HEADING OF WINTER LETTUCE ON STEAMED SOIL: INFLUENCE OF NITROGEN FORM, MANGANESE LEVEL AND SHADING

by

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CONTENTS

Introduction .......................... 2
Lay-out of the experiments ........... 2
Results .............................. 4
Heading ................................ 4
Morphogenetic study of the leaf .... 7
Dry weight and heading ............... 8
Mineral composition of the plant ... 10
Discussion ........................... 12
Light - dry weight and heading ...... 12
Nitrogen form - dry weight and heading 13
Mn-accumulation - dry weight ...... 15
Mn-accumulation symptoms - heading 16
Summary ............................. 18
Literature ........................... 19
Figures
INTRODUCTION

Heading of winter glasshouse lettuce on steamed soil can be poor. In our first paper (Jager et al., 1969a) the changes in the soil properties due to steaming were discussed. In a second paper (Jager et al., 1969b) the growth of lettuce on steamed and not steamed soil, its heading and chemical composition were compared and discussed. Although a better dry-matter production was obtained on steamed soil, due to an improved nutrient availability, the marketing quality of the lettuce was reduced, due to bad heading and leaf-margin necrosis.

Steaming causes the following changes in soil properties:

a. accumulation of nitrogen in the ammonium form,
b. high quantities of manganese,
c. formation of injurious organic compounds from organic matter decomposed during the heat treatment.

In this paper a study of the effects of ammonium and manganese accumulations on the performance of lettuce in sand culture whether or not combined with reduced light intensities is presented. It is very probable that these soil factors are the quintessence of the failure of lettuce growth on steamed soils under the poor light conditions during autumn and early winter.

The appearance of poor heading may be described as follows.
At first the plants are growing normally and rapidly. Half-way the growth stops. The outside leaves of the head are showing a more steep attitude than normal, the main vein is growing almost as fast as the blade, the inner leaves of the head are poorly or not developed so that the head is more or less hollow. Because the outside leaves are a little bent outwards, the whole gives the impression of a tulip - the nick-name of the growth disorder (Fig.1). The malformation, however, has not one typical appearance, and many of these phenomena may be caused by other growth disturbances, not connected with the after-effect of steaming (Bensink, 1958; Hartmann, 1961; Dullforce, 1962; Sonneveld, 1966, 1968; Wiebe, 1968).

LAY-OUT OF THE EXPERIMENTS

Five experiments were carried out with the variety Proeftuin's Blackpool, three in the period from October 1963 to April 1964 and two in the period
from October 1964 to March 1965. The first experiment included the combination of three factors at two stages: two nitrogen levels, two kinds of nitrogen, viz. $\text{NO}_3^-$ and $\text{NH}_4^+$, and two light intensities, viz. the prevailing intensity and one reduced by shading with musling during the day from 10 a.m. to 4 p.m. or to 2 p.m. under bright or dark weather conditions, respectively. In the other experiments the two levels of nitrogen were reduced to one, but two levels of manganese were included.

Plastic pots of 4-liter capacity were filled with 5900 g moderately fine sand; particle size between 0.255 and 2 mm. Per pot two nozzles of a trickle irrigation were placed. One to three times a day, depending on the need, the culture solution was trickled and this was continued during 5 minutes after a leachate started to emerge from the spout of the pot.

The nutrient contents of the solution used in the first experiment are given in Tables 1 and 2.

Table 1. Nutrient concentration of solutions (m-equiv./l) used in the first experiment, and pH of nutrient solution and of culture medium

<table>
<thead>
<tr>
<th></th>
<th>$\text{NH}_4^-$</th>
<th>$\text{NO}_3^-$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$1N$</td>
<td>$4N$</td>
</tr>
<tr>
<td>K</td>
<td>6.32</td>
<td>6.32</td>
</tr>
<tr>
<td>Ca</td>
<td>3.00</td>
<td>3.00</td>
</tr>
<tr>
<td>Mg</td>
<td>6.32</td>
<td>6.32</td>
</tr>
<tr>
<td>$\text{NH}_4^+$</td>
<td>4.38</td>
<td>17.52</td>
</tr>
<tr>
<td>$\text{SO}_4^-$</td>
<td>10.32</td>
<td>17.18</td>
</tr>
<tr>
<td>$\text{H}_2\text{PO}_4$</td>
<td>3.00</td>
<td>4.08</td>
</tr>
<tr>
<td>$\text{HPO}_4$</td>
<td>5.08</td>
<td>9.18</td>
</tr>
<tr>
<td>$\text{NO}_3$</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$\text{HCO}_3$</td>
<td>1.64</td>
<td>2.72</td>
</tr>
<tr>
<td>pH of solution</td>
<td>7.0</td>
<td>7.0</td>
</tr>
<tr>
<td>pH of culture (sand + 1% CaCO$_3$ + nutrient solution)</td>
<td>7.0</td>
<td>7.0</td>
</tr>
</tbody>
</table>

Table 2. Manganese concentrations used in the nutrient solutions

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Mn-level (mg Mn/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>low</td>
</tr>
<tr>
<td>Vp 597</td>
<td>1.2</td>
</tr>
<tr>
<td>Vp 674</td>
<td>1.2</td>
</tr>
<tr>
<td>Vp 692</td>
<td>1.2</td>
</tr>
<tr>
<td>Vp 737</td>
<td>1.2</td>
</tr>
<tr>
<td>Vp 758</td>
<td>1.2</td>
</tr>
</tbody>
</table>
Because of the difference in pH of the ammonium- and nitrate solutions, the sand was mixed with 1% CaCO₃ to minimize differences in growth reactions. To secure a sufficient microelement supply Hoagland A-Z-solution was administrated iron was added as NaFeEDTA (1 mg Fe/l).

