slechts een beperkte grootte en gewicht bereiken. De zeer hoge (C – A)-gehalten in de dode bladeren, vooral in die van het begin van het groeiseizoen, wijzen ook op een zeer actieve periode wat betreft reductie van nitraat (en sulfaat). Dat de eerst gevormde bladeren klein en gering in gewicht blijven, werd aannemelijk door de hypothese dat deze bladeren, door concurrentie met nieuw blad om de door hen geproduceerde bouwstoffen (eiwitten en koolhydraat), weinig in hun eigen oppervlak en gewicht kunnen investeren. Maximale bladgrootte en bladgewicht werd gevonden bij het 10^e–15^e blad. Het aantal bladeren dat deze maximale grootte en gewicht kon bereiken werd in deze proef bepaald door de stikstofbemesting. Later gevormde bladeren konden deze maximale grootte niet meer bereiken door een tekort aan licht, water, mineralen en/of tijd.

Grote verschillen werden binnen één oogst gevonden in gehalten aan kationen en anionen in de verschillende plantedelen met name in bladschijven en bladstelen van onderscheiden leeftijd. Vooral voor Na, Ca, Mg en (C – A) werden de hoogste concentraties gevonden in het oudste materiaal. Ook voor NO_3 bleken de hoogste gehalten voor te komen in de oudste bladstelen en de oudste bladschijven. Voor H_2PO_4, K en organisch-N werd het omgekeerde gevonden. Minimale concentraties werden voor deze elementen gevonden in het dode materiaal. Deze waren in het bladmoes voor organisch-N, K en H_2PO_4 respectievelijk 1000, 300–400 en 25–50 meq·kg^{-1} droge stof. In de bladstelen was dit alleen voor H_2PO_4 duidelijk met een waarde van 25 meq·kg^{-1} droge stof. Van de mineralen met de hoogste gehalten in de oudste bladeren bleek het Ca-gehalte het meest constant te zijn gedurende het groeiseizoen.

De daling van de gehalten aan som kationen, som anionen, (C – A) en organisch-N gedurende het seizoen in het loofmateriaal kon ten dele worden verklaard door de verliezen ten gevolge van bladval. Door gehalten te berekenen, aannemende dat geen bladeren verloren zouden zijn gegaan, werden vanaf half augustus vrijwel constante gehalten gevonden. Daar in gewasmateriaal de meeste gehalten dalen met het ouder worden van het gewas, zullen de zogenaamde kritische concentraties afhankelijk zijn van de leeftijd.

De extra stikstofbemesting op 4 juli, 1 augustus en 29 augustus hadden een invloed op opbrengst, bladoppervlak, droge stofgehalten en suikergehalten. De uiteindelijke suikeropbrengst was echter voor de diverse objecten vrijwel gelijk. Elke extra stikstofbemesting resulteerde, een maand na de toediening, in een extra toename van de bladoppervlakte index (LAI) met een 0,5 eenheid. Het suikergehalte werd in dezelfde tijd met 1% verlaagd. De laatste extra stikstofbemesting op 26 september had geen invloed meer op het bladoppervlak, de drogestofopbrengst en de suikeropbrengst. Wel was er een duidelijke toename in de NO_3 en organisch-N gehalten.

Contents

1 Introduction

Nitrogen dressings has several effects on sugar-beet.

With increasing nitrogen shoot growth is enhanced with an increase in weight and area (Jorritsma, 1962; Stout, 1961; and many others) and especially the growth of new leaves is stimulated (Stout, 1961).

Root growth too is stimulated; a certain maximum in fresh root weight is reached (Jorritsma, 1962). According to literature sugar content of the roots and sap purity decrease inversely with nitrogen dressing. A decreasing sugar content combined with a maximum root weight led to an optimum sugar yield. However, Boyd et al. (1970) found no decrease in sugar yield with nitrogen dressing in several trials on mineral soils.

Early in the growth period the supply of nitrogen to the plants must be sufficient to build up the photosynthetic system as soon as possible.

Total dry-matter production is maximum when an optimum canopy is produced as early as possible and lasts as long as possible (Storer et al., 1970). However, this situation does not mean an optimum sugar yield, because production of sugars and other dry matter compete for the produced assimilates. Furthermore a large canopy will lead to inefficiency due to mutual shading (Tanaka & Kawano, 1966; Bremner et al., 1967; Loomis & Ulrich, 1969, 1962; Loomis & Nevins, 1963).

If the final sugar yield of a sugar-beet crop could be correlated with one or more properties in an early stage of growth, it might be possible to change the growing conditions and so influence the growth and sugar yield. Growth or nutritional characteristics can be used for this purpose.

The growth of sugar-beet is mainly influenced by nitrogen dressing and water supply. However, under field conditions, it is only possible to control the amount of available water in irrigated systems. Therefore this study is restricted to the influence of nitrogen supply.

The growth pattern of sugar-beet can be characterized by dry matter production of the whole crop and of specific parts of the plants, and by leaf area. These characteristics are usually measured at intervals of one or two weeks. With these data the growth rate and, for instance, the rate of sugar accumulation can be calculated and compared with the leaf area of the crop.

The growth characteristics which are in use are: the crop growth rate, the relative growth rate, the leaf area index, the leaf area duration, the relative leaf growth rate, the net assimilation rate and the leaf area ratio. For this study the following parameters are used (A = leaf area; W = dry weight; t = time):

a. crop growth rate (CGR) $= (W_2 - W_1)/(t_2 - t_1)$
b. leaf area index (LAI) = leaf area per unit of soil area
c. net assimilation rate (NAR) $= 1/A \cdot \mathrm{d}W/dt$; this is the rate of dry weight increase per unit of leaf area.

To solve Equation (c) either the relation between A and W or the relation between both A and W with time has to be known (Radford, 1967).

1. If the relation between A and W is linear ($W = c + bA$), then NAR $= [(W_2 - W_1)/(A_2 - A_1)] \cdot [(\ln A_2 - \ln A_1)/(t_2 - t_1)]$.
2. If the relation between A and W is of quadratic form ($W = c + bA^2$), then NAR $= 2(W_2 - W_1)/[(A_2 + A_1)(t_2 - t_1)]$.
3. If the relation between A and W is of the form $W = c + bA^x$, then NAR $= [x/(x-1)] \cdot [(W_2 - W_1)/(t_2 - t_1)] \cdot [(A_2^{x-1} - A_1^{x-1})/(A_2^x - A_1^x)]$.
4. If the relation between A and W is of the form $W = c + bA + \mathrm{d}A^2$, then NAR $= [b(\ln A_2 - \ln A_1) + 2d(A_2 - A_1)]/(t_2 - t_1)$.

The influence of a nitrogen dressing on the leaf area is evident: with increasing fertilization leaf area increases up to a certain maximum. A very large leaf area causes shading of the lowest leaves which influences the photosynthetic capacity of these leaves. Hypothetically a stage could be reached where the dissimilation of these leaves is higher than the photosynthesis (Donald, 1961).

However, data from literature indicate that leaf area is a better criterion for dry matter yield of sugar-beet than the net assimilation rate, sometimes called the efficiency (Watson, 1952, 1956; Goodman, 1967).

The increase of leaf area of sugar-beet always follows the same pattern: a very slow increase in the beginning of the growth season followed by a quick, more or less linear increase with time up to a maximum value. Afterwards the leaf area decreases because the oldest leaves die, their area is larger than that of the newly formed leaves (Watson, 1956; Loach, 1970). Nitrogen dressings produce more leaves per unit time; the area per leaf for well fertilized plants also increases. Loomis & Nevins (1963) found that with adequate nitrogen supply 4 ± 1 new leaves appeared on each plant every week. This rate was found to be more or less constant during the whole season. Plants, that became deficient in nitrogen showed a decline in this rate to a minimum of less than one leaf per week by the sixth week of deficiency. After a renewal of nitrogen supply these plants increased their rate of leaf appearance again to 4 ± 1 per week, as before. The number of leaves that died was not significantly affected by nitrogen nutrition.

According to Watson (1963) many studies on growth analysis have shown that a variation in the nutrient supply has little or no effect on the net assimilation rate, but often has a very pronounced effect on leaf area and weight. He suggested that the net assimilation rate increased with increasing nutrient supply at low nutrient levels but that it became independent at higher levels. However, in pot trials (Watson et al., 1958, 1963), where the NAR was increased by an increase in nitrogen supply, a wider range was found due to less mutual interference of the plants.

The leaf area duration (LAD), which is the integral of the leaf area curve over a given period of time, takes into account both the magnitude and the life span of the leaves. It is usually expressed in weeks. By nitrogen application the LAD is increased by an increase in size and number of leaves (Storer et al., 1970). Although Watson (1958) proposed LAD as a good indicator for the production capacity of a plant or a crop Storer et al. (1970) found quite different sugar yields with the same LAD value. These same LAD values were produced by different nitrogen treatments: a pre-sowing nitrogen dressing and a late nitrogen dressing. When nitrogen was supplied before sowing, the shoot developed more quickly so that the leaf area was larger early in the season, when solar radiation and air temperature were high. Furthermore sugar yield decreased with the late nitrogen dressing, because of an induced vegetative growth of the crop.

Besides growth parameters, the nutritional status is an important indication for crop behaviour. From literature it is clear that there are large differences in contents of cations and anions in the various plant part. Differences are found not only between various parts of the plant, but also in the same parts at different positions on the plant (Vickery, 1961; Coic et al., 1962; Kirkby & de Kock, 1965). In general the total cation concentration (Na+K+Ca+Mg) is high in old laminae and low in young ones. The sum of inorganic anions (A) in the laminae is usually lower than the sum of cations (C).

Differences in anion content between laminae of different age can be small (Vickery, 1961), but sometimes great differences are found, for instance, for nitrate (Kelley & Ulrich, 1966). More organic nitrogen was found in young expanding laminae than in old ones (Sörensen, 1962; Coic et al., 1962). In the petioles of sugar-beet plants the concentration of anions was much higher than in the laminae (van Egmond & Houba, 1970; Houba et al., 1971). Also differences between old and young petioles were found, for example, for nitrate (Kelley & Ulrich, 1966).

As a result of these differences in contents, the cation minus anion content (C−A) (de Wit et al., 1963) or carboxylate content is higher in old laminae than in young ones.

De Wit et al. (1963) concluded from experiments with perennial ryegrass that a certain carboxylate content is a condition for good growth. For orchard grass and perennial ryegrass, the range should be 900–1000 meq per kg dry matter. For wheat, it should be about 1000 meq per kg dry matter (Kostic et al., 1967). According to van Tuil (1965), a normal carboxylate content for sugar-beet foliage in an early stage of growth is 3500 meq per kg dry matter.

However, for wheat (Slangen, 1971) and for sugar-beet plants grown on culture solutions (van Egmond & Houba, 1970; Houba et al., 1971), the carboxylate content was not constant, but decreased during the growth period.

The formation of carboxylates is mainly the result of reduction of nitrate and sulphate in living plant material (Dijkshoorn, 1962, 1963). The relative amount of organic sulphur to organic nitrogen is for many plants only 6% when calculated on an ion equivalent basis (Dijkshoorn & van Wijk, 1967). Thus the (C−A) content of the plants is mainly dependent on nitrate reduction.

Houba et al. (1971) found for sugar-beet plants on culture solutions that, for plants well fertilized with nitrate, the amount of organic nitrogen produced by these plants was equal to the amount of carboxylates formed. For plants deficient in nitrogen the production of organic nitrogen was stopped soon after nitrogen depletion. However, at the same time the production of carboxylates continued at a lower rate.

About 80–90% of the (C−A) could be detected as carboxylates (malate, citrate, oxalate etc.). What remained was probably polyuronates (van Tuil, 1965) and other carboxylates that are difficult to extract (Houba et al., 1971).

Usually in literature the growth of a crop is characterized either by describing the change in growth parameters as dry weight and leaf area, or by continuous measurement of the crop's chemical composition. The two approaches to crop growth and development are seldom combined. This field trial with sugar-beet was so designed that the influence of nitrogen on characteristics of growth and nutrition could be determined simultaneously.

In this experiment some of the sugar-beet plots were fertilized with nitrogen throughout the season. Some received a rather low basic dressing with nitrogen and other plots received one or more extra nitrogen dressings.

Plants were harvested every 14 days. The plants were divided into different parts, such as laminae and petioles of different age. In this way it could be checked whether any one characteristic in a young stage of development was related to the final sugar yield.

2 Methods

2.1 General

The field trial was carried out in 1967 on a gravelly sandy soil near Wageningen, the Netherlands.

The pH-KCl of the field was 5.0; the organic matter content 3.3%; phosphorus extracted with a buffered ammonium lactate-acetic acid solution of pH = 3.75 (P-AL) was 47 mg P_2O_5 per 100 g soil and potassium extracted with 0.1 *N* HCl was 10 mg K_2O per 100 g soil.

The plots were two by two meters with ±30 cm distance between the plants in the row and 40 cm between the rows. This amounts to 30 plants per plot or 75000 plants per hectare. Each plot was surrounded by two rows as border.

The borders were sown with a machine, but in the plots the seeds were sown by hand on the spot where a plant had to grow.

A plot of two by two meters is usually small for sugar-beet. For that reason a non-commercial diploid hybrid, being genetically more homogeneous was used (No. P 2167 of the van der Have firm, Kapelle Bieselinge, the Netherlands).

When necessary the crop was spray irrigated.

The plants were sown on 5 May, which is fairly late, and thinned to 30 plants per plot on 20 June. Starting from 4 July plants were harvested every fortnight.

2.2 Manuring

The entire experimental field was fertilized according to Table 1. The basic slag was applied in the autumn of 1966. The other fertilizers were applied in 1967 before

Table 1. Basic rates and kinds of fertilizers used.

		Rate ($kg \cdot ha^{-1}$)
P_2O_5	(basic slag)	85
K_2O	(potassium chloride 40 %)	120
MgO	(kieserite and dolomitic limestone)	57.5
CaO	(dolomitic limestone)	400
B	(borax)	2
N	(nitrochalk and Chilean nitrate)	120

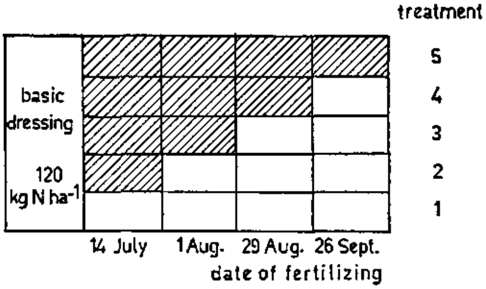


Fig. 1. Scheme of the experiment (each lined square represents an additional dressing of 50 kg N/ha and 20 kg K_2O/ha at the dates indicated).

sowing (beginning of May).

In addition to this basic dressing different quantities of nitrogen were applied according to the scheme presented in Figure 1.

The nitrogen was applied as nitrochalk (23% N). The extra potassium (as potassium chloride 40%) was applied to ensure that the sugar-beet, that was well fertilized with nitrogen, would not suffer from potassium deficiency.

About two month after sowing (on 4 July) the first additional nitrogen dressing was applied and this was repeated every four weeks (on August 1, August 29 and September 26). These extra dressings were carefully added to the soil so that the fertilizer did not come in contact with the leaves.

2.3 The harvest

Starting from 4 July three plots per treatment were harvested every 14 days up to the last harvest on 24 October. All the plots were harvested between 6 and 9 a.m. to avoid any changes in chemical composition (nitrate, sugar etc.) of the plant material related to the time of day.

All 30 plants were dug out of each plot and separated on the field in root (beet) and shoot. The shoot included about 2–3 cm of the upper part of the beet.

At the laboratory the beets were washed, weighed and rasped to pulp. From this pulp a sample was dried at 70°C to determine the dry matter content. Two samples, both 26 g, were preserved frozen for a determination of sugar content.

After weighing the shoots of the 30 plants, ten plants were arbitrarily chosen and set aside. The remaining shoots were cut into small pieces and mixed thoroughly. From this material a sample was taken to determine the dry matter content (drying at 70°C).

From the ten plants, selected at random, the dead and dying (=yellow) leaves were collected and called dead material. The leaf area of the living (=green) leaves was measured (see Section 2.6). The green leaves were then separated into three different groups: the five oldest leaves, the next five leaves and the rest of the leaves.

The area of the leaves of each plant was measured in the sequence of their appearance so that the area of each group of leaves could be calculated.

In these four groups of leaves (dead, oldest five, following five and the rest) the petioles were separated from the laminae. The midrib was included in the laminae.

From each group the laminae and petioles, and the rest of the shoot (crown of the beet plus a very small part of the petioles) were weighed separately and after that cut into pieces. The dry matter content of a sample from each group was determined (70°C).

The samples for the dry matter determinations were ground and stored in the dark in sealed plastic bags for chemical analysis (see Section 2.4).

On 20 June the plots were thinned to 30 plants. The plants taken out were regarded as the first harvest.

These plants were too small to be separated into laminae, petioles etc. Only roots and shoots could be distinghuished.

The selected plants from the next harvest (4 July) were still too small to be separated into the different groups of laminae and petioles. On 18 July and 1 August only two groups of living leaves could be collected. From the harvest of 15 August onwards three different groups of living laminae and petioles could be separated.

2.4 Chemical analysis

Only plants of treatments 5 and 1 were chemically analysed (see Fig .1). The chemical analysis was carried out according to procedures of the Laboratory of Soils and Fertilizers of the Agricultural University, Wageningen, the Netherlands (van Schouwenburg & Walinga, 1971, and internal reports).

From all the plant parts, subsamples were analysed after digestion in concentrated sulphuric acid and hydrogen peroxide (Lindner & Harley, 1942). Concentrations of Na, K and Ca were estimated with a flamephotometer (Eppendorf), with propane as fuel for estimation of Na and K, and acetylene as fuel for Ca. The concentration of Mg was estimated by atomic-absorption spectrophotometry (Techtron AA 100). Phosphate was measured colorimetrically (Vitatron colorimeter) by the molybdenum blue method with antimonyl tartrate, ascorbic acid being used as reducing agent. Nitrogen in the digest was estimated as follows: The digest was made alkaline, distilled over into a boric acid solution, and titrated with potassium biiodate. Since the material was digested without salicylic acid, the values for nitrogen do not include all the nitrate since a minor part is lost (N-Kjeldahl).

Other subsamples were extracted with 0.5 *N* acetic acid. In this extract the Cl concentration was estimated coulorimetrically, with a chlorocounter (Marius, Utrecht). The nitrate in the extract was estimated by nitration of 3,4-dimethylphenol in an acid medium. The nitro-xylenol that formed was distilled into a sodium hydroxyde solution and the resulting colour was measured with a Vitatron colorimeter. Sulphate was precipitated with barium chloride and kept in suspension with Tween-80. The turbidity was measured colorimetrically (Vitatron colorimeter).

All concentrations are given on the basis of oven-dried material (70°C).

The variation coefficient of the analysis was not higher than 10%.

2.5 Sugar estimation

Sugar content was estimated at the Institute for Research on Varieties of Field Crops, Wageningen. The pulped root samples were mechanically shaken for 2½ min after addition of a basic lead acetate solution. After repeated filtration (3 times), the sugar content in the filtrate was measured with a polarimeter according to the method of Sachs-le-Docteur.

2.6 Measurement of leaf area

During the growth season of 1966 leaves of different size of the variety used in this trial were collected. Photogrammes of these leaves were made and the area of the prints was measured with a planimeter.

With these prints a scale was made of leaves of sugar-beet plants with an area from one cm^2 up to an area of about 600 cm^2 (Table 2).

In the experiment, the area of the leaves from sugar-beet plants were compared with the area of the prints and the corresponding scale number was recorded.

2.7 Climate

The day and night temperature and the radiation during the experiment were recorded and given as means of 10-day periods in Table 3. The mean daily temperature was in the beginning of the growth season (May) higher than normal. In June, July, August and September the temperature was normal, except for cold periods in September. However, at the end of September and in the beginning of October the temperature was higher than normal, especially at night.

Table 2. Scale number and the corresponding area of leaves of a sugar-beet plant.

Scale number	Area (cm^2)	Scale number	Area (cm^2)	Scale number	Area (cm^2)
1	1.0	11	10.9	21	106.8
2	1.2	12	12.8	22	140.7
3	1.5	13	16.9	23	174.3
4	1.8	14	20.8	24	203.5
5	2.5	15	25.9	25	266.3
6	3.4	16	32.2	26	336.3
7	4.3	17	48.4	27	378.0
8	5.7	18	52.0	28	430.5
9	6.9	19	66.7	29	512.0
10	8.7	20	81.3	30	608.8

Table 3. Mean day and night temperature and radiation during 1967.

Period	Mean temperature		Mean daily radiation ($cal \cdot cm^{-2}$)
	during day light (°C)	during the night (°C)	
May 11–May 21	16.3	12.5	350
May 21–May 31	14.8	10.8	290
May 31–June 10	15.1	11.5	368
June 10–June 20	14.1	10.2	404
June 20–June 30	17.2	13.3	303
June 30–July 10	18.3	13.7	352
July 10–July 20	20.8	15.7	396
July 20–July 30	19.7	14.3	340
July 30–Aug. 9	19.8	14.7	337
Aug. 9–Aug. 19	17.1	14.4	215
Aug. 19–Aug. 29	17.9	13.4	339
Aug. 29–Sept. 8	16.2	13.0	192
Sept. 8–Sept. 18	13.9	10.9	191
Sept. 18–Sept. 28	14.9	12.1	173
Sept. 28–Oct. 8	14.5	11.8	146
Oct. 8–Oct. 18	14.2	11.5	106

Dry periods were recorded in the beginning of May, during June and July and in the beginning and at the end of August. On 12 May, 16 June and 14 July about 20 mm of water was sprayed to make sure that the crop would not suffer from drought. During September and October the amount of rainfall was normal.

3 Growth analysis of a sugar-beet crop

During the experiment it became evident, that losses due to leaves dying were so high, that for a study of this crop's growth and development they could not be ignored.

Although in recent literature (Terry, 1968; Loach, 1970; Milford & Watson, 1971) the importance of dry weight loss was mentioned, no measurements of weight were reported.

For sugar-beet plants, grown in nutrient solutions, Loomis & Nevins (1963) found no differences in the amount of dead leaves for different nitrogen treatments. Under growth chamber conditions, Terry (1968) found that for sugar-beet, grown at different temperatures and under different light intensities, the rate of unfolding and senescence of leaves was effectively constant during growth.

For sugar-beet in the field, Humphries & French (1969) found a death rate of 0.7–1.3 leaves per plant per week.

In this field trial with sugar-beet it was not originally intended to study leaf senescence. However, in a few additional plots of Treatment 5 (Fig. 1), the yellow leaves were collected every 14 days. From 18 July to 1 August three leaves turned yellow during every 14 days.

3.1 Losses due to leaf fall

To be able to estimate the losses due to leaf fall the following assumptions were made:

1. that gathering the yellow leaves from plants in the field did not affect the maturing of the other leaves,
2. that there was no significant difference in number of dead leaves from the plants of the various nitrogen treatments according to the findings of Loomis & Nevins (1963),
3. that during maturation the area and the dry weight of the leaves did not change appreciably.

Assumption 3 had to be made because the dry weight and the area of the dead and yellow plant material was not measured.

Based on these assumptions the losses in dry weight and leaf area during this trial were calculated from data of the five oldest living laminae and petioles (see Section 2.3). The 3/5 part (three leaves were lost per 14 days) of the dry weight and leaf area of this group of laminae and petioles was considered to be the losses in the next 14-day period.

As the first yellow leaves were observed on 18 July, the first losses could be expected in the period from 18 July to 1 August.

The calculated losses of dry material of laminae and petioles and the losses of leaf area are given in Table 4 for all the 14-day periods.

The loss in leaf area was highest in August and September with values between 0.5 and 0.7 m^2 leaf area m^{-2} soil area (Table 4). The total accumulated loss in leaf area during the growth season was lowest for Treatment 1 (pre-sowing nitrogen dressing only), mainly because the losses in September and October were lower for Treatment 1 than for the other treatments.

Higher losses in leaf area in August and September at a constant rate of loss of leaves means that the laminae lost during these months are larger than the laminae lost before and after this period. So, the first laminae formed must have been smaller than those formed later. With the assumed loss of three leaves per 14 days, the largest laminae must be situated somewhere between the fourth and the fifteenth leaf. The

Table 4. Calculated losses throughout the season of dry weight and leaf area of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data								Total
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10	
a. Losses of leaf area (m^2 leaf area·m^{-2} soil area)									
1		0.33	0.55	0.57	0.52	0.46	0.41	0.37	3.20
2		0.38	0.57	0.54	0.55	0.53	0.53	0.46	3.56
3				0.59	0.60	0.56	0.50	0.43	3.63
4						0.63	0.55	0.49	3.89
5								0.49	3.89
b. Losses of dry matter from laminae (g·m^{-2})									
1		19.0	31.8	34.8	40.2	28.8	25.8	24.6	205.0
2		22.4	33.0	34.2	39.0	36.6	31.2	30.0	226.4
3				32.4	45.0	39.0	29.4	29.4	236.6
4						36.0	35.4	31.2	235.4
5								31.2	235.4
c. Losses of dry matter from petioles (g·m^{-2})									
1		11.0	25.8	28.2	36.0	33.6	33.6	35.4	203.6
2		13.4	23.4	27.6	30.0	37.8	43.6	39.0	214.8
3				28.8	34.8	41.4	44.6	40.8	227.2
4						41.4	44.4	37.8	224.0
5								36.6	222.8
d. Losses of dry matter from petioles and laminae (g·m^{-2})									
1		30.0	57.6	63.0	76.2	62.4	59.4	60.0	408.6
2		35.8	56.4	61.8	69.0	74.4	74.8	69.0	441.2
3				61.2	79.8	80.4	80.0	70.2	463.8
4						77.4	79.8	69.0	459.4
5								67.8	458.2

laminae that formed later did not have such a large area before they died off.

The loss in dry matter of the laminae, showed a similar trend to the loss in leaf area (Table 4b), and was highest from 29 August to 12 September for all the treatments. So the laminae formed first were lighter than those formed later. The heaviest lamina was situated somewhere between the ninth and the twelfth one.

The overall picture for the loss in dry weight of petioles shows increasing loss throughout the growth period with only a small loss for the last period from 10 October to 24 October (Table 4c).

The accumulated dry matter loss of shoots for the entire season, based on the assumptions mentioned before, was lowest for Treatment 1 with a value of 409 $g \cdot m^{-2}$ (±4000 kg $DM \cdot ha^{-1}$) (Table 4d). For the other treatments the loss was about 460 $g \cdot m^{-2}$ (±4600 kg $DM \cdot ha^{-1}$). These dry matter losses were about 70–100% of the yield of shoots on 24 October (see Section 3.2.2).

In Sections 3.3 and 4.4 some arguments are given that these calculated losses of dry matter are not more than 25% too high.

Although these losses in leaves were calculated with some assumptions, it is clear that they are substantial and that they may not be ignored when discussing growth or uptake of minerals for this crop (see Section 4.1).

3.2 Yield analysis

In this section the growth of sugar-beet during this experiment is first described in the conventional way, without taking into account the calculated losses. In the second part, the calculated losses are included as part of the dry matter produced.

3.2.1 Yield analysis without allowing for calculated losses

The main data describing the production of this sugar-beet crop are given in Table 5.

The dry weight of the shoots was highest for treatments 4 and 5 (well fertilized) and lowest for Treatment 1 (once fertilized with nitrogen) (Table 5a). Shoot yield reached a maximum of ±4500 kg dry matter per hectare on 29 August with Treatment 1 and a maximum of ±6600 kg dry matter per ha on 26 September with Treatment 5. After these maxima, the dry weight of the shoots decreased, mainly because of high dry matter losses. The data for Treatment 3 were irregular.

Although there were great differences in shoot yield between the treatments, the data of the dry matter yield of roots were almost the same (Table 5b).

As was expected, there were large differences in the data for leaf area index (Table 5c). The effect of an extra nitrogen dressing on 4 July, 1 August and 29 August was clearly shown by the sharp increase of the LAI measured 14 days after the extra dressing. The similar results obtained for treatments 4 and 5 on 10 October and 24 October showed that the extra nitrogen dressing on 26 September did not increase the LAI further.

Between the treatments the differences in sugar yield were small (Table 5d), although there is an indication that the sugar yield for Treatment 5 was lower than for the treatments 1, 2 and 3.

There were marked differences in the percentage sugar and the percentages dry matter of the shoot and root (Table 5e, f and g). The highest percentages were found

Table 5. Yield data of a sugar-beet crop during the growth period with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Dry matter yield of the shoot ($g \cdot m^{-2}$)								
1	148	310	379	449	410	398	366	366
2	175	313	415	504	519	470	570	435
3			431	551	636	509	540	574
4					649	664	642	622
5							651	621
b. Dry matter yield of the roots ($g \cdot m^{-2}$)								
1	71	231	395	595	808	1074	968	985
2	70	208	392	566	698	863	912	1051
3			381	579	734	815	900	1062
4					743	803	1010	967
5							914	937
c. Leaf area index ($m^2 \cdot m^{-2}$)								
1	1.48	2.41	2.58	2.44	2.10	1.90	1.55	1.30
2	1.76	2.80	3.00	2.86	2.42	2.43	2.40	1.81
3			3.37	3.31	3.01	2.59	2.20	2.39
4					3.63	3.11	2.98	2.67
5							2.86	2.58
d. Sugar yield ($g \cdot m^{-2}$)								
1	42	147	264	418	566	773	728	733
2	40	131	247	404	462	610	659	793
3			234	410	496	622	667	787
4					510	566	687	689
5							614	695
e. Sugar content as percentage of fresh root weight								
1	8.01	10.85	12.04	14.39	15.33	16.84	17.87	18.08
2	7.13	9.63	10.97	13.45	14.51	16.06	16.85	17.65
3			9.96	12.27	12.50	15.25	16.09	17.13
4					13.74	14.37	14.69	15.60
5							14.32	16.50
f. Percentage dry matter of the shoot								
1	8.8	9.8	10.1	11.2	12.6	12.9	13.9	14.9
2	8.0	8.8	9.7	11.1	11.7	11.8	12.4	13.7
3			8.8	10.1	11.2	11.0	12.1	11.9
4					10.4	10.8	11.7	11.9
5							11.7	11.4

Table 5. Continued.

Treatment	Yield Data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
g. Percentage dry matter of the root								
1	13.5	17.1	18.0	20.5	21.7	23.4	23.8	24.3
2	12.5	15.4	17.2	18.9	21.6	22.7	23.3	23.4
3			16.2	17.3	18.5	20.1	21.7	23.1
4					20.0	20.4	21.6	21.8
5							21.2	22.2
h. Dry weight of sugar-free root ($g \cdot m^{-2}$)								
1	29	84	131	177	242	301	240	252
2	30	77	145	162	236	253	253	258
3			147	169	228	193	233	275
4					233	237	323	278
5							300	242

in the treatments with the lowest nitrogen dressing and the lowest percentages with Treatment 5. Again, the data of treatments 4 and 5 were almost identical.

The percentages sugar, based on fresh weight of the beets, increased gradually with time up to 24 October. Maximum value was 18.08% for Treatment 1 and 16.50% for Treatment 5. The influence of the extra nitrogen dressings on 4 July, 29 August and 26 September can be seen from the smaller increase in percentage sugar, in the harvest after the date of dressing, than with the treatments without additional fertilizer.

The percentages dry matter of roots and shoots, however, decreased (shoots) or remained equal (roots) in the first 14 days (20 June up to 4 July). Thereafter these percentages increased gradually with a faster increase for roots than for shoots. The sugar-free root weight increased rapidly until about 12 September (Table 5h). Thereafter the increase was slow and irregular. The increase in weight of the treatments with low nitrogen dressing was almost zero.

The percentage sugar, based on the root dry weight, was about 60% on 18 July and increased gradually until 24 October. On this date, the values were 70–75%, the highest for the low fertilized treatments.

The leaf area index (LAI) for the different groups of laminae is shown in Table 6. The greatest differences between the treatments were seen from the leaf area of the 'rest of the laminae', the youngest laminae (Table 6c). Especially for this group of laminae the area was smallest for Treatment 1. With increasing nitrogen fertilization this area increased. The same increase was observed in the area of the laminae 1–5 (Table 6a) and the laminae 6–10 (Table 6b), although the differences between the treatments were much smaller than in the group 'rest of the laminae'.

On 24 October the difference in leaf area index between treatments 1 and 5 was

Table 6. Leaf area index during the season of different groups of leaves of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Leaf area index of the five oldest living laminae ($m^2 \cdot m^{-2}$)								
1	0.55	0.91	0.94	0.87	0.77	0.68	0.62	0.50
2	0.64	0.95	0.90	0.91	0.88	0.88	0.76	0.72
3			0.99	1.00	0.93	0.83	0.72	0.77
4					1.05	0.92	0.82	0.76
5							0.81	0.85
b. Leaf area index of the laminae 6–10 ($m^2 \cdot m^{-2}$)								
1	0.60	0.70	0.79	0.66	0.60	0.51	0.48	0.40
2	0.73	0.86	0.77	0.76	0.67	0.60	0.59	0.45
3			0.91	0.86	0.82	0.67	0.57	0.56
4					1.02	0.78	0.72	0.62
5							0.63	0.61
c. Leaf area index of the rest of the laminae ($m^2 \cdot m^{-2}$)								
1	0.32	0.79	0.86	0.90	0.74	0.71	0.45	0.42
2	0.39	1.00	1.38	1.19	0.87	0.95	1.05	0.65
3			1.47	1.46	1.25	1.10	0.90	1.06
4					1.57	1.42	1.43	1.29
5							1.42	1.16

0.35 for the 5 oldest living laminae, 0.20 for the laminae 6–10 and 0.75 for the 'rest of the laminae'.

During the experiment the number of laminae from the plants were counted, starting with leaves of an area larger than 1 cm^2 (number 1 on the scale; see Section 2.6). The number of measurable living laminae was the same for all treatments until about 15 August. Thereafter, there were 2.5 laminae more in Treatment 5 than in Treatment 1. There were more laminae than are accounted for in the tables, because many were too small to handle.

The dry-matter yield for the living laminae and petioles of the different groups (Table 7) was lower for Treatment 1 from 12 September onwards; for Treatment 2 it was only lower on 24 October. From 12 September onwards the laminae and petioles of the leaves 1–5 for treatments 2 and 3 were heavier than those of the leaves 6–10. The same holds for the treatments 4 and 5 from 26 September onwards. Up to the end of August the dry weight of the petioles of the leaves 1–5 and 6–10 was lower than the corresponding weight of the laminae. In September and October just the opposite was so. The laminae of the leaves 1–5 and 6–10 were remarkably heavy on 29 August.

The dry-matter content of the different groups of laminae (Table 8a, b and c) was always higher than the corresponding contents in the petioles (Table 8d, e and f).

Table 7. Dry matter yield during the season of different groups of laminae and petioles of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Dry matter yield of the laminae 1–5 ($g \cdot m^{-2}$)								
1	32	53	58	67	48	43	41	41
2	38	55	57	65	61	52	50	48
3			54	75	65	49	49	57
4					60	59	52	53
5							52	57
b. Dry matter yield of the laminae 6–10 ($g \cdot m^{-2}$)								
1			48	62	38	34	31	26
2			47	76	49	35	40	31
3			52	70	58	38	38	42
4					63	45	48	43
5							39	41
c. Dry matter yield of the rest of the laminae ($g \cdot m^{-2}$)								
1	51	82	41	81	42	41	30	29
2	64	94	74	72	56	57	65	42
3			73	88	90	56	56	79
4					98	85	91	95
5							92	78
d. Dry matter yield of the petioles 1–5 ($g \cdot m^{-2}$)								
1	18	43	47	60	56	56	59	42
2	23	39	46	50	63	73	65	53
3			48	58	69	66	68	70
4					69	74	63	60
5							61	71
e. Dry matter yield of the petioles 6–10 ($g \cdot m^{-2}$)								
1			49	58	47	46	44	29
2			46	56	57	55	55	34
3			58	63	74	50	54	51
4					81	64	62	53
5							53	54
f. Dry matter yield of the rest of the petioles ($g \cdot m^{-2}$)								
1	35	84	45	70	48	48	30	27
2	44	91	68	78	71	68	80	39
3			83	101	111	73	66	81
4					112	110	113	106
5							99	81

Table 8. Percentage dry matter during the season of the different groups of laminae and petioles of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Percentage dry matter of the laminae 1–5								
1	9.0	9.2	10.1	13.2	11.9	11.7	12.8	14.6
2	8.9	9.4	10.7	12.7	11.9	11.3	12.3	13.6
3			9.3	13.6	12.1	11.2	12.6	13.4
4					11.4	10.7	10.8	12.9
5							11.5	12.5
b. Percentage dry matter of the laminae 6–10								
1			11.1	16.5	12.7	12.3	13.5	14.4
2			11.2	17.5	13.9	11.8	12.6	14.0
3			11.0	15.3	12.8	11.4	12.7	14.3
4					12.1	11.0	11.9	13.1
5							11.3	12.7
c. Percentage dry matter of the rest of the laminae								
1	11.2	11.3	11.4	17.8	12.6	12.7	14.2	14.7
2	10.4	10.9	11.2	13.9	12.6	12.2	12.2	14.4
3			10.5	12.1	13.6	11.7	13.2	13.8
4					12.6	10.8	11.9	13.4
5							12.2	13.2
d. Percentage dry matter of the petioles 1–5								
1	7.0	8.3	9.3	10.8	11.1	11.4	12.0	11.8
2	6.4	7.5	8.5	9.1	9.7	10.6	10.1	11.7
3			7.8	9.1	8.5	9.6	10.4	10.4
4					8.7	8.6	9.5	9.7
5							9.1	9.8
e. Percentage dry matter of the petioles 6–10								
1			10.0	11.1	11.5	11.3	12.8	12.4
2			8.7	10.1	10.4	11.2	10.9	12.1
3			8.4	8.9	9.7	9.9	11.0	11.6
4					9.4	9.0	10.3	9.8
5							9.8	10.4
f. Percentage dry matter of the rest of the petioles								
1	7.3	9.1	9.8	11.0	11.5	11.9	12.4	12.9
2	6.7	8.1	8.1	10.3	10.1	11.5	11.1	12.3
3			8.3	9.2	10.0	10.5	11.1	10.8
4					9.8	9.2	10.3	10.6
5							9.5	10.5

Table 9. Dry matter yield and percentage dry matter during the season of the crowns of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Dry matter yield ($g \cdot m^{-2}$)								
1	7	19	26	52	56	60	46	56
2	10	29	32	44	54	53	92	68
3			32	71	68	82	69	86
4					69	93	108	83
5							98	91
b. Percentage dry matter								
1	15.2	17.2	17.0	19.6	20.6	21.2	21.7	22.7
2	13.8	15.6	14.8	17.6	19.1	19.7	20.1	21.2
3			15.4	17.4	18.5	18.9	19.4	19.1
4					17.6	17.9	18.7	19.6
5							17.9	18.5

Furthermore this content was always higher when less nitrogen was applied. Throughout the season the dry-matter content of the youngest laminae and petioles was nearly always higher than the content in the oldest laminae and petioles. In the beginning of the season the dry-matter contents of laminae and petioles of the leaves 6–10 were highest. Gradually the dry-matter contents of this group of leaves reached values in between those of the other two groups.

The dry-matter yield of crowns was low early in the season, but increased up to very fluctuating values late in the season (Table 9a). This fluctuation was connected with the way the plants were harvested (see Section 2.3).

A more regular pattern was shown by the dry matter content of the crowns. These values were somewhat lower than the dry matter content of the roots (Table 9b). Again, these percentages were higher when less nitrogen was applied.

3.2.2 Yield analysis, including calculated losses

If the yield data of Section 3.2.1, are compared with those of this section the main changes will be found in the data for shoot yield, for yield of laminae and petioles and for leaf area. To obtain the data of Table 10, the total loss in the period before a certain harvest date was added to the dry-matter yield or leaf area of the living plant material on this particular date. The result was a gradual increase in leaf area and shoot dry weight troughout the season instead of a decrease later in the season, as indicated by the actual harvest data (compare Table 10 with Table 5a and c).

The LAI, calculated for the case when no leaves had died off, showed a decrease in rate with diminishing applications of nitrogen (Table 10a). Only the last nitrogen

Table 10. Calculated yield data of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data							
	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
a. Calculated leaf area index ($m^2 \cdot m^{-2}$)								
1	1.48	2.73	3.45	3.88	4.06	4.32	4.38	4.50
2	1.76	3.18	3.95	4.35	4.46	5.00	5.50	5.37
3			4.32	4.85	5.15	5.29	5.40	6.02
4					5.77	5.96	6.38	6.56
5							6.26	6.47
b. Calculated dry matter yield of shoots ($g \cdot m^{-2}$)								
1	144	311	404	601	561	619	629	659
2	178	343	464	593	634	691	818	755
3			494	670	767	726	790	930
4					785	840	928	952
5							884	931
c. Calculated dry matter yield of the laminae ($g \cdot m^{-2}$)								
1	83	154	199	296	254	274	282	301
2	102	171	234	302	295	309	350	347
3			235	311	346	315	349	415
4					354	358	395	426
5							386	412
d. Calculated dry matter yield of the petioles ($g \cdot m^{-2}$)								
1	54	138	179	253	251	285	301	302
2	66	143	198	247	285	329	376	340
3			227	288	353	329	372	429
4					362	389	425	443
5							400	428
e. Calculated total dry matter yield ($g \cdot m^{-2}$)								
1	215	542	799	1196	1369	1693	1597	1644
2	248	551	856	1159	1332	1554	1730	1806
3			875	1249	1501	1541	1690	1992
4					1528	1643	1938	1919
5							1798	1868

dressing on 26 September did not influence this leaf area. About one month after the time of application of additional nitrogen, the increase in LAI was about 0.5 unit.

The same continuous increase with time was found in the calculated dry weight of shoots (Table 10b). This increase in dry weight of shoots was lower when less nitrogen was applied, except for Treatment 4. The dry weight of shoots was calculated by adding the actual dry matter weight of living laminae and living petioles, including the accumulated losses (Table 10c and d), and the dry weight of the crowns (Table 9a). This calculation was necessary because the dry weight material, actually harvested, (Table 5a) always contained some dead plant parts. The data for Treatment 3 were

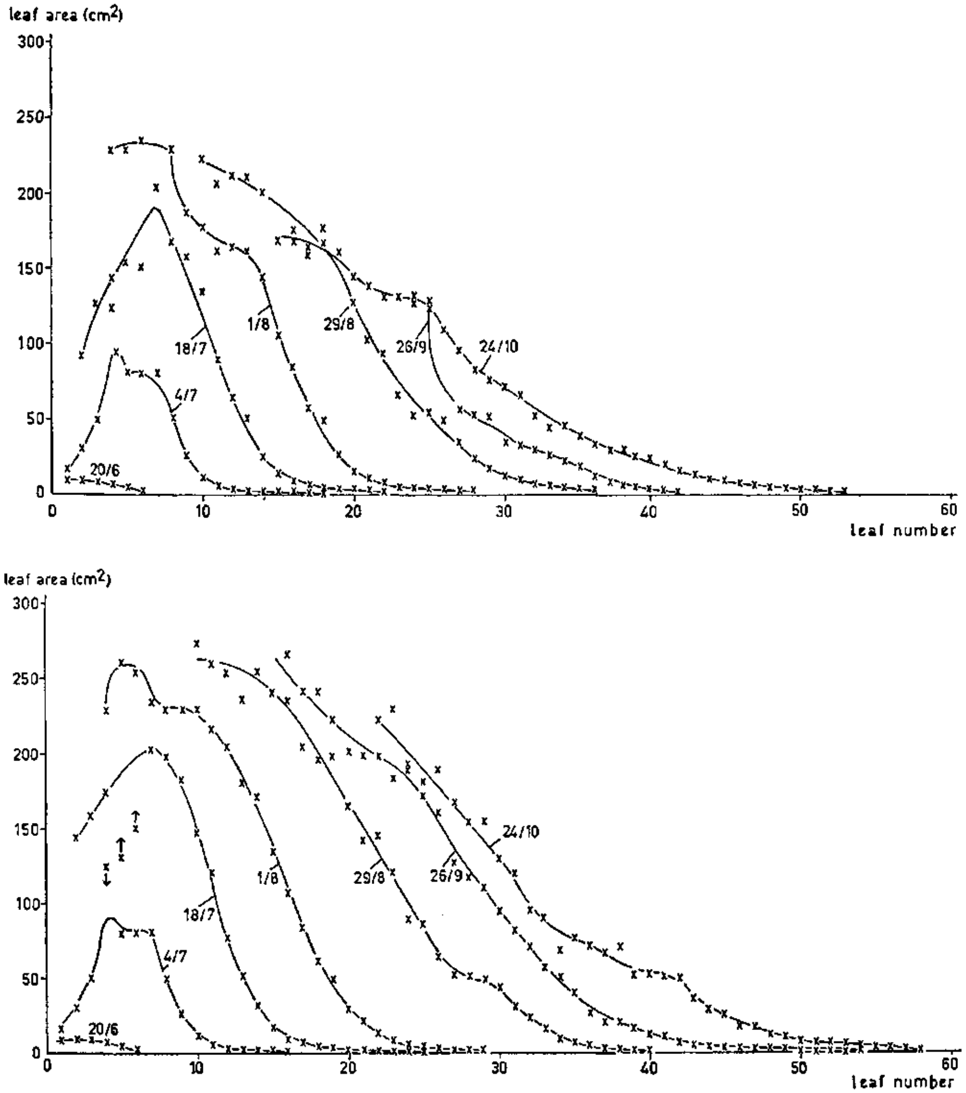


Fig. 2. Seasonal changes in area of leaves of a sugar-beet plant with low rates of nitrogen (Treatment 1, on top) and a high rate of nitrogen (Treatment 5, below).

unfortunately very irregular.

The gradual increase in the calculated dry weight of shoots is reflected both in the calculated dry weight of laminae and of petioles (Table 10c and d).

From the extreme treatments 1 and 5, the leaf area per lamina (average of 10 measurements) was calculated. With the assumption that three leaves died per 14 days, figures 2a and b were constructed. These diagrams give an impression about the formation of the leaf area of sugar-beet with time.

The laminae formed first never became large. The largest lamina of Treatment 1 was situated around leaf number 8 (harvest on 15 August) and of Treatment 5 around leaf number 13 (harvest on 12 September). The laminae formed earlier died off without becoming as large and the later formed ones never reached this size. The largest mean area of laminae of this sugar-beet crop was 260–280 cm^2. Starting in August, many laminae of the plants of Treatment 5 reached this mean value. The plants of Treatment 1 developed somewhat later only 1–2 laminae with an area of this mean value.

3.2.3 Distribution of dry matter

According to the classical conception of the development of a sugar-beet plant in the first (vegetative) year three phases can be distinguished.

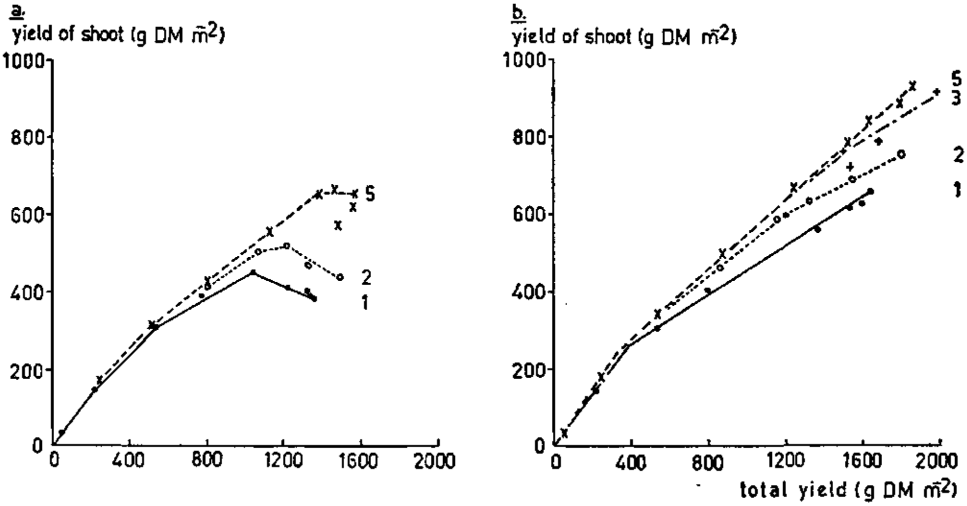
1. A phase of leaf development, in which most of the dry matter produced is used to build up a leaf canopy by formation of new leaves and by expansion of the existing leaf.
2. A beet forming phase, in which most of the dry matter produced is used for the growth of the beet.
3. A ripening phase, in which much sugar accumulates in the root.

A 'phase of development' is indicated if the dry matter yield of a plant part and the total dry matter produced show a linear relationship (van de Sande Bakhuysen, 1937, 1950). According to van de Sande Bakhuysen (1937, 1950), the distribution of dry matter produced is constant within one growth phase. When a next phase is entered the direction of the line changes abruptly.

In Fig. 3 the shoot dry weight is plotted against total dry matter produced. In Fig. 3a these dry weights are the actual harvested amounts. In Fig. 3b the calculated losses are added to the harvested living amounts. In Fig. 3c the calculated losses are reduced by 25% (see Sections 3.3 and 4.4).

The curves in Fig. 3a for both the extreme treatments (5 and 1) are built up from three straight lines. The first straight part of the curve is the same for both treatments and ends somewhere between 17 July and 1 August. In this first development phase, about 60–70% of the dry matter produced is used for shoot growth. In the second part of these curves this percentage is much lower, which indicates an enhanced root growth. Here there is a clear difference between the treatments: the lower the nitrogen dressing the less dry matter is stored in the shoot. Between the end of August and the beginning of September this distrubition pattern changes again. The curves then indicate that all the dry matter produced is stored in the roots. The actual gain in dry weight of the roots is even higher, because of dry matter loss due to leaf fall.

In Fig. 3b, however, the pattern is quite different. Here, the actual living shoot and total dry weight are both corrected for the calculated losses. The first part of the curve, which is almost the same for all treatments, continuous until a point between 17 July and 1 August. In this first phase about 70% of the dry matter produced is used for shoot growth and only 30% for root growth. In the second part of the



c. as b but the calculated losses reduced by 25%

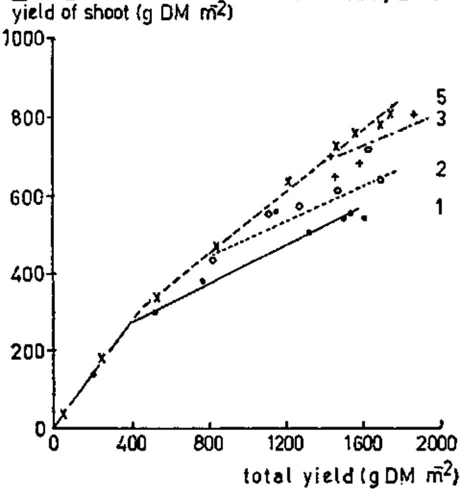


Fig. 3. Relation between actual harvested (a) and calculated (b and c) shoot and total dry weight of a sugar-beet crop with different rates of nitrogen.

curve the distribution pattern for the treatments diverge: for Treatment 1 about 70% of the dry matter produced is now used for root growth and 30% for shoot growth; for Treatment 5 55% for root growth and 45% for shoot growth. As soon as the extra nitrogen dressings are stopped in treatments 2 and 3, the distribution pattern becomes similar to that of Treatment 1.

In Fig. 3c the calculated dry weight losses are reduced by 25%. The pattern of the curves is the same as in Fig. 3b, only the distribution data in the second part of the curves is different. In this case 40 and 26% of the dry matter produced is used for shoot growth for treatments 5 and 1, respectively.

In Fig. 4 the calculated dry weight of laminae and petioles is plotted against the calculated total dry weight. Here again, the points are in two straight lines. In the first phase, in which the data for the treatments 1 and 5 are almost equal, about 40%

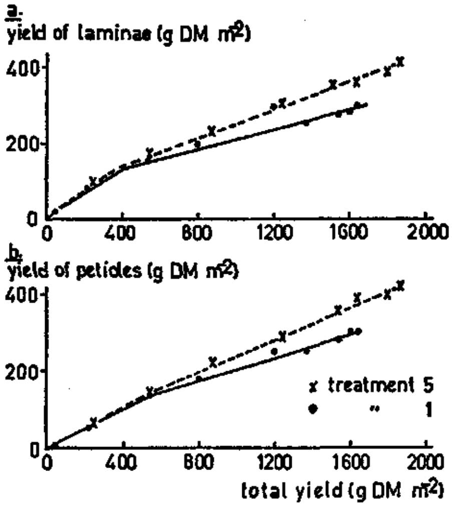


Fig. 4. Relation between calculated dry weight in laminae (a) and petioles (b) and total calculated dry weight of a sugar-beet crop with different rates of nitrogen.

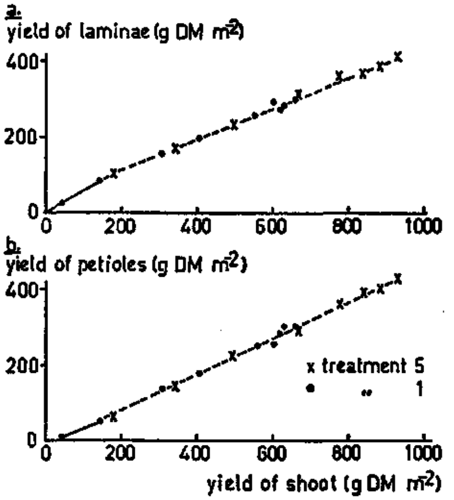


Fig. 5. Relation between calculated dry weight in laminae (a) and petioles (b) and calculated shoot dry weight of a sugar-beet crop with different rates of nitrogen.

of the dry matter produced is used for the growth of the laminae and about 25% for the growth of the petioles. In the second part of these curves the lines for the treatments 1 and 5 differ so that in Treatment 1 a smaller amount of the total dry matter produced is used for the growth of petioles and laminae than in Treatment 5.

In Fig. 5 the calculated dry weights of laminae and petioles are plotted against the calculated dry weight of shoots. Here it is shown that the distribution of dry matter within the shoot is the same for both the extreme treatments, and does not change when the calculated losses are reduced by 25%. The difference between the treatments is the higher yield for Treatment 5 compared with Treatment 1. In the first phase, which is now, at least for the petioles, less pronounced, about 60% of

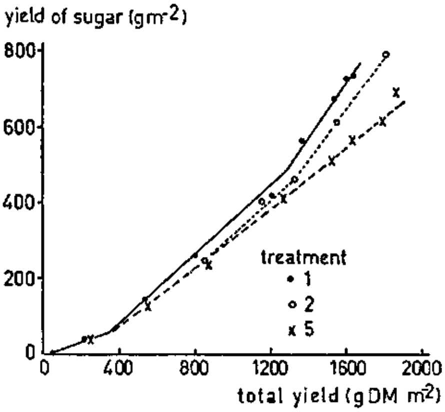


Fig. 6. Relation between the sugar yield and the calculated total dry weight of a sugar-beet crop with different rates of nitrogen.

the dry weight of shoots is stored in the laminae, 35–40% in the petioles and the remainder (0–5%) in the crowns. In the second phase, these data are ±40% for the laminae, ±50% for the petioles and the remainder for the crowns.

In Fig. 6 the sugar yield is plotted against the total calculated dry matter. In the first phase, until the end of June, about 17 g out of 100 g total dry matter produced is stored as sugar. In the second phase this amount increased to 40 g for Treatment 5. Up to September about 48 g per 100 g total dry matter produced is stored as sugar for Treatment 1. Still later in the season this increases to about 70 g, or 74 g when the calculated dry weight losses are reduced by 25%. This implies that for Treatment 1 the total increase of dry matter in the root in this last period is sugar and that there is almost no increase in sugar-free root dry weight (Table 5h).

All these distribution figures are summarized in Table 11.

Treatments 2, 3 and 4 tend to maintain their distribution pattern as in Treatment 5 as long as enough nitrogen is present. They change to the distribution pattern of

Table 11. Distribution of the calculated dry matter (%) in different plant parts of a sugar-beet crop with different rates of nitrogen.

	Shoot				Root		
	petiole	laminae	crown	total	sugar	sugar-free	total
Growth period 1 (till the end of July)							
Treatment 1 and 5	25	40	0–5	70	17	13	30
Growth period 2 (end of July–end of October)							
Treatment 1 beginning	13–(16)[1]	9–(13)	4	26–(32)	48	20–(26)	68–(74)
Treatment 1 later on	13–(16)	9–(13)	4	26–(32)	68–(74)	–	68–(74)
Treatment 5	20–(23)	16–(18)	4	40–(45)	40	15–(20)	55–(60)

1. Depending on the way of calculation.

Table 12. Percentage of ground covered by the shoot of a sugar-beet crop.

Date	20 June		5 July		19 July	
Angle of incidence	30°	60°	30°	60°	30°	60°
Percentage ground cover	5	3	60	43	ca. 100	ca. 100

Treatment 1 when there is sufficient nitrogen for unlimited growth under these circumstances. This means that the third phase, the ripening phase, only shows up when there is a lack of nitrogen.

3.2.4 Soil covering rate

In the beginning of the experiment, the percentage of soil covered by leaves, was measured by looking through a camera obscura at a plot, (Baeumer & de Wit, 1968). The camera obscura was placed at the corners of the plot and made an angle with the field of 30 or 60 degrees. As the camera was rotated, it was noted whether spots on an arc of the plot were covered by plant material or not.

In the very beginning of the growth of this sugar-beet crop, on 20 June, the percentage of soil, covered by the shoots, was very small (Table 12). But about 14 days later, half of the field was covered and another 14 days later almost the entire soil area was covered by plant material.

3.2.5 Growth rates

The growth rate (GR) in $g \cdot m^{-2}$ soil area per week was calculated with $GR = (W_2 - W_1)/(t_2 - t_1)$, in which W = dry weight of the crop, and t = time.

This growth rate can be calculated for the whole crop or for every plant part such as shoot and root; similarly the accumulation rate for sugar can be estimated. Furthermore, these growth rates can be calculated from the actual harvest values or from the calculated harvests. In the latter case, the growth rates give an impression about the rate of new production of dry matter.

As soon as leaves die off, the crop growth rates, based on the calculated harvest data, are higher than the corresponding rates, based on the actual harvests. The crop growth rate (CGR), based on the calculated harvest data (Table 13) increased from about 100 $g \cdot m^{-2} \cdot week^{-1}$ ($= \pm 140$ $kg \cdot ha^{-1} \cdot day^{-1}$) in the beginning of July to 180–200 $g \cdot m^{-2} \cdot week^{-1}$ (=260–280 $kg \cdot ha^{-1} \cdot day^{-1}$) at the end of August. In September and October these rates were lower, but unfortunately fluctuated. The mean values for the period 4 July – 29 August (period of more or less linear growth) and for the period 29 August – 24 October (period of diminishing growth) were much higher in the first period than in the second period. The lowest CGR values were found in treatments 1 and 2. The crop growth rate, based on actual harvested yields,

Table 13. Growth rate of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data										
	4/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10	4/7–29/8	29/8–24/10
a. On the basis of calculated yields ($g \cdot m^{-2} \cdot week^{-1}$)											
1		85	163	129	198	82	162	−48	24	144	56
2		100	151	153	151	82	111	88	38	139	81
3				162	187	126	20	75	151	150	93
4						140	58	147	−10		84
5								72	35		77
b. On the basis of actual (harvested) yields ($g \cdot m^{-2} \cdot week^{-1}$)											
1		86	161	116	135	87	137	−69	8	125	38
2		98	138	143	132	73	58	74	2	128	52
3				145	159	120	−23	58	98	136	63
4						131	38	92	−31		57
5								50	−4		54

Table 14. Rate of increase in dry weight of sugar-beet shoots with different rates of nitrogen.

Treatment	period 4/7–29/8	period 29/8–24/10
a. On the basis of calculated yields ($g \cdot m^{-2} \cdot week^{-1}$)		
1	71	7
2	69	20
3	79	33
4		36
5		32
b. On the basis of actual (harvested) yields ($g \cdot m^{-2} \cdot week^{-1}$)		
1	52	−11
2	58	−9
3	65	3
4		9
5		9

showed the same trend as the crop growth rate, based on calculated yields, but with lower data.

The data for the rate of increase of the shoot dry weight in the two different growth periods showed high values in the first period with somewhat lower values for treatments 1 and 2 (Table 14). The calculated rates of increase in shoot weight for the second period (29 August – 24 October) showed that for Treatment 1 new shoot material was also produced. This production of new material was seen in the field

Table 15. Rate of increase of dry weight and sugar in roots of a sugar-beet with different rates of nitrogen.

Treatment	Yield data										
	4/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10	4/7–29/8	29/8–24/10
a. Rate of increase of dry weight ($g \cdot m^{-2} \cdot week^{-1}$)											
1		31	80	82	100	106	133	−53	8	73	49
2		31	69	92	87	66	82	24	70	70	61
3				86	99	78	41	42	81	71	60
4						82	30	103	−21		48
5								56	11		45
b. Rate of accumulation of sugar ($g \cdot m^{-2} \cdot week^{-1}$)											
1		18	52	58	77	74	103	−22	3	52	39
2		18	45	58	78	29	74	25	67	50	49
3				51	88	43	63	23	60	51	46
4						50	23	60	1		35
5								23	40		36

too, although it did not show up in the rate of increase of shoot dry weight, based on the actual harvested amounts. When the calculation was based on actual harvested amounts this rate of increase of shoot dry weight was even negative.

In the very beginning the rate of increase of root dry weight and the sugar accumulation rate were low (Table 15). Thereafter these rates increased till at the end of August the highest production rates were obtained. In September and October these rates were lower, but still high compared with the rate of increase of shoot dry weight (Table 14).

The rate of increase of the leaf area index was very high in the first weeks of the growth period and afterwards decreased (Table 16). Between the treatments the differences were clear from the beginning. The rate of increase of measured leaf area was already negative for all treatments at the end of August. This indicates, as was explained earlier, that the losses in leaf area in this period were already higher than the newly formed leaf area.

To calculate the net assimilation rate (NAR), a quadratic relationship between dry weight and leaf area was assumed (see Chapter 1). This function fitted the data very well up to the end of August. From that time the measured leaf area decreased with increasing total dry weight. Only the actual harvested values were used in the calculation, because the leaves that had fallen off did not contribute any more to the production. The results gave high values of 60–80 $g \cdot m^{-2} \cdot week^{-1}$ in the beginning of the growth period (Table 17). Then NAR decreased to very low values and late in the season even became negative.

In the same way as for the NAR, a sugar accumulation rate was calculated. This sugar accumulation rate represents the increase in g $sugar \cdot m^{-2}$ leaf area per week.

Table 16. Rate of increase in leaf area index of sugar-beet with different rates of nitrogen.

Treatment	Yield data										
	4/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10	4/7–29/8	29/8–24/10
a. On the basis of calculated leaf areas ($m^2 \cdot m^{-2} \cdot week^{-1}$)											
1	0.46	0.62	0.36	0.21	0.09	0.13	0.03	0.06		0.42	0.08
2	0.60	0.71	0.38	0.20	0.06	0.27	0.25	−0.07		0.48	0.13
3			0.57	0.26	0.15	0.07	0.05	0.31		0.54	0.15
4					0.46	0.10	0.21	0.09			0.21
5							0.15	0.10			0.20
b. On the basis of measured leaf areas ($m^2 \cdot m^{-2} \cdot week^{-1}$)											
1	0.46	0.46	0.08	−0.07	−0.17	−0.10	−0.17	−0.13		0.24	−0.14
2	0.60	0.52	0.10	−0.07	−0.22	0.00	−0.01	−0.30		0.26	−0.13
3			0.28	−0.03	−0.15	−0.21	−0.20	0.09		0.35	−0.12
4					0.16	−0.26	−0.06	−0.15			−0.08
5							−0.13	−0.14			−0.09

Table 17. Net assimilation rate of a sugar-beet crop with different rates of nitrogen.

Treatment	Yield data								
	4/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
On the basis of measured leaf area and actual (harvested) total dry weight ($g \cdot m^{-2}$ *leaf area* $\cdot week^{-1}$)									
1	85	83	47	58	38	25	5	6	
2	86	61	49	28	28	24	31	−1	
3			47	48	38	−8	24	43	
4					38	11	30	−11	
5							17	−1	

Table 18. Sugar accumulation rate of sugar-beet with different rates of nitrogen.

Treatment	Yield data								
	4/7	18/7	1/8	15/8	29/8	12/9	26/9	10/10	24/10
On the basis of measured leaf areas ($g \cdot m^{-2}$ *leaf area* $\cdot week^{-1}$)									
1	18	27	23	31	33	27	15	2	
2	15	20	20	27	11	30	10	32	
3			17	26	14	22	9	26	
4					14	8	20	0.4	
5							8	15	

Again, a quadratic relationship between sugar weight and leaf area was assumed. This function fitted the data fairly well for the beginning of the season. This rate was lower for treatments which were fertilized with nitrogen repeatedly (Table 18). For most treatments the highest rates were found in August.

3.3 Discussion

Because the sugar yields of the treatments were almost equal (Table 5d) the discussion of the results of this field trial is restricted to the effects of split nitrogen dressings and to the effects of the calculated losses on the various characteristics.

The calculation of losses in leaf area and dry matter, both due to leaf fall, was based on several assumptions (Section 3.1). One assumption, namely that the leaf area and especially the dry weight of a leaf will not change during senescence, is questionable. Normally, dry material of different origin will be transported from older leaves to younger developing leaves and to the root (see also Section 4.5). To get an idea about the amount translocated, let us suppose that the amount of organic nitrogen (N-Kjeldahl) translocated to younger plant parts during the period of senescence of older leaves is about 85 proteins$\cdot$kg^{-1} dry matter (see Section 4.4). The amount of dry matter in the leaves at the end of their life span has therefore decreased by 8–10% with this form of nitrogen transport.

The estimate for the loss of dry matter, based on 3/5 part of the five oldest, living leaves that die off in the 14 days after a harvest date, was too high, at least in the beginning of the growth period. In this period the dry weight of each of the succeeding numbered laminae increased up to a maximum till about leaf number 12[1]. The losses in dry weight as calculated in this experiment were again about 8–10% too high because the differences in weight of the succeeding leaves were neglected[1].

For these reasons, the dry matter losses due to leaf fall were calculated again assuming that the earlier calculations were about 25% too high (see Section 4.4).

The calculated losses in this experiment for the different treatments should therefore be considered as maximum losses. They were for the LAI 3.2–3.9 units (Table 4a) and for the dry matter 4100–4600 kg$\cdot$ha^{-1}. When the calculated dry matter losses were reduced by 25%, the loss of dry matter was 3000–3400 kg dry matter$\cdot$ha^{-1}.

The number of leaves lost during the growing season was calculated to be 21 per plant in this experiment with a plant density of 75000 plants$\cdot$ha^{-1}. At a lower plant density (67000 plants$\cdot$ha^{-1}), Humphries & French (1969) found a loss of 17–18 leaves per plant at the end of the season.

Although loss of leaves in the period of increasing leaf area and shoot dry weight have been reported (French & Humphries, 1969; Humphries & French, 1969; Loomis & Nevins, 1963; Follet et al., 1970; Loach, 1970) literature only gives data of losses as a decrease in shoot dry weight and as a decrease in leaf area in the last part of the

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[1] F. van Egmond, pers. commun.

season. The leaf area losses (as LAI), calculated from the growth curves and data of Follet et al., (1970) and Storer et al., (1970) were 2–3.5 units. They were lower when extra nitrogen was applied later in the season (Loomis & Nevins, 1963; Campbell & Viets, 1967). The shoot dry matter losses were very low or zero when calculated from the data of Follet et al. (1970), or of the order of 2000–3000 $\text{kg} \cdot \text{ha}^{-1}$ when calculated from the data of van Ginneken (1966) and Lüdecke & Nitzsche (1959).

When the calculated losses of leaf dry weight are included in the production pattern of this sugar-beet crop, a growth scheme can be developed, which in some respects is different from the generally accepted growth schemes. A production pattern is the distribution of the total dry matter produced over the different plant parts in time.

When enough nitrogen was available for unlimited growth in this crop situation, the development of the sugar-beet crop could be divided into two phases. In the first phase, which lasted till the end of July, about 70% of the produced dry matter was used for shoot growth and the remainder for root growth. In the second phase these percentages were 40–45 for shoot growth and 55–60 for root growth. A third phase of development, the 'ripening phase' (van de Sande Bakhuysen, 1950; Bouillenne et al., 1940) was not found. The crop, dressed with an amount of nitrogen too low for unlimited shoot growth (Table 5a, Treatment 1), stored 26–32% of the dry matter produced in the shoots and the remainder in the roots in the second phase[2]. In this treatment with a restricted nitrogen dressing, the 'normal' pattern of enhanced root growth was found. A third growth phase became evident at the moment that no more sugar-free dry matter accumulated in the roots (Fig. 6). In Treatment 5 up to the end of the growth period sugar-free dry matter was formed in the roots. In treatments 2 and 3 the distribution of the dry matter produced changed as soon as the nitrogen became more or less depleted. From that time onwards the distribution of the produced dry matter was almost equal to that of the plants of Treatment 1 (Fig. 3). The same holds for the distribution within the root (Fig. 6). This suggests that the ripening phase (van de Sande Bakhuysen, 1950; Bouillenne et al., 1940) may be a physiological status induced by a limited availability of nitrogen for shoot growth. It is also possible that the ripening phase is described in literature because losses due to leaf fall have been ignored.

Normally, the measured quotient shoot dry weight over root dry weight decreases throughout the season. A value of 0.7–0.8 at the time of harvest is supposed to be optimum for sugar yield (Lüdecke & Müller, 1965). The distribution pattern of dry material in this experiment between shoot and root (Table 11) implies that this value is more than one in the first development phase and gradually decreases to less than one in the second phase. This decrease in value during the growth season will be also found for the calcaluted yield, but the decrease will be faster when dry matter losses are ignored. In this experiment the quotient shoot dry weight/root dry weight for the measured yield decreased from 2.1–2.5 in the middle of July to 0.37 (Treatment 1)

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[2] The amount of nitrogen was, however, sufficient to develop a leaf area which covered the soil completely.

and 0.66 (Treatment 5) at the final harvest. Based on the calculated shoot yields, this value decreased to 0.68 and 0.99 respectively, or, if the calculated losses were reduced by 25%, to 0.57 and 0.88, respectively. So, even with a low value of 0.37, based on actual harvest data, a high sugar yield of 7000 $\text{kg}\cdot\text{ha}^{-1}$ was obtained.

The distribution of dry matter within the shoot was equal for all treatments (Fig. 5). In the first development phase, more dry matter was used in growth of laminae (± 60%) than in growth of petioles (35–40%). In the second growth phase just the opposite was the case (± 40 and ± 50% resp.). The same enhanced growth of laminae in the beginning of the season has been reported often in literature (Milford & Watson, 1971; Humphries & French, 1969; French & Humphries, 1969; Follet et al., 1970). Therefore the quotient laminae dry weight over petiole dry weight will be more than one in the beginning of the season and gradually decrease to less than one at the end of the season. The values of the quotient in this experiment were 1.5–1.6 on 18 July and 0.9–1.0 at the final harvest. This decrease was enhanced by the loss of leaves because the dead leaves had higher quotients than the living ones.

The distribution of dry matter in the root between sugar and non-sugar material was also the same for all treatments until no more sugar-free dry matter was built up in the roots. In the first development phase about 60% of the weight increase of the beets was sugar and 40% was non-sugar. In the second phase these percentages were ± 70 and ±30 respectively. This distribution pattern is also seen from the sugar percentage on dry matter basis. In the first phase it was almost 60% and in the second phase it increased gradually to ± 75% (Treatment 1) and ±70% (Treatment 5).

There was a clear linear relationship between the percentage sugar (on fresh weight basis) and the percentage dry matter of the root (Fig.7). In this experiment the percentage dry matter of the roots minus 4.5 equals the sugar content. Nitzsche & Winner (1970) found for several experiments with sugar beets in different years the relation:

$$\%\ \text{dry matter} - 6.8 = \%\ \text{sugar}$$

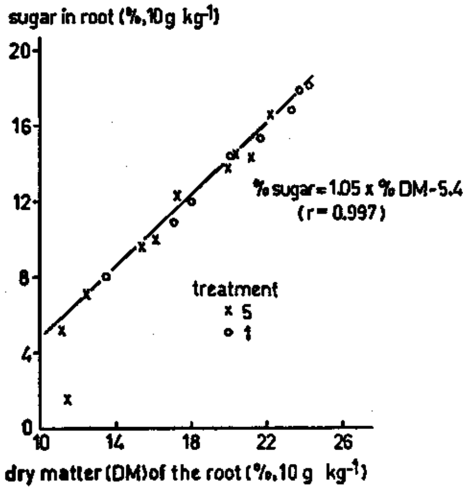

Fig. 7. Relation between the percentage sugar and percentage dry matter of the root during the growth season of a sugar-beet crop with different rates of nitrogen.

This relation indicates that it is very difficult to observe a difference in distribution of dry material within the roots as a result of differences in the nitrogen fertilization.

The marked change in development from phase one to phase two in this experiment was somewhere between 18 July and 1 August. In that period the soil was entirely covered with foliage (Table 12). Because of the late sowing date (5 May) the change over from phase one to phase two was relatively late in the season. The date at which the soil was fully covered was also late for the same reason. It was not clear what the reason was for the marked change in development of this sugar-beet crop. That the soil was covered completely at that time could be a coincidence.

In the period, when the soil was not completely covered by green cover, the main part of the dry weight increase was used for the growth in size and number of laminae. During this period the dry matter production per unit leaf area per week (NAR, Table 17) was highest for the entire growth period. The same holds for the increase in leaf area (Table 16). Later in the growth season these values decreased. A decrease with time of NAR is in agreement with data presented by Watson (1958), Campbell & Viets (1967), Storer et al. (1970), Follet et al. (1970) and others. A high NAR in the early period means that the leaves, present at that time, produce dry matter most efficiently. These leaves were also very efficient in producing sugar (sugar accumulation rate, Table 18) and new leaf area (Table 16). The highest values of NAR were reached in this experiment with a LAI of 1.5–2.0 (Table 5c), which is lower than that found by Campbell & Viets (1967), Storer et al. (1970) and Follet et al. (1970). They found the highest values for NAR when LAI was between 2–4. However, radiation, earliness of the crop and a more or less erect position of the leaves will also influence these LAI values for maximum NAR (Follet et al., 1970).

The most efficient leaves which arise early in the season, however, do not grow large, especially the leaves formed first had small laminae (Fig. 2a and b). The same was found by French & Humphries (1969), Humphries & French (1969) and Fernando (1958, cited by Watson (1963)). Excluding the coleoptiles, the largest leaves were situated around leaf number 8 for Treatment 1 and around leaf number 13 for Treatment 5 with a largest mean area of 260–280 cm^2. The leaves formed later were smaller again.

The course of development in area and weight of the leaves could be explained by the following hypothesis. The relative small number of leaves present in the beginning of development are subject to stronger competition with the newly formed leaves than leaves formed in the later stages of development. Although the leaves formed first are very active in production, the material produced is transported rapidly elsewhere to form new leaves and root. Thus the early formed leaves have less oppertunity to increase their own area and weight. Later formed leaves, around leaf number 10 and higher, are in a much less competative situation. The need for the supply of dry material for the formation of new leaves is now divided over numerous older leaves and therefore enough assimilate is available to enlarge their own area. The number of leaves that could reach the mean maximum area in this experiment was also restricted by nitrogen. About 15 leaves from Treatment 5 could enlarge their mean area to at

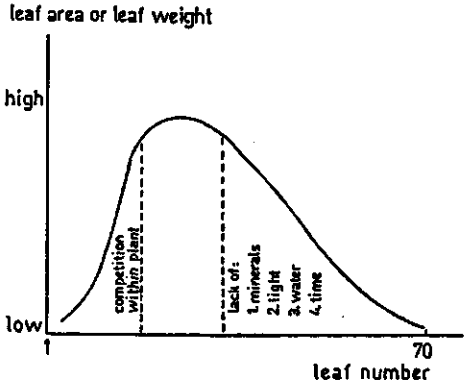

Fig. 8. Development of the area and weight of subsequent leaves of a sugar-beet plant.

least 200 cm^2, but only two leaves from Treatment 1 (Fig. 2a and b) reached that mean maximum. Individual leaves reached much larger areas, even more than 600 cm^2. The leaves that developed later than those with a mean maximum area and weight, were also in a less competative situation than the earlier ones. However, these leaves could not grow large due to lack of nutrients (N), light (lower light intensities and shadowing), water, and possibly other growth factors. Furthermore, for many of the leaves, developed late in the season, the available growing period was too short to reach large areas and high weights (Fig. 8).

The dry matter increase per unit soil area per week for the whole crop was highest in the beginning of the second growth period in August (Table 13). Especially the rates of increase of root dry weight and sugar (Table 15) were high in this period. The same high sugar-accumulation rate in this early period is often reported in literature (e.g. van Ginneken, 1956; Lüdecke & Nitsche, 1959). Although the rate of the dry matter production per unit leaf area in this period was lower than in the preceding period, the situation for the crop was more favourable because of still relatively high light intensities in that period together with a high LAI (Table 5c). Later in the season the accumulation rates of dry matter and sugar were lower than in the preceding period. Although the temperature decreased, the light intensity decreased even faster and therefore the dissimilation losses were relatively high. However, the leaf area in this late period was still relatively high.

The influence of extra nitrogen applications was clearly demonstrated in higher growth rates for shoots (Table 14) and for leaf areas (Table 16). These growth rates were low (Treatment 5) to very low (Treatment 1) at the end of the season, but new shoot material (dry weight and leaf area) was still produced. Each additional nitrogen dressing resulted in an extra increase of the LAI by 0.5 unit, one month after the date of application. At the same time the sugar content was reduced by about 1%. Only the last additional nitrogen dressing did not influence the growth characteristics of sugar-beet. The crop of Treatment 5 reached maximum shoot yield (based on actual data) one month later than the crop fertilized only once (Treatment 1).

The influence of nitrogen on the percentages of sugar or dry matter was clear: high

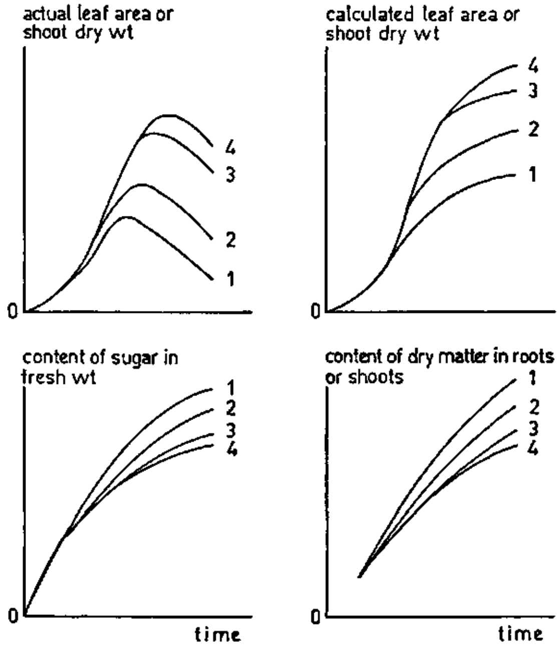

Fig. 9. Hypothetical scheme of the influence of additional nitrogen during the growth season on some growth characteristics of a sugar-beet crop (1, 2, 3 and 4 are the numbers of extra nitrogen dressings).

percentages with low nitrogen dressings and increasing values during the season. The effects of additional nitrogen dressing on some growth characteristics of sugar-beet are summarized in Fig. 9.

4 Mineral composition of sugar-beet

4.1 Losses due to leaf fall

As a result of some assumptions (Section 3.1) it was possible to get an idea about the dry weight and leaf area losses due to leaf fall. The same procedure can be followed for minerals.

The mineral composition of the dead laminae and petioles was estimated. The mineral losses were calculated by multiplying the contents on a certain harvest date by the dry weight losses in the preceding 14-day period (see section 3.1).

The calculated losses in $meq \cdot m^{-2}$ soil area are given in Table 19. In Table 20 the uptake in $kg \cdot ha^{-1}$, based on the actual amounts harvested on 24 October, is given together with the calculated uptake on the same date. This calculated uptake is the amount of minerals in the living part of the crop on 24 October increased with the accumulated losses for the entire season (Table 19). The losses were calculated a second time, assuming that the calculated losses in dry weight were 25% too high.

Although it can be expected that the losses of some elements, such as K and NO_3, are higher than calculated here (due to leaching of the leaves by rain during the period of senescence) the data from Table 20 give an impression of the total mineral uptake.

The calculated losses of minerals from Treatment 5 were nearly always higher than those from Treatment 1, especially the nitrate and N-Kjeldahl losses. The losses of Na, Ca, Mg and Cl in both treatments and NO_3 only in Treatment 1 were almost equal

Table 19. Accumulated mineral losses due to leaf fall ($meq. m^{-2}$)

	Na	K	Ca	Mg	H_2PO_4	NO_3	Cl	SO_4	N-Kj.	C−A
a. Treatment 1										
laminae	190	67	304	437	8	7	107	42	197	837
petioles	256	174	154	144	5	22	298	7	120	398
total	446	241	458	581	13	29	405	49	317	1235
75 % of total	334	181	344	435	10	22	304	37	238	927
b. Treatment 5										
laminae	249	88	350	484	10	48	115	40	360	960
petiole	307	260	157	187	5	88	393	8	252	416
total	556	348	507	671	15	136	508	48	612	1376
75 % of total	417	261	380	503	11	102	382	36	459	1030

Table 20. Uptake of minerals by a sugar-beet crop based on the harvest date at the end of the season (24 October) with and without the calculated losses (kg·ha^{-1}).

	Na	K	Ca	Mg	H_2PO_4	NO_3	Cl	SO_4	N-Kj.	C−A
a. Treatment 1										
shoot	43	82	40	21	25	2	66	18	61	75
root	3	62	12	14	37	1	12	9	55	32
uptake as harvested	46	144	52	35	62	3	78	27	116	107
calculated uptake	136	223	121	95	75	20	199	45	146	236
calculated uptake − 25 %	110	199	98	78	72	16	163	38	135	196
b. Treatment 5										
shoot	92	176	63	46	46	88	135	38	181	70
root	8	66	11	13	21	27	10	12	114	28
uptake as harvested	100	242	74	59	67	115	145	50	295	98
calculated uptake	176	347	147	116	75	164	260	53	341	234
calculated uptake − 25 %	145	314	122	96	72	143	214	48	319	200

Table 21. Uptake of minerals by a sugar-beet crop.

Fresh yield (ton·ha^{-1})		Uptake (kg·ha^{-1})						
root	shoot	Na	K	Ca	Mg	H_2PO_4	N	
42[1]	54[1]	145–176	314–347	122–147	96–116	72–75	319–341[2]	Treatment 5 (calc.)
41[1]	25[1]	110–136	199–223	98–121	78–95	72–75	135–146[2]	Treatment 1 (calc.)
42[1]	54[1]	100	242	74	59	67	295[2]	Treatment 5 (as harvested)
41[1]	25[1]	46	144	52	35	62	116[2]	Treatment 1 (as harvested)
45	20	–	195	68	54	94	180	von Boguslavski & Jacob (1957)
45	50	94	308	49	36	102	225	Lüdecke & Nitzsche (1959)
50	35	–	280	84	55	139	226	Anonymus (1967)
40	30	59–89	158–232	50–64	39–48	68–82	140–240	Lüdecke & v. Müller (1965)

1. Yield on 24 October.
2. N-Kjeldahl only.

to the actual uptake on 24 October. For K, H_2PO_4 and N-Kjeldahl in both treatments and NO_3 and SO_4 in Treatment 5 the losses were lower than the harvested uptake.

If 60% of the nitrogen fertilizer is used during the growth period, the amount of nitrogen delivered by this soil is 135–146 (actual uptake+losses)−72 (=60% of fertilized)=63–74 kg N·ha^{-1} in Treatment 1.

In a trial field of 20 cm soil depth, with an organic matter content of 3.3%, of which 50% is C, and a C/N value of 10, there is almost 3300 kg N in organic form per ha.

If mineralization is 2%, about 66 kg N becomes available for uptake during the growth period. This amount is comparable to the earlier calculated amount.

A comparison of the calculated uptake of sugar-beet with uptake data from literature (Table 21), reveals that the data from this experiment are much higher, except for phosphorus. When the losses due to leaf fall were included, the uptake of elements with high concentrations in the other plant parts was much higher (see Section 4.2.1).

Compared to the total crop, the fallen leaves were rich in Na, Ca, Mg, (C−A) and poor in N-Kjeldahl, H_2PO_4 and K.

4.2 Mineral content in different plant parts during growth

Most of the analytical data are presented in figures 10–15[3].

Naturally there are inaccuracies in the analytical data. An important error is introduced during harvesting, when the sugar-beet plants are damaged. When the plants were separated into shoot and root and during the transport to the laboratory some of the older leaves broke off. Therefore the content of an element in the laminae or petioles could refer to the group of leaves 2–6 or 7–11 instead of 1–5 or 6–10.

4.2.1 Content in laminae and petioles

The mineral content of laminae and petioles depends on leaf age and on the course of the growth season. Data are presented in figures 10–13. First the differences in mineral content of laminae and petioles of different age will be discussed.

The contents of Na, Ca, Mg, NO_3, Cl, total cations, total anions and (C−A) were higher in old laminae and petioles than in young ones. The differences in total cation content and (C−A) content between the petioles of the group 6–10 and the rest were small. The differences in the total anion content of the different groups of laminae, especially those of Treatment 1 were not clear.

The contents of K, H_2PO_4 and N-Kjeldahl in the old laminae and petioles were lower than in the young ones, except for the K content in the dead petioles. This K content was highest in most harvest data, especially in the beginning of the season. The pattern of the SO_4 content in the green laminae was the same as for the contents of Na, Ca, etc., i.e. the older the material the higher the content. The SO_4 content of the dead laminae was between the contents of the living laminae. The pattern of the SO_4 content in the living (green) petioles, however, was the same as that for the content of K, H_2PO_4 and N-Kjeldahl. The SO_4 content of the dead petioles has again an intermediate value.

The change in content with time was quite different for the minerals estimated. The Mg content in the laminae of the different groups decreased throughout the season (figs. 10 and 11). Because the Mg content was very high compared to the other cations,

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[3] If desired, the actual data are available from the Laboratory of Soils and Fertilizers, Agricultural University, Wageningen.

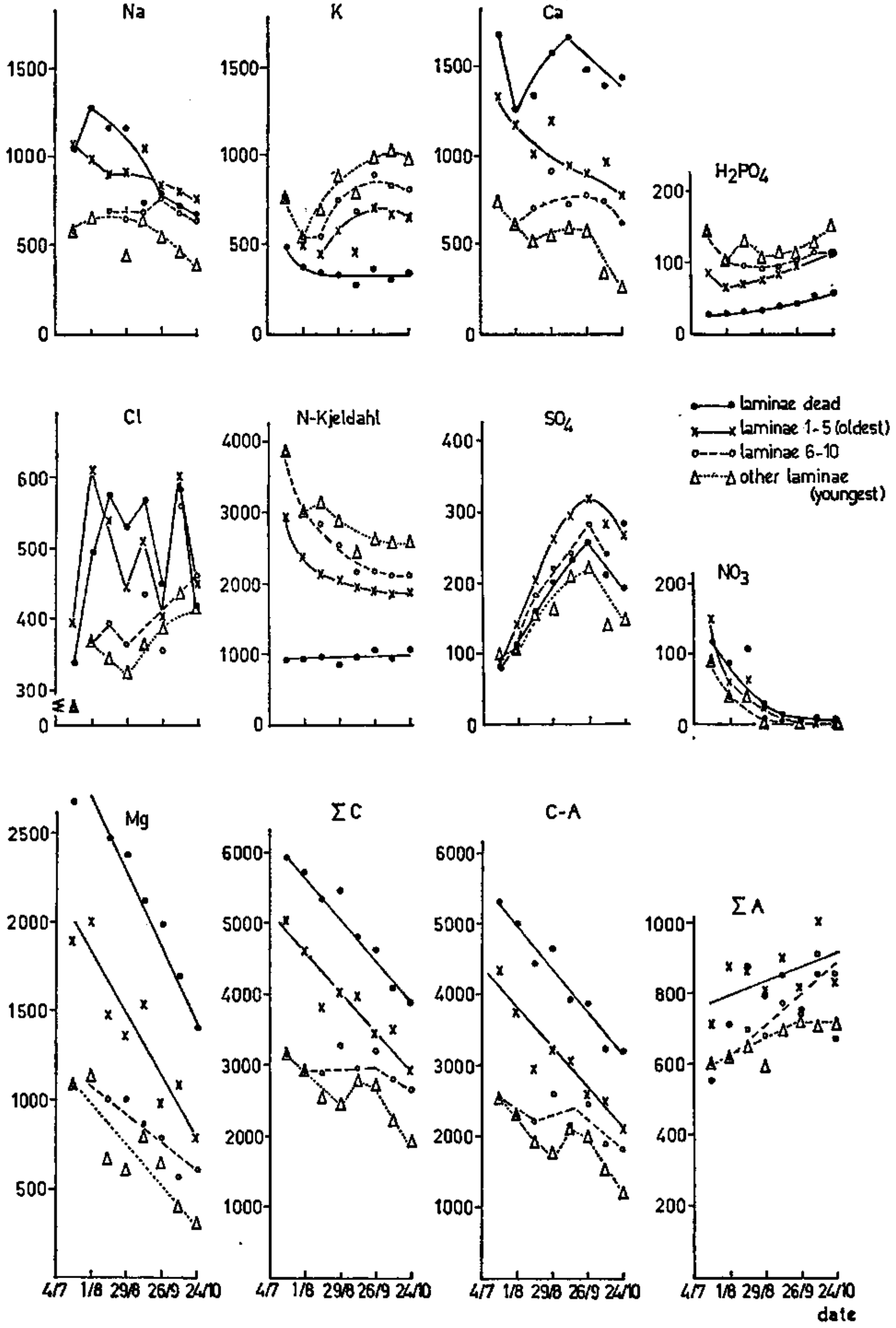


Fig. 10. Mineral content (meq·kg^{-1} dry matter) in laminae of different age of a sugar-beet crop during the season with a low rate of nitrogen.

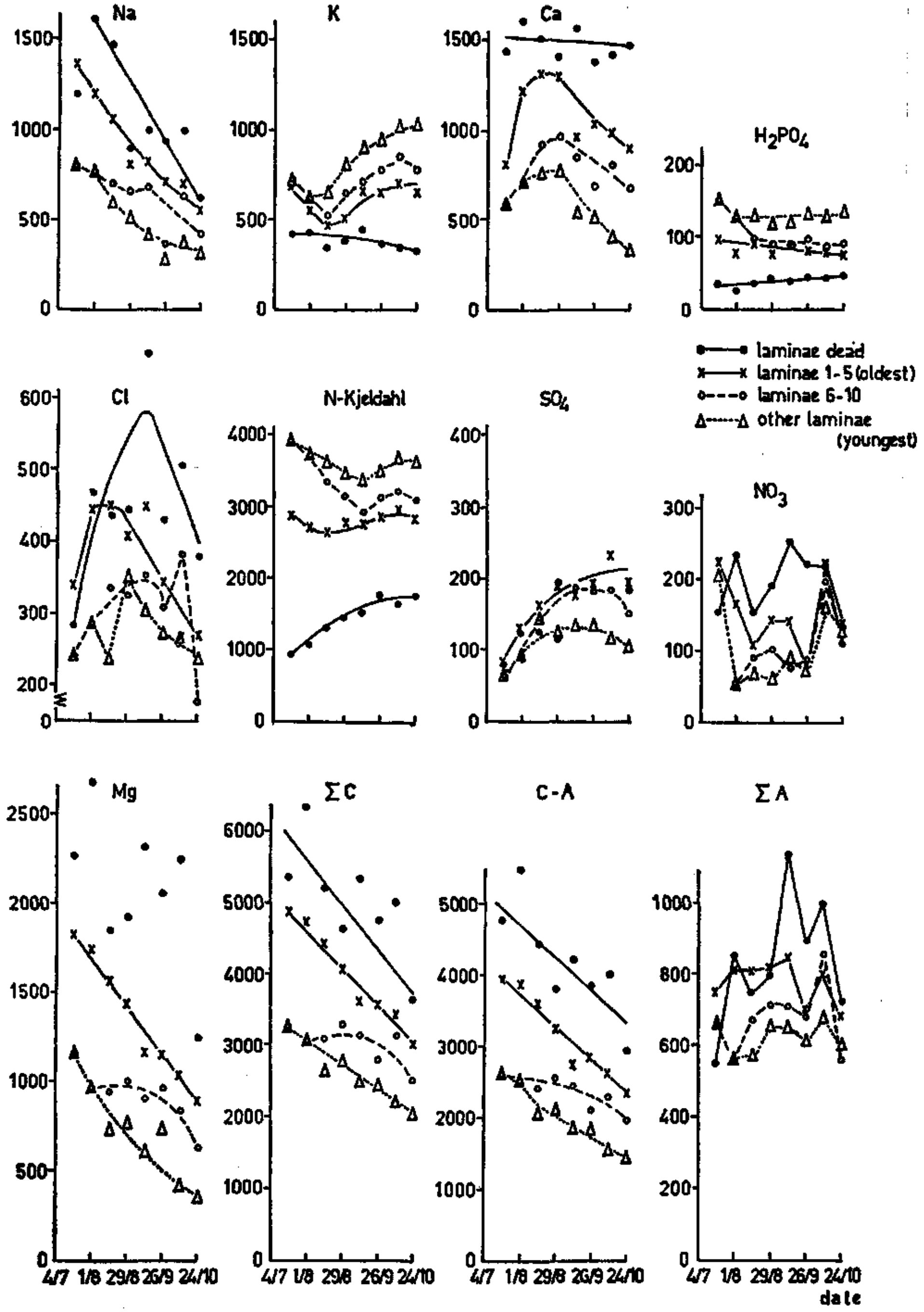


Fig. 11. Mineral content (meq·kg^{-1} dry matter) in laminae of different age of a sugar-beet crop during the season with a high rate of nitrogen.

the same decrease was found in the total cation content and also in the (C – A) content, although it was not so clear in the younger laminae.

The same decrease in content was found for Na and Ca, especially in the second half of the growth period. However, the K content in the green laminae first decreased and then steadily increased. Between treatments 1 and 5 there were large differences in the NO_3 and the N-Kjeldahl contents. For Treatment 1 the NO_3 content in the laminae decreased rapidly to a very low value in contrast to the high and fluctuating values for Treatment 5. The N-Kjeldahl content in the green laminae of Treatment 1 decreased gradually and was constant in the dead laminae. For Treatment 5 this content in the green laminae increased slightly after an initial decrease. In the dead laminae of Treatment 5, the N-Kjeldahl content increased rather quickly with time upto a more or less constant value at the end of the season. The Cl content in the laminae was very irregular. The SO_4 content increased first and decreased at the end of the season. The H_2PO_4 content was most stable with very little change in Treatment 5 and a slight increase in Treatment 1.

The mineral content of the lamina differed from that of the petiole of the same leaf. The NO_3 and Cl contents were much higher in the petioles than in the laminae (Figs. 12 and 13). Furthermore, in the beginning of the season both the Na content and the K content in the dead leaves were higher in the petioles than in the laminae.

As a result of the higher NO_3 and Cl contents in the petioles, the total anion content was also highest in the petioles. The contents of the other elements estimated were lower in the petioles than in the laminae.

During the growth period the change in mineral content in the petioles was for some elements very consistent as it was in the laminae. The NO_3 content in Treatment 1 decreased rapidly to very low values. For Treatment 5 the NO_3 content also decreased, but remained rather stable for the last two months at a much higher value than for Treatment 1. The Cl content decreased throughout the season. Because of the very high content of Cl compared with the other anions, the change in content of total anions was more or less the same as for the Cl. The SO_4 content increased after a sharp decrease in the beginning. This increase in SO_4 content was particularly evident in the youngest petioles. During the growth period, the H_2PO_4 content in the petioles was the most stable as it was in the laminae, with the exception of the youngest petioles. In the green (living) petioles the H_2PO_4 content for Treatment 5 was higher than for Treatment 1, but in the dead petioles it was equal for both treatments.

The Na content in the dead petioles decreased. In the living petioles of Treatment 1 the Na content was more or less stable. In Treatment 5, however, it fluctuated: first a decrease until the end of August and an increase thereafter. The K content decreased gradually in the dead petioles but after a sharp decrease in the beginning remained rather stable in the living petioles. At the end of the growth period there was some increase in the K content of the youngest petioles. The Ca content in the dead petioles fluctuated. In the living ones it decreased gradually, except for an initial increase in Treatment 5. More or less the same trend was found for the Mg content. The total cation content decreased throughout the season, especially in the older petioles.

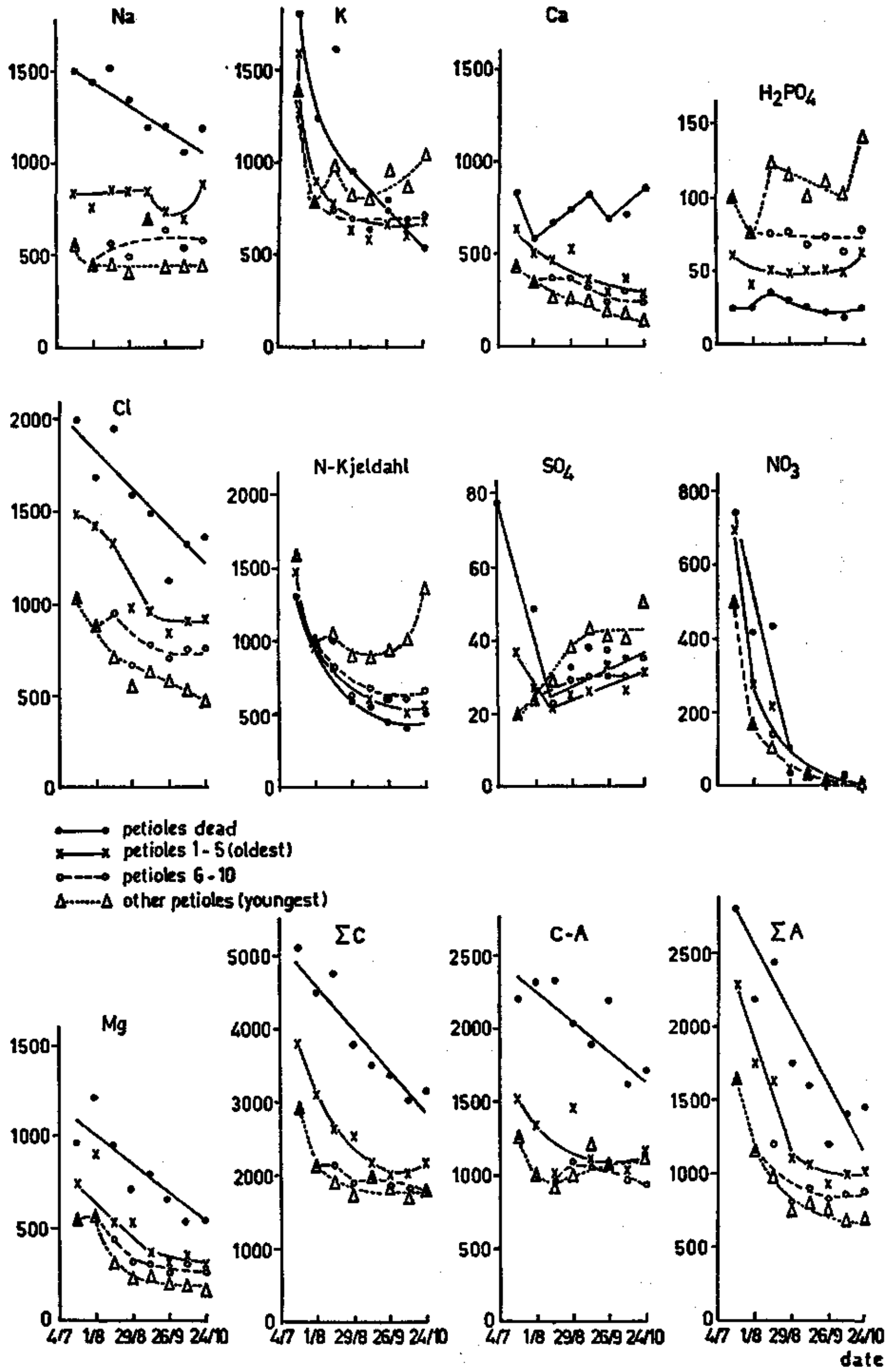


Fig. 12. Mineral content (meq·kg^{-1} dry matter) in petioles of different age of a sugar-beet crop during the season with a low rate of nitrogen.

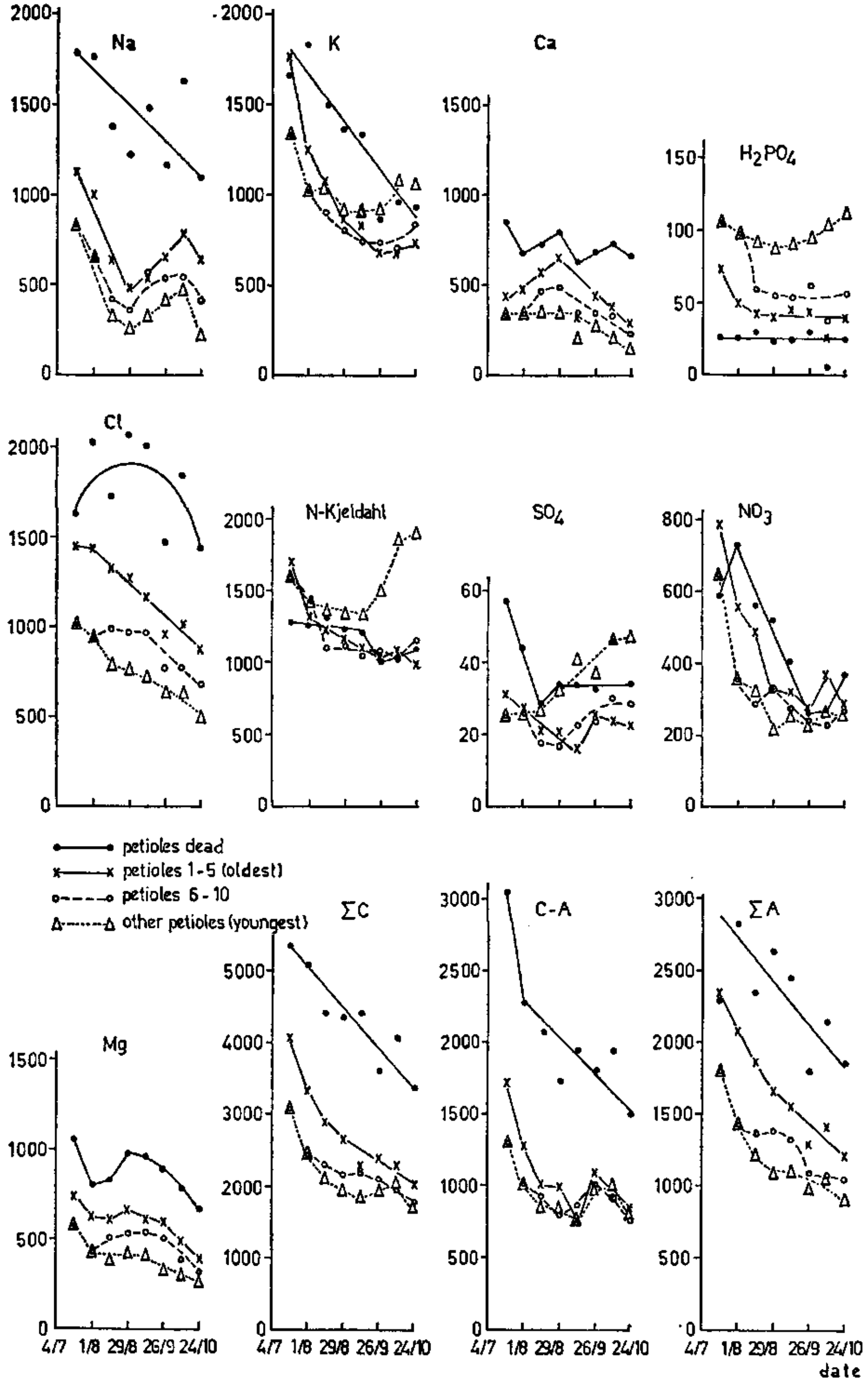


Fig. 13. Mineral content (meq·kg⁻¹ dry matter) in petioles of different age of a sugar-beet crop during the season with a high rate of nitrogen.

In the younger petioles this content was stable after a decrease in the beginning of the growth season.

The N-Kjeldahl content in the petioles decreased gradually with constant values for the last part of the growth period. The N-Kjeldahl content only increased in the youngest petioles at the end of the season.

The (C−A) content in the dead petioles decreased throughout the season. In the living petioles, however, this content did not change during August, September and October. In this period the differences in content of all groups of living petioles were very small.

4.2.2 Mineral content in shoot and root

The contents of the elements analysed in the shoot are contents of a mixture of laminae, petioles and crowns including dead leaves present in the actual harvested shoot (Fig. 14).

In young sugar-beet plants the Na content in the shoot increased from about 500 meq to 1200 $meq \cdot kg^{-1}$ dry matter. Thereafter the Na content decreased very fast till 18 July, followed by a slow decrease to about 600 $meq \cdot kg^{-1}$ dry matter at the end of the growth period. After the first extra dressing on 4 July the Na content of the shoot of plants of Treatment 5 compared to plants of Treatment 1 was first higher, then lower and at the end of the season again higher.

The Na content in the roots also increased in the first 14 days, but decreased thereafter to a low value of 10 $meq \cdot kg^{-1}$ dry matter for Treatment 1 and to about 40 $meq \cdot kg^{-1}$ dry matter for Treatment 5 (Fig. 15). During the entire growth period the Na content in the beets of Treatment 5 was always the highest. The higher Na content was a result of the additional K dressing, supplied at the same time as the extra nitrogen. The K was given as K-40, which contains about 33% NaCl.

The K content in the shoot remained at about 1300 $meq \cdot kg^{-1}$ dry matter during the first three harvest periods. During July this content decreased rapidly to 650–750 $meq \cdot kg^{-1}$ dry matter and afterwards was almost constant. The constant level was higher for Treatment 5 than for Treatment 1.

The K content in young roots on 6 June was very high (± 1370 $meq \cdot kg^{-1}$ dry matter) but decreased rapidly to about 400 $meq \cdot kg^{-1}$ dry matter at the end of July. Thereafter the content decreased gradually to about 170 $meq \cdot kg^{-1}$ dry matter. In the last period the content in the beets of Treatment 5 remained higher than in Treatment 1.

The Ca content of the shoot fluctuated. In the beginning of the growth period, the Ca content increased from 550 to 700 $meq \cdot kg^{-1}$ dry matter, at the end of the season it was 500–550 $meq \cdot kg^{-1}$ dry matter.

The Ca content in the roots dropped very fast in the first 6 weeks from 260 to ± 60 $meq \cdot kg^{-1}$ dry matter. For the rest of the season this content was stable with a somewhat higher value in the roots of Treatment 5.

The Mg content in the shoot fluctuated considerably: a sharp increase in the first 6

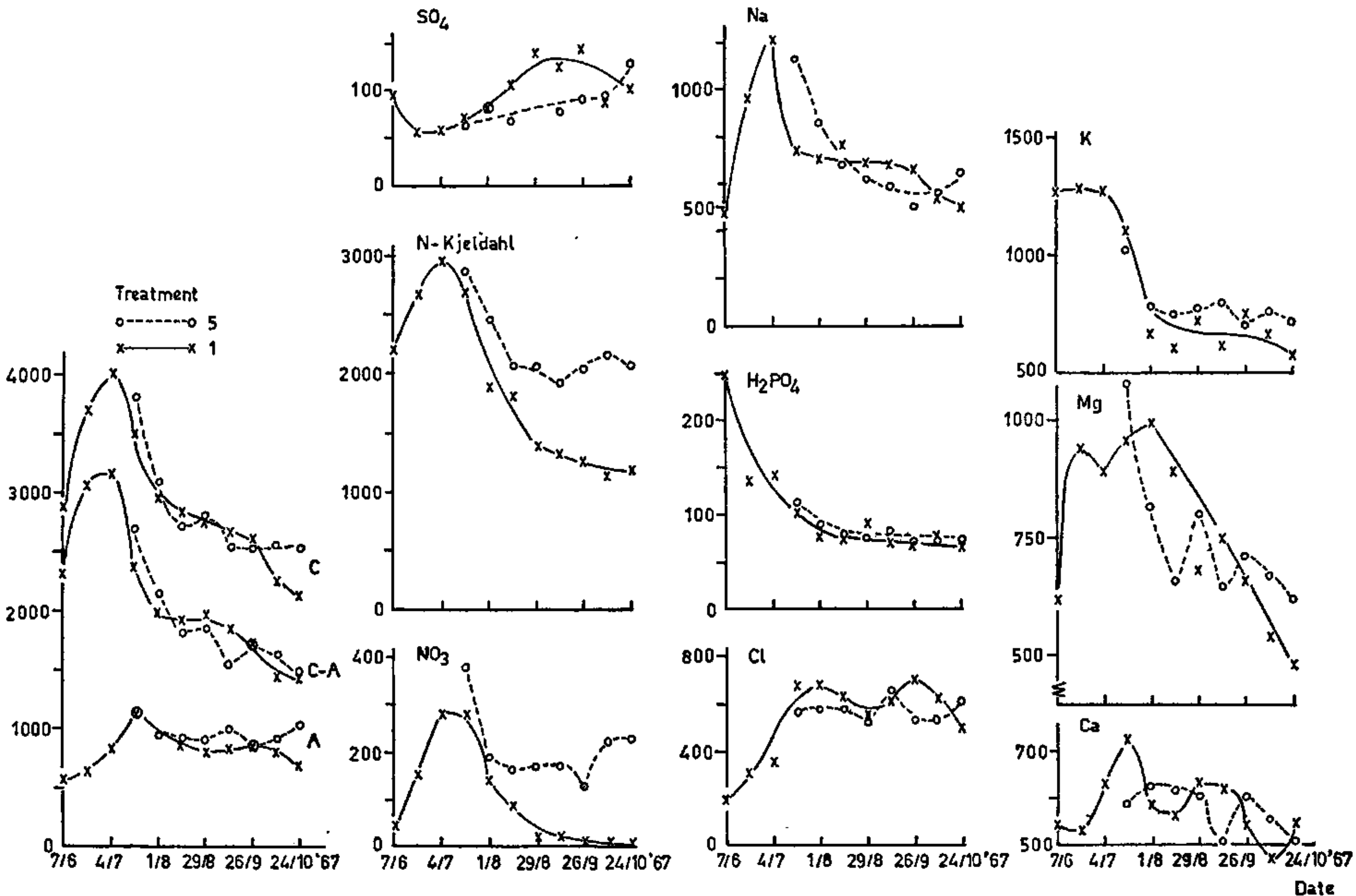


Fig. 14. Mineral content in dry matter (meq·kg^{-1}) of the shoot of a sugar-beet crop at high and low rates of nitrogen.

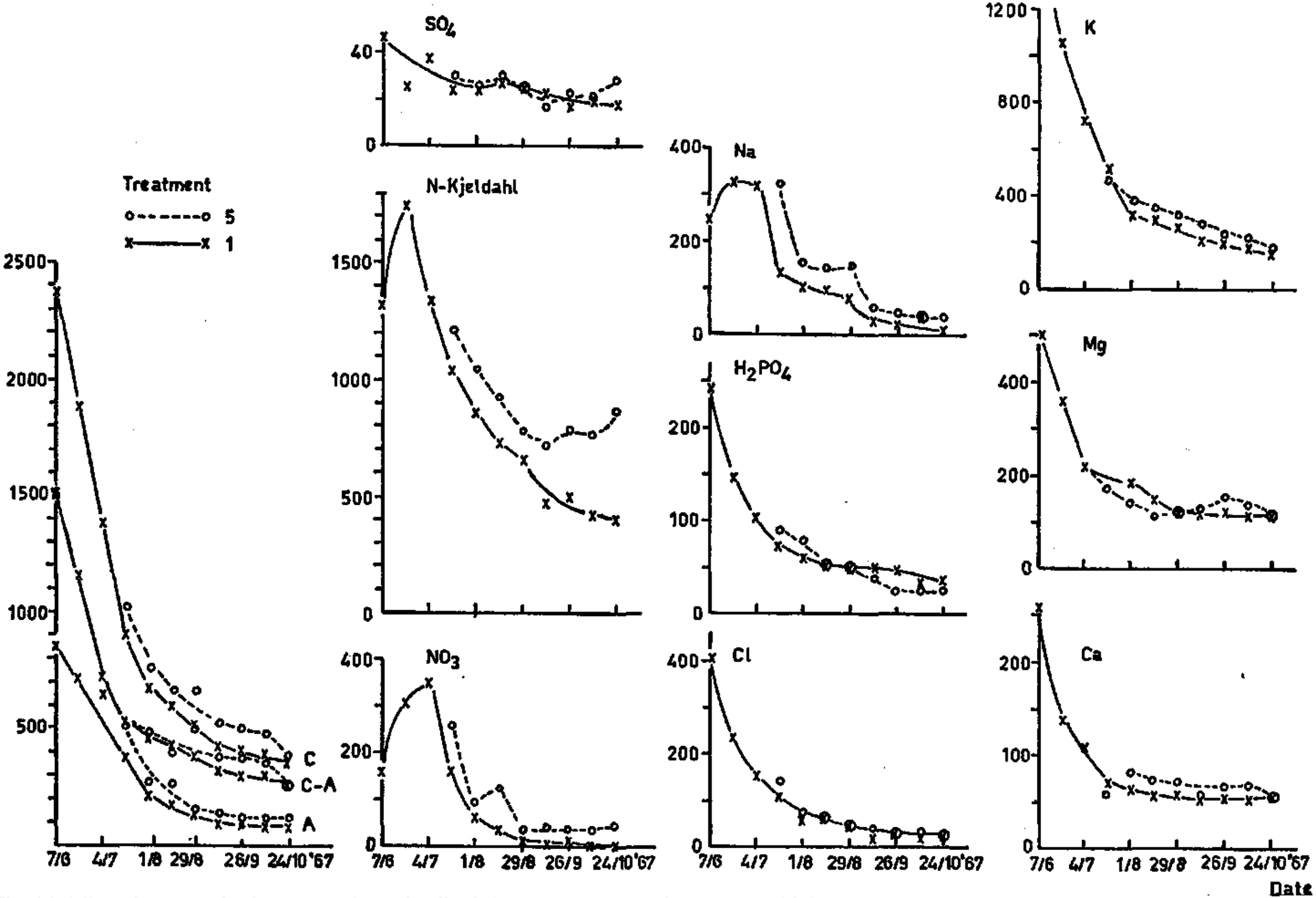


Fig. 15. Mineral content in dry matter (meq·kg^{-1}) of the root of a sugar-beet crop at high and low rates of nitrogen.

weeks followed by a decrease in content. Due to the fluctuations the differences between the two treatments were not clear.

The Mg content in the roots decreased quickly from 500 to 100-150 meq$\cdot$kg^{-1} dry matter during June and July. Thereafter the Mg content did not change very much. The differences between the treatments were small and irregular.

The NO_3 content in the shoot increased the first month from 50 to 270 meq$\cdot$kg^{-1} dry matter. Thereafter this content decreased fast to almost zero at the beginning of September for Treatment 1. The plants of Treatment 5 had a much higher nitrate content in the shoot compared to Treatment 1. During August and September, the NO_3 content in these shoots was almost constant at 170 meq$\cdot$kg^{-1} dry matter. Due to the last extra nitrogen dressing on 26 September, the nitrate content increased to about 220 meq$\cdot$kg^{-1} dry matter.

The NO_3 content in the roots increased in the first month from 150 to 350 meq$\cdot$kg^{-1} dry matter and decreased thereafter to almost zero at the end of August for Treatment 1. In the beets of Treatment 5 the NO_3 content became more or less constant at 40 meq$\cdot$kg^{-1} dry matter at the end of August.

The Cl content in the shoots increased in the beginning of the season from 200 to about 600 meq$\cdot$kg^{-1} dry matter. For the rest of the growth period it fluctuated around this value. On most harvest dates the content for Treatment 5 was somewhat lower than for Treatment 1.

For both treatments the Cl content in the roots was equal. It decreased from 400 meq$\cdot$kg^{-1} dry matter for very young beets to 30 meq$\cdot$kg^{-1} dry matter in mature beets.

The SO_4 content in the shoots decreased from 100 to 50 meq$\cdot$kg^{-1} dry matter in the first 14 days and increased thereafter gradually to about 125 meq$\cdot$kg^{-1} dry matter at the end of the growth period. The SO_4 content in the shoots of Treatment 5 was for most of the season lower than that in the shoots of Treatment 1.

The SO_4 content in the roots was equal for both the treatments and it decreased gradually from 40 to 20 meq$\cdot$kg^{-1} dry matter.

The H_2PO_4 content in the shoots decreased fast from 250 meq $\cdot$ kg^{-1} dry matter in the beginning of the season to 75 meq $\cdot$ kg^{-1} dry matter in the beginning of August For the rest of the growth period this content varied little. The differences between the two treatments were negligible.

The H_2PO_4 content in the roots showed more or less the same trend as in the shoots. Only in August, September and October did it decrease somewhat. The H_2PO_4 content in the roots on 24 October were 40 and 25 meq $\cdot$ kg^{-1} dry matter for the treatments 1 and 5, respectively.

The N-Kjeldahl content (almost N-organic) in the shoots increased from 2200 to 3000 meq $\cdot$ kg^{-1} dry matter in the beginning of the season. In Treatment 1, this was followed by a sharp and later by a gradual decrease to a content of 1200 meq$\cdot$kg^{-1} dry matter on 24 October. The N-Kjeldahl content in the shoots of Treatment 5 decreased from 3000 to 2000 meq$\cdot$kg^{-1} dry matter on 15 August and remained more or less constant for the rest of the season.

In the roots, the N-Kjeldahl content increased in the first 14 days form 1300 to

1750 meq·kg^{-1} dry matter. Then it decreased gradually to 400 meq·kg^{-1} dry matter in the beets of Treatment 1. For Treatment 5 it decreased to 700 meq·kg^{-1} dry matter on 12 September and then increased to almost 900 meq·kg^{-1} dry matter on 24 October.

An overall picture of the contents of the different minerals is presented as the sum of anions (A), the sum of cations (C) and the (C – A) content.

The total cation content in the shoots showed only small differences between the two treatments. After an increase from 2900 to 4000 meq·kg^{-1} dry matter in the first month, the total cation content decreased to a value of 2200 – 2600 meq·kg^{-1} dry matter at the end of the season. Only in the last month was the total cation content in shoots of well fertilized plants higher than that in the plants dressed with less nitrogen.

The total cation content in very young sugar-beet roots was very high (2400 meq·kg^{-1} dry matter). However, it decreased first sharply and then gradually to about 400 meq·kg^{-1} dry matter on 24 October. During the whole season the total cation content of the beets of Treatment 5 was about 100 meq·kg^{-1} dry matter higher than that in the beets of Treatment 1.

The total anion content in the shoots increased in the first 6 weeks from 600 to about 1000 meq·kg^{-1} dry matter and fluctuated for the rest of the season between a value of 800 and 1000 meq·kg^{-1} dry matter. On most of the harvest dates the anion content in the shoots of the well fertilized plants was a little higher.

The total anion content in the roots was highest for the roots of Treatment 5. This anion content decreased from 800 meq·kg^{-1} dry matter on 7 June to about 100 – 120 meq·kg^{-1} dry matter in the beginning of September. Thereafter it was more or less constant.

The (C – A) content in the shoots showed the same trend as the total cation content. After an increase from 2300 – 3200 meq·kg^{-1} dry matter in the beginning, it decreased sharply and then gradually to 1400 – 1500 meq·kg^{-1} dry matter at the end of the growth period. The differences between the two treatments were small.

In the roots the trend of the (C – A) contents was also equal to that of the cation content. It decreased from 1500 meq·kg^{-1} dry matter in the beginning of the season to about 250 meq·kg^{-1} dry matter at the last harvest. Only from the end of August until the beginning of October was the (C – A) content in the beets of Treatment 5 about 100 meq·kg^{-1} dry matter higher than the (C – A) content of the beets of Treatment 1.

4.3 Balance of uptake and utilization

For a correct idea about the balance of uptake and utilization, the amount of minerals lost by leaf fall (see Section 4.1) cannot be ignored. The uptake of elements during the growth period is therefore calculated by adding the uptake by laminae, petioles, crown and beet to the accumulated losses in the period preceding a harvest date.

The result is shown in Table 22 and Fig. 16. The uptake of minerals was higher in Treatment 5 than in Treatment 1 for all minerals, except H_2PO_4 and SO_4. Because some minerals, especially NO_3 and SO_4, are metabolized to organic forms and the chemical estimation of plant material gives the minerals as such, one should keep in mind that the actual uptake will be higher than the apparent uptake based on the estimated value indicates. Marked differences were found in the amount of N-Kjeldahl and NO_3 between plants of both treatments. In the uptake of NO_3 in Treatment 5 the direct influence of an extra dressing was shown by a stepwise increase in the amount of NO_3 present in the crop (dates of dressing were 4/7, 1/8, 29/8 and 26/9).

Most of the uptake curves were more or less linear from the starting of the sampling up to 29 August. After this date the uptake diminished. For these two periods the uptake was calculated in $\text{meq} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$, based on the curves from Fig. 16 (Table 23). For all minerals, except H_2PO_4 and SO_4, the rate of uptake in the first period was highest for Treatment 5. In the second period the rate of uptake in both treatments was much lower, although for most minerals still higher in Treatment 5 than in Treatment 1. In the second period the rate of Ca uptake was equal for both treatments and there was no more H_2PO_4 uptake. In the same period there was no increase of N-Kjeldahl in the plants of Treatment 1 whilst there was still an increase in $(C-A)$

Table 22. Calculated uptake during the growth of minerals by a sugar-beet crop with high and low rates of nitrogen ($\text{meq} \cdot \text{m}^{-2}$).

Date	Na	K	Ca	Mg	C	H_2PO_4	NO_3	Cl	SO_4	A	N-Kj	C−A	$g \cdot m^{-2}$
a. Treatment 1													
4/7	49	55	25	36	165	6	14	15	2	37	124	128	47
18/7	119	200	112	155	586	21	54	110	13	198	474	388	215
1/8	283	292	240	465	1280	36	60	268	32	396	774	884	542
15/8	363	395	284	455	1497	51	64	332	50	497	914	1000	799
29/8	495	582	467	624	2168	74	46	411	83	614	1236	1554	1196
12/9	514	516	466	686	2182	75	40	439	84	638	1002	1544	1369
26/9	545	640	526	748	2459	91	48	478	95	712	1202	1747	1693
10/10	579	588	564	761	2402	71	37	535	89	732	1027	1760	1597
24/10	590	572	607	789	2558	77	32	561	93	763	1047	1795	1644
b. Treatment 5													
4/7	49	55	25	36	165	6	14	15	2	37	124	128	47
18/7	219	213	107	203	742	26	85	110	13	234	588	508	248
1/8	337	358	252	359	1306	47	108	256	30	441	979	865	551
15/8	425	513	399	481	1818	59	168	366	52	645	1335	1173	875
29/8	539	697	569	693	2498	75	165	507	74	821	1747	1677	1249
12/9	618	833	572	815	2838	82	212	636	83	1013	1937	1825	1528
26/9	653	827	654	918	3052	75	211	629	91	1006	2095	2046	1643
10/10	780	906	709	965	3360	74	258	715	102	1149	2298	2211	1798
24/10	767	891	737	970	3365	78	265	733	111	1187	2435	2178	1868

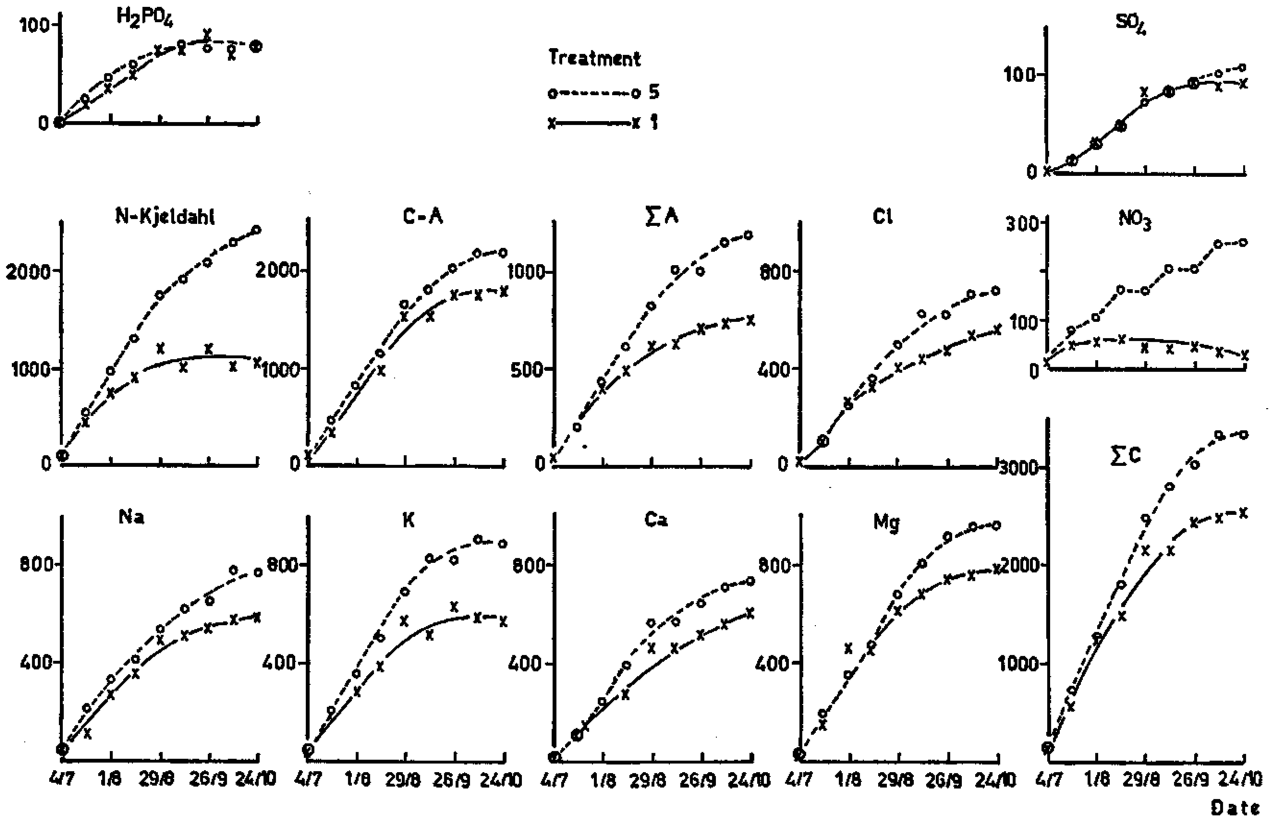


Fig. 16. Calculated uptake (meq.m^{-2}) on different dates at high and low rates of nitrogen.

Table 23. Uptake of minerals ($meq \cdot m^{-2} \cdot week^{-1}$) by a sugar-beet crop at low and high rates of nitrogen.

	Na	K	Ca	Mg	C	H_2PO_4	NO_3	Cl	SO_4	A	N-Kj	C−A
Treatment 1												
4/7–29/8	54	56	44	74	228	9	4	50	9	72	122	156
29/8–24/10	16	3	28	21	68	0	−2	19	2	19	0	49
Treatment 5												
4/7–29/8	61	80	63	82	286	9	19	61	9	98	203	188
29/8–24/10	29	24	26	35	114	0	13	28	5	46	86	68

or carboxylates. This prolonged increase in (C−A), after the increase in N-Kjeldahl stopped in Treatment 1, is also shown in Fig. 17. From this figure it is also clear that in Treatment 5 the production of (C−A) is almost equal to the production of N-Kjeldahl. Because part of the NO_3 in the plant material was included in the N-Kjeldahl data, the N-Kjeldahl production was somewhat higher than the N-organic production (see Section 2.4).

When the calculated losses are reduced by '25%', the curves show a somewhat higher N-organic production than the (C−A) production in Treatment 5 (Fig. 18).

Figures 17 and 18 show that from a date between 18 July and 1 August until the end of the growth period, the relation between the calculated dry weight and the calculated uptake (or production) is linear. As these straight lines do not pass through the origin, the contents of total cations, total anions, (C−A) and N-Kjeldahl in the calculated dry matter are decreasing throughout the growth period. The differences in calculated contents of the last four harvests, however, were very small and almost negligible because of the small increase in dry matter in this period.

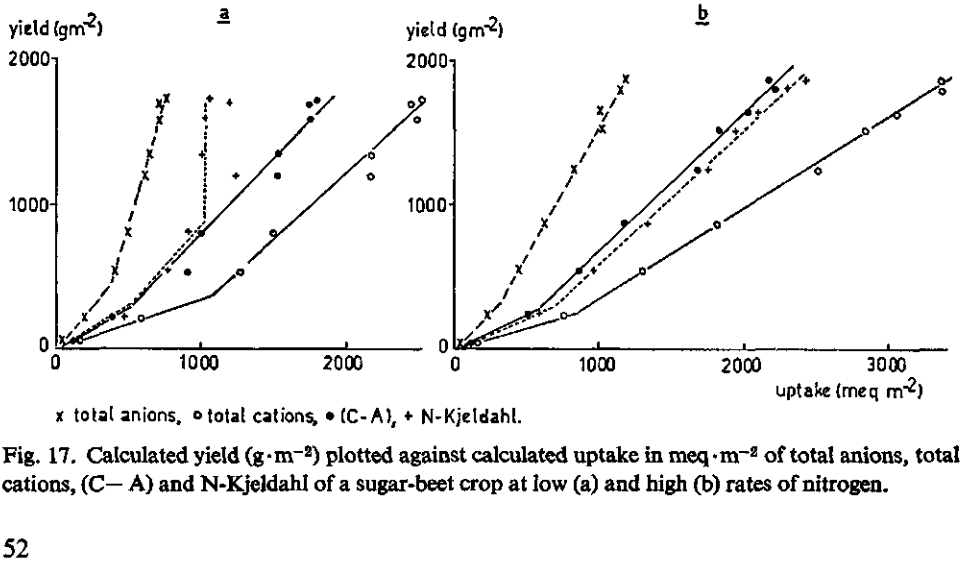


Fig. 17. Calculated yield ($g \cdot m^{-2}$) plotted against calculated uptake in $meq \cdot m^{-2}$ of total anions, total cations, (C− A) and N-Kjeldahl of a sugar-beet crop at low (a) and high (b) rates of nitrogen.

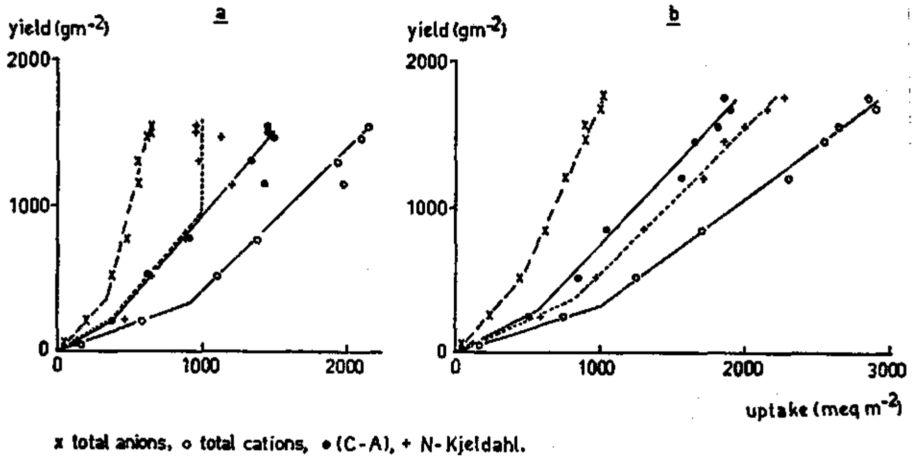


Fig. 18. As figure 17 but the calculated losses reduced by 25 %.

From the calculated dry matter production and the calculated uptake or production, the uptake of cations and anions and the production of (C–A) and N-Kjeldahl per 100 g dry matter produced was calculated (Table 24). This was done for the period starting from the beginning of August. In this period, the uptake (or the amount not yet metabolized by the plant) of cations and anions per unit dry matter was highest for the well fertilized sugar-beet plants (Treatment 5). The (C–A) production per unit of dry matter was also highest for the well fertilized plants but the difference between Treatment 5 and Treatment 1 with regard to the (C–A) production was only

Table 24. Uptake and production per 100 g total dry material (calculated) of a sugar-beet crop at low and high rates of nitrogen (from August 1).

	Total cations	Total anions	(C–A)	N-Kjeldahl
a. Treatment 1				
Whole plant	109–128[1]	29–32	80– 96	→0
Root	31– 22	9– 3	22– 19	→0
Shoot	78–106	20–29	58– 77	→0
Laminae	42– 59	8–13	34– 46	→0
Petiole	34– 45	12–16	22– 29	→0
b. Treatment 5				
Whole plant	140–163	50–56	90–107	102–107
Root	25– 23	7– 4	18– 19	34– 40
Shoot	115–140	43–52	72– 88	68– 67
Laminae	55– 69	13–16	42– 53	31– 34
Petiole	54– 65	28–34	26– 29	25– 26

[1] The range shown is variation through different methods of calculation.

about 10%. Furthermore, the production of N-organic (N-Kjeldahl in this experiment) was equal to the (C − A) production for the well fertilized plants, or when the calculated leaf losses were reduced by 25% was about 10% higher. In the plants of Treatment 1 the N-organic production decreased very soon to zero. The differences in uptake and production of (C − A) were mainly found in the shoot. The data for the roots were almost equal, except for N-Kjeldahl, which was found in fairly large quantities in the roots of Treatment 5. In the shoot the largest differences in uptake of cations and anions were found in the petioles.

4.4 Discussion

In this section the importance of leaf fall on nutrient uptake will be discussed. Not only the magnitude of the losses due to leaf fall is of importance, but also the effect that ignoring these losses has on the calculation of a balance of uptake and utilization of cations and anions. Furthermore, the internal transport of nutrients in sugar-beet plants, will be discussed.

The loss of nutrients was calculated from estimated contents in dead material and from assumed losses of dry matter. As was explained in Section 3.3, these calculated losses may be too high. The assumption that during senescence the dry weight of a leaf will not change is certainly questionable. The main cause for this change will be transport of organic nitrogen to other plant parts. The difference between the N-Kjeldahl content in the dead laminae and the five oldest living laminae is for both treatments for most of the growth period about 1000 meq·kg^{-1} dry matter (Figs 10 and 11). Thus during senescence about 1000 meq organic nitrogen/kg dry matter leaf must have been transported to other plant parts: that is 1000×14 mg N or $1000 \times 14 \times 6.25 = 87500$ mg protein if the transport took place in the form of amino acids. Calculated on a dry matter basis this means a decrease in dry weight by this transsport of about 8–9%. Because the differences in dry weight of the succeeding leaves were neglected, the estimates of the dry weight loss were an additional 8–10% too high (see Section 3.3). However to include all possible changes in dry matter, the losses in this experiment were calculated again with a reduction of 25%. The overall picture was not really altered by this recalculation. The real losses will probably be somewhere in between both sets of results.

The result for both calculations shows an enormous loss of nutrients during the growth period, especially of those elements that reach high concentrations in older laminae and petioles. For those elements the losses may even be higher than the uptake based on the last harvest data, which is the normal uptake figure found in literature. Therefore in sugar-beet, which loses older leaves continuously, the real uptake is much higher than is given in literature (Table 21). The real uptake is much higher than is usually accepted, but the fertility status of the soil is not affected because the extra uptake is returned to the soil.

In this experiment only the calculated uptake of phosphorus was equal or lower than the uptake data given in literature. This observation suggests that the amount of phosphores available for this sugar-beet crop during the growth period may be limited. Even a slight P deficiency is possible, although there was no indication from the P content.

All calculated uptake data were higher than data for the uptake based on the analysis of the last harvest. As minimum amounts of N, P and K were left in the dead material, this higher calculated uptake also holds for elements that were transported within the plant from old leaves to other plant parts.

In agreement with the results of Kelley & Ulrich (1966) and van Egmond & Breteler (1972), the highest nitrate concentrations were found in the oldest plant parts. In this experiment relatively high concentrations were found in the oldest plant parts with, at the same time, very low concentrations in younger plant parts. These results mean that transport of nitrate in sugar-beet plants is difficult from old to young plant parts unlike the transport of organic nitrogen. The loss in nitrogen by leaf fall is increased by the 'accumulation' of nitrate in older plant parts.

An increasing concentration (%) of nutrients in older plants parts may be brought about by accumulation of these nutrients and by transport of other material to other plant parts. Decreasing concentrations of nutrients in older plant parts may be caused by consumption of these nutrients (e.g. nitrate and sulphate), by transport to other plant parts and by accumulation of other forms of dry matter.

To decide if transport or accumulation takes place, the same plant part must be examined continuously during growth. This examination is, however, very difficult, especially when plant material has to be sampled for chemical analysis. In this experiment it was possible to calculate the amount of nutrients present in the laminae per leaf area.

With an assumed loss of three leaves per 14 days (see Section 3.1), the laminae in the middle position, laminae 6 – 10, will become laminae 1 – 5 after one month of growth, and one month later will be dead laminae. With the measured areas of laminae 6 – 10 and 1 – 5 and with the assumption that during senescence the leaf area does not change, the amount of nutrients$\cdot m^{-2}$ leaf area was calculated. The result is given in Table 25. The amount of dry matter$\cdot m^{-2}$ leaf area was almost constant throughout the season with a value of 60 $g \cdot m^{-2}$, except for the laminae 6 – 10 on 29 August and the laminae 1 – 5 on 24 October which had higher to much higher weights per unit of area. If these unlikely high dry weight yields were excluded, the general trend was a decrease in the amount of K, H_2PO_4 and especially N-Kjeldahl per unit of leaf area. These decreases were very clear at the transition from living to dead laminae. The changes in amounts of nutrients$\cdot m^{-2}$ leaf area for the transition from laminae 6 – 10 to laminae 1 – 5 were not so clear and for some elements not even present. The amount of Ca, Mg and $(C-A)\cdot m^{-2}$ leaf area showed an increase with age, although not always too distinct, especially in the living laminae.

The uptake of cations and anions and the production of organic nitrogen and $(C-A)$ per unit dry matter produced, can be divided into two different periods (Table 24 and Figs. 17 and 18), just as for the distribution of the dry matter produced. This can

Table 25. Change in the quotient amount of nutrient to leaf area with age of leaf (meq·m^{-2} leaf area).

Harvest date	18/7	15/8	1/8	29/8	15/8	12/9	10/10	29/8	26/9	24/10	12/9	10/10	26/9	24/10
Leaf position	1–5 →	dead	1–5 →	dead	6–10 →	1–5 →	dead	6–10 →	1–5 →	dead	6–10 →	1–5	6–10 →	1–5
Treatment 1														
Na	62	68	57	72	42	65	47	60	51	46	42	53	51	62
K	44	20	29	19	33	29	20	70	44	21	43	45	59	54
Ca	76	79	68	97	43	59	88	86	57	97	47	63	53	64
Mg	109	145	116	147	61	96	108	94	62	94	55	71	53	64
H_2PO_4	5	2	3	2	6	5	3	9	6	4	5	8	8	10
NO_3	9	6	4	2	1.8	0.8	0.7	0.9	0	0.5	0.5	0.3	0.4	0.2
Cl	24	33	35	34	24	32	37	35	25	27	28	40	23	36
SO_4	5	9	8	12	11	18	13	21	21	12	15	19	20	22
N-Kj	169	55	138	53	173	121	54	239	121	70	137	121	145	154
C–A	251	262	220	288	134	192	208	247	165	207	139	166	165	176
dry matter	58	–	58	–	61	62	–	94	63	–	63	66	66	82
Treatment 5														
Na	83	86	69	49	41	48	65	55	46	37	42	46	22	28
K	41	19	32	20	30	38	22	54	42	20	44	46	45	45
Ca	48	88	70	76	53	54	92	78	67	90	52	64	40	60
Mg	109	107	101	104	54	67	146	82	75	76	56	67	56	60
H_2PO_4	6	2	4	2	6	5	3	7	5	3	5	5	5	5
NO_3	14	9	10	10	5	8	14	8	5	7	5	14	5	9
Cl	20	24	26	24	20	26	33	27	22	24	22	17	18	18
SO_4	5	7	7	6	9	10	14	16	12	11	12	15	10	13
N-Kj	173	75	157	79	192	158	108	257	183	106	180	190	180	190
C–A	236	257	226	207	139	159	260	211	185	180	151	169	123	156
dry matter	60	–	58	–	57	57	–	81	64	–	62	63	58	67

only be done when the calculated yield and uptake data are considered. In the first period, from the beginning of the growth period until a certain time between 18 July and 1 August, the uptake and production per unit dry matter produced was relatively high and for both treatments equal. In the second period which lasted till the end of the growth period, the uptake of ions and the production of N-organic and (C−A) per unit dry matter produced was much lower than in the first period. Moreover, the data for the well fertilized plants were higher than for the plants of Treatment 1, especially the uptake of cations and anions.

The data of Treatment 5 indicated that the amount of N-organic and (C−A) produced was almost equal. Dependent on the calculation of the losses due to leaf fall, the amount of N-organic produced (or in this experiment N-Kjeldahl) was equal or somewhat higher than the amount of (C−A) produced.

In this experiment the sugar-beet crop was grown under field conditions and the calculated data for yield and uptake were taken into consideration. The same result was found for young sugar-beet plants on culture solutions (van Egmond & Houba, 1970 and Houba et al., 1971).

For well fertilized sugar-beet plants the production of N-organic and (C−A) was almost the same. Almost no decarboxylation could be shown in these plants. This was in contradiction to the findings in perennial ryegrass (Dijkshoorn et al., 1968). Sugar-beet plants which were dressed with an insufficient amount of nitrogen (for unlimited growth) stopped the production of N-organic almost completely when the nitrate in the plant was exhausted in about the middle of August. The carboxylate production continued, however, at a lower rate than in the well fertilized plants. This result is in agreement with those of Houba et al. (1971) for young sugar-beet plants on culture solutions. Most of the differences in uptake of cations and anions per unit dry matter produced were found in the data of the petioles (Table 24).

The difference in nitrogen dressings was clearly shown by the great differences in NO_3 and N-Kjeldahl content in the root and the shoot. Although the influence of the last nitrogen dressing was not reflected in an increase in leaf area or an increase in dry weight, this nitrogen was taken up by the plant, as can be seen by the increase in NO_3 content in the shoots during October (Fig. 14). The influences on the differences of the other cations and anions between the two treatments were very small or absent.

Great differences, however, were found in the contents of cations and anions in laminae and petioles of different age.

The highest concentrations of Ca, Na, Mg and (C−A) were found in the oldest laminae and petioles. The potassium content, however, was lowest in the oldest laminae. It is well-known that potassium is transported from old plant parts towards roots and younger leaves. A certain minimum concentration was found in dead laminae. This minimum concentration was 300–400 $\text{meq}\cdot\text{kg}^{-1}$ dry matter, which was higher than the critical value of 250 $\text{meq}\cdot\text{kg}^{-1}$ dry matter mentioned for mature laminae (Ulrich et al., 1959). Somewhat higher values were found for the laminae of the well fertilized plants. A minimum concentration was also found for N-Kjeldahl in the dead laminae of Treatment 1 with a value of 1000 meq$\cdot$kg^{-1} dry matter. For the well fertilized plants, the N-Kjeldahl in the dying laminae was not reduced to this same low value, except for the dead laminae at the start of the growth season. The result was an increasing concentration of N-Kjeldahl with time in the dead laminae of Treatment 5 to a value of 1700–1800 meq$\cdot$kg^{-1} dry matter. Phosphorus was also transported from older plant parts to other plant parts, resulting in a minimum concentration of 25 meq $H_2PO_4\cdot$kg^{-1} dry matter in the dead petioles and 25–50 meq$\cdot$kg^{-1} dry matter in the dead laminae. According to Ulrich & Hills (1967) a critical concentration for H_2PO_4 in petioles of sugar-beet is about 25 meq$\cdot$kg dry matter, which is close to the concentration found in dead petioles in this experiment.

Most nutrient contents in laminae and petioles of different age fluctuated with time, especially Mg in the laminae. Together with the potassium concentration in the dead laminae, the calcium concentration in the dead laminae and petioles was the most stable cation concentration with time. Unlike K, the Ca content was highest in the older plant parts. In this experiment, values of 1400–1600 meq Ca$\cdot$kg^{-1} dry matter in the dead laminae and 600–800 meq Ca$\cdot$kg^{-1} dry matter in the dead petioles were reached.

According to the hypothesis developed in Section 3.3, the first leaves formed were very active in the production of dry matter, most of which was transported to other plants parts and there used for growth. The reduction of mainly nitrate in these leaves results in a production of organic nitrogen together with organic anions (Dijkshoorn, 1962; de Wit et al, 1963). The produced organic nitrogen is very mobile and is transported to other plant parts. The organic anions, which for sugar-beets are mainly oxalates, are very likely immobile (van Egmond & Houba, 1970; van Egmond, 1971). They remain in the leaves, accompanied by cations such as Mg, Ca and, in sugar-beet, probably also Na. If we assume that there is almost no transport of organic anions from older leaves to other plant parts, the organic anion content or (C – A) content is a measure of the $NO_3(SO_4)$ reduction activity of the leaves in the past. High (C – A) contents in the leaves reflect a high activity during their active lifetime.

Figure 19 illustrates the (C – A) and N-organic contents in laminae of different age of a sugar-beet plant.

The first laminae formed, which never became large or heavy (see Section 3.3), had the highest (C – A) contents. This means that they have reduced most nitrate. Leaves formed later reduced less nitrate. The difference in (C – A) content between the first dead laminae and the dead laminae at the end of the growth period was almost 2000 meq$\cdot$kg^{-1} dry matter. Consequently the leaves that died early in the season, are considered to have been much more active than those that died later in the season. The very high (C – A) content in these dead laminae is accompanied by about 50% Mg, 20% Na and 30% Ca in the beginning of the growth season. At the end of the season these figures are about 35% Mg, 15% Na and 50% Ca. The more or less constant Ca content in the dead laminae and petioles may account for the death of leaves: the Ca content was so high that these leaves could not continue to function normally. The Ca content in the dead plant parts was almost independent of the

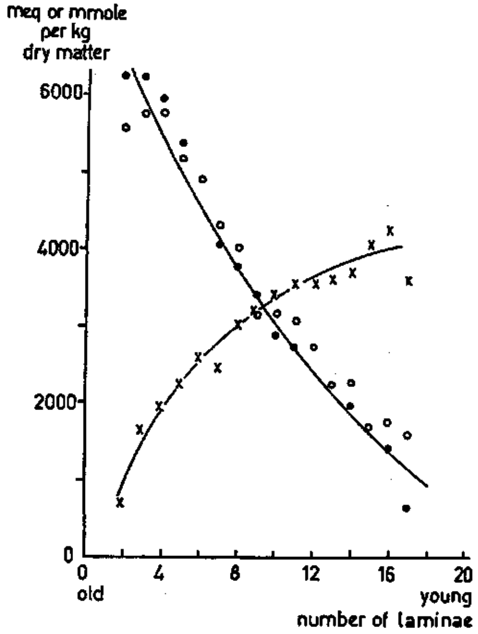


Fig. 19. Relation between number of leaf and organic N (x), C – A (·), sum of carboxylates (o) in a young sugar-beet crop with a high nitrogen fertilization (van Egmond, 1971).

activity of the plant part during its lifespan.

In the petioles, a large part of the (C – A) seems to be accompanied by Na. It is most likely, that the K in dead petioles is mainly present in ionic form, as is the case with Cl. However, it is very difficult to decide with which cation the organic anions are precipitated, if they are precipitated at all.

The relatively high content of some elements in the dying plant parts imply a decrease in content of these elements in the remaining plant material, when the old plant parts are lost. This is shown in figures 14 and 15, where the decreasing contents in the root and shoot are illustrated. In the root the decrease in nutrient content is mainly caused by an increase in sugar. When the contents of anions, cations, (C – A) and N-Kjeldahl in the roots were calculated on sugar-free dry matter (Fig. 20), the data, however, fluctuated. It seems that these contents, especially in the sugar-free dry weight of the roots of Treatment 1, also decreased. In the shoots the decrease of most nutrient contents during the growth was partly caused by the loss of dry matter which was rich in those elements. When these contents in the dry matter of the shoot were calculated under the supposition that no leaves died off (Fig. 21), the contents of total cations, total anions and (C – A) remained almost equal from the beginning of August until the end of the growth period. Only in the beginning of the growth period did these contents change with time. The calculated N content in the shoots of Treatment 1 decreased continuously, because there was little or no production of organic nitrogen in these plants (Table 24). In the period beginning early in August, there was a constant uptake of cations and anions per unit dry matter produced and a constant production of (C – A) and N-organic (Figs. 17 and 18 and Table 24). The experimental results showed differences between the two treatments, resulting in differences in calculated contents.

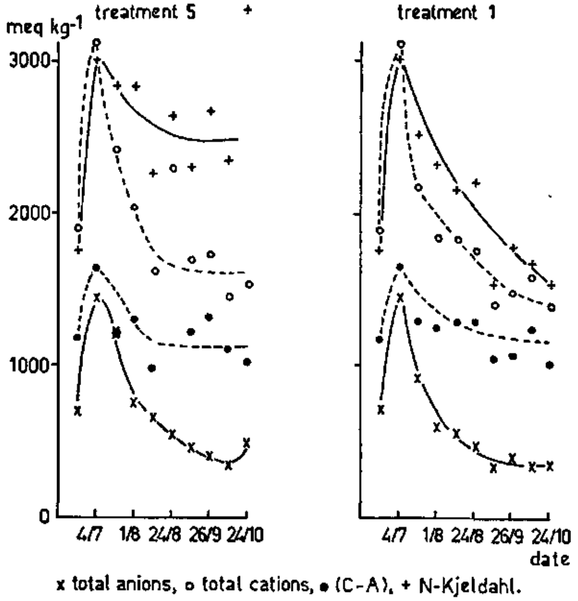
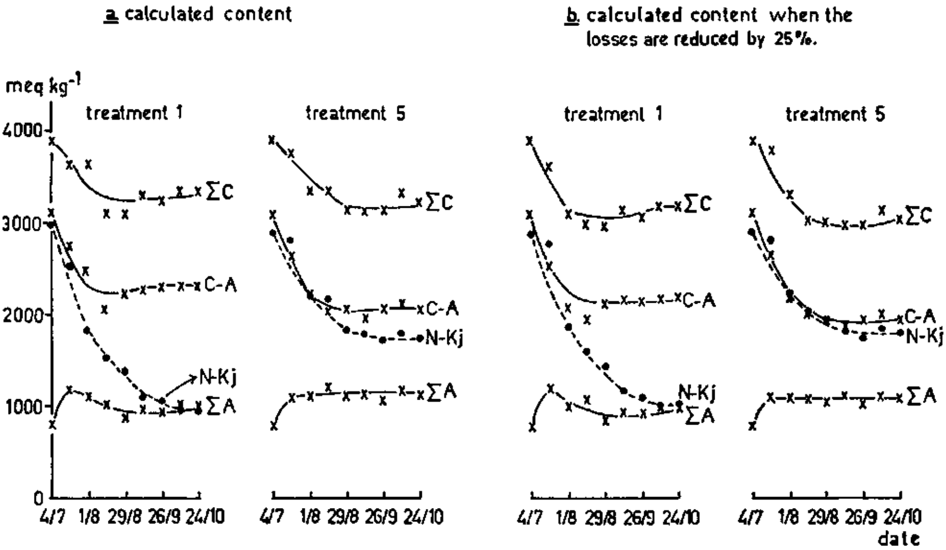


Fig. 20. Mineral content in the sugar-free dry matter of the roots of a sugar-beet crop at different rates of nitrogen.



a. calculated content

b. calculated content when the losses are reduced by 25%.

Fig. 21. Calculated content in dry matter of the shoot of sugar-beet with different rates of nitrogen.

Most contents in the harvested shoot material changed with time. To assess the nutritional status of a sugar-beet crop with data from chemical analysis, not only the plant part sampled must be known but also its physiological age. If for a sugar-beet crop a certain (C−A) content is used as an indication for healthy growth, as was proposed for perennial ryegrass by de Wit et al. (1963), its dependence on age of tissue must be kept in mind.

5 Summary

In a field trial, the influence of split dressings of nitrogen on growth and development and on the chemical composition of sugar-beet was studied. The growth and development was measured from dry matter yields and from leaf area. The chemical composition was estimated from different parts of the crop, such as laminae and petioles of different age, and from the root.

During the growth period it became evident that for a correct interpretation of growth, development and uptake of minerals, the loss by leaf fall could not be ignored. In a number of plots it was estimated that from about the middle of July until the end of the growth period, an average of three leaves were lost per fortnight. Because 21 leaves died off during the growth period, 4100 kg dry matter per ha and 3.2 m^2 leaf area$\cdot m^{-2}$ soil area were lost at a low nitrogen supply. With high nitrogen application, these data were 4600 kg dry matter per ha and 3.9 m^2 leaf area$\cdot m^{-2}$. The loss of minerals by leaf fall was especially high for those elements that were accumulated or retained in the oldest leaves. Losses of 90–140 kg nitrogen per ha, 80–105 kg potassium per ha and 5–13 kg phosphorus (H_2PO_4) per ha were calculated. Because these mineral losses are returned to the soil, they have little effect on soil fertility. In a study about a crop's growth, development and chemical composition, however, it is necessary to include these losses.

By adding up these losses to the measured production and uptake, a production pattern was found that deviated from the one mentioned in literature. In this experiment sugar-beet with sufficient nitrogen showed only two phases of development. In the first phase, most of the dry matter produced was used for enlarging the shoot; in the second phase most was used for the beet. More dry matter was used in the beet of a crop with nitrogen shortage than of a crop well fertilized with nitrogen. Moreover, in the crop with nitrogen shortage a third phase could be distinguished. The moment at which this third phase started was probably related to the moment of nitrogen shortage. In this third phase, no increase in sugar-free dry matter was found in the beet, whereas there was an increase in amount of sugar. The dry matter, used to maintain and increase the shoot material, was within each phase distributed over laminae and petioles with no dependence on the nitrogen dressings. The uptake of cations and anions and the production of organic nitrogen and organic anions ($C-A$) per unit dry matter produced was also constant within a phase. However, differences between treatments with high and low nitrogen dressings were found.

In this experiment the greatest increase in dry matter and sugar per unit of time was in August. The increase in dry matter per unit leaf area per unit of time was greatest in the beginning of the growth period. The first leaves formed, which were very active in this period, could only reach a limited size and weight. The very high (C – A) content in dead leaves, especially in those at the beginning of the growth period, indicates that these leaves were very active in reducing nitrate (and sulphate). The first leaves formed remained small and low in weight. This could be explained by the hypothesis that these leaves could use little dry matter produced for their own area and weight, due to competition for the produced materials (proteins and carbohydrates) between these leaves and the new leaves. Maximum leaf area and weight was found for the 10th to 15th leaf. The number of leaves that could reach this maximum area and weight depended on the nitrogen dressings. Leaves formed later did not reach this maximum size and weight due to shortage of light, water, minerals and/or time.

Great differences within one harvest were found in contents of cations and anions in different plant parts, particularly in laminae and petioles of different age. Especially for Na, Ca, Mg and (C – A), highest concentrations were found in the oldest material. Also for NO_3 highest contents were found in the oldest petioles and laminae. For H_2PO_4, K and organic-N the opposite was found. Minimum concentrations for these elements were found in the dead material. These were in the laminae for organic-N, K and H_2PO_4 1000, 300–400 and 25–50 $meq \cdot kg^{-1}$ dry matter, respectively. In the petioles a minimum concentration was only clear for H_2PO_4 with a value of 25 $meq \cdot kg^{-1}$ dry matter. From the minerals with the highest contents in the oldest leaves, the Ca content was the most constant during the growth period.

The decrease in contents of the sum of cations, the sum of anions, (C – A) and organic-N during the season in the shoot material could partly be explained by the losses due to leaf fall. By calculating the contents and assuming that no leaves were lost, almost constant contents were found from the middle of August onwards. Because in plant material most contents decrease with age, the critical values will be dependent on age.

The extra dressings of nitrogen on 4 July, 1 August, and 29 August had an influence on yield, leaf area, content of dry matter and sugar content. The final sugar yield was, however, almost equal for the different treatments. Each additional nitrogen dressing resulted one month after application in an extra increase in leaf area index (LAI) by 0.5 unit. The sugar content was at the same time reduced by 1 %. The last extra nitrogen dressing on 26 September, had no further influence on leaf area, dry matter yield and sugar yield, although there was a clear increase in NO_3 and organic-N content.

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