In the four following trials, N was supplied in the half concentration of 4N. Instead of 1% CaCO₃ now 0.2% was given. The two manganese levels in these experiments were as shown in Table 2.

The experiment was laid out as a splitplot in four replications, and with five pots per plot. CO₂ was supplied during the experiments and thus could not be a limiting factor in photosynthesis.

RESULTS

Heading

Light conditions

Light conditions were restricted by means of shading with muslin. Shading diminished light intensity with 25 to 50%. During the experiment, the light intensity, however, was not constant, decreasing during the experimental period in autumn just as in practice, but increasing in the experiments during the spring, also a contrast with the light pattern in the autumn. The improved light conditions during the experiment VP 692, in which the plants were growing from 19/3/1964 until 29/4/1964, prevented the appearance of poor heading in spite of shading. In the other four experiments shading appeared to be an important factor for promoting "tulip" formation, indicating that poor light conditions in the autumn, especially in unfavourably built glass-houses are a main factor for the appearance of the malformation. The symptoms of the shaded plants in experiments VP 737 were almost identical to the phenomena of poor heading and "tulip" form.

In practice, the light conditions in this experiment already induced poor heading (Table 3).

Table 3. The effect of light conditions on heading of lettuce

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Growing period</th>
<th>Treatment*</th>
<th>Statistical evaluation**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vp 597</td>
<td>30 Sep.-16 Dec. 1963</td>
<td>2.5</td>
<td>8.8</td>
</tr>
<tr>
<td>Vp 674</td>
<td>23 Dec.1963-4 March 1964</td>
<td>1.7</td>
<td>6.8</td>
</tr>
<tr>
<td>Vp 737</td>
<td>1 Oct.-11 Dec. 1964</td>
<td>4.9</td>
<td>6.8</td>
</tr>
<tr>
<td>Vp 758</td>
<td>18 Dec.1963-4 March 1964</td>
<td>4.8</td>
<td>6.1</td>
</tr>
</tbody>
</table>

* 0 = good head; 10 = poor head.

** (+) = P 0.10; + = P 0.05; ++ = P 0.01; +++ = P 0.001; n.s. = not significant.
The study of soil factors in combination with or without shading gave the following results.

**NH₄⁺-accumulation**

After steaming NH₄⁺-N accumulates in the soil. The amount of nitrate in the soil is reduced or has altogether disappeared. Nitrification is delayed and recovers only slowly. The effect of ammonium on heading was studied by comparing plant development on nutrient solutions containing NH₄⁺-N with those containing NO₃⁻-N.

Nitrification of NH₄⁺-N occurred in these experiments already after a few days and proceeded at a high rate. Therefore the first experiments may not be wholly representative, although there has been an excessive ammonium supply every day. So the leach-water of the NH₄⁺-object of VP 674 contained at 3 February 1964, 42 days after the start of the experiment, 54 ppm NH₄⁺-N and 33 ppm NO₃⁻-N, while 105 ppm NO₃⁻-N was found for the nitrate object.

In the last two experiments N-serve (2-chloro-6-(trichloromethyl)pyridine) was supplied to both NH₄⁺- and NO₃⁻-nutrient solutions (Goring, 1962a, b). In a preliminary experiment 5 and 10 ppm N-serve proved to give an irregular and retarded growth. Therefore a concentration of 1 ppm N-serve was used which appeared sufficient to prevent nitrification completely. The growth of the lettuce plants, however, seemed somewhat irregular compared with that fertilized with nitrate without N-serve. Ammonium supply stimulated the appearance of bad heading (Table 4, Fig.2).

### Table 4. The effect of the form of nitrogen on heading of lettuce

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Difference between NH₄⁺ and NO₃⁻</th>
<th>Statistical evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NH₄⁺-NO₃ light shadow</td>
<td></td>
</tr>
<tr>
<td>Vp 597</td>
<td>-0.1 +0.4</td>
<td>+0.2 n.s. n.s.</td>
</tr>
<tr>
<td>Vp 674</td>
<td>+0.8 +1.7</td>
<td>+1.2 ++ n.s.</td>
</tr>
<tr>
<td>Vp 737</td>
<td>+0.9 +0.1</td>
<td>+0.5 n.s. n.s.</td>
</tr>
<tr>
<td>Vp 758</td>
<td>+0.6 +0.7</td>
<td>+0.6 + n.s.</td>
</tr>
</tbody>
</table>

Footnotes: see Table 3.
It was found that this was especially the case during unfavourable light conditions; the interaction nitrogen form x light, however, being not significant.

The general impression was that nitrate supply gave a firmer, more flat, yellowish green plant. The darker green leaves of the plants supplied with ammonium, were somewhat narrower and showed a more steep position. The latter seemed more fated to show the studied growth disturbances if conditions were favourable for these. A necessary condition is an ample amount of nitrogen and a fast growth of the plant, which is usually the case after steaming of the soil. This follows from the results of the first experiment, in which two levels of nitrogen supply were compared. At the low nitrogen level the plants failed completely to head because their development was retarded too much; the plants with the high nitrogen level headed well with light, but if shaded the plants showed a poor performance.

Mn-accumulation

In preliminary sand and water culture experiments it was tried to evoke the poor heading of the lettuce. From these experiments it was found that "tulip"-formation may be seen as a border-case of manganese excess. High doses of manganese markedly reduced the growth of the plant and the latter showed symptoms of manganese excess in leaves: in the oldest leaves fine brown necrotic spots over the whole leaf, later on yellowing and dying of the leaf margins, proceeding from the outside inwards. The fine necrotic dotting of the leaves was found after steaming especially on sandy soils with a low pH. At low levels of Mn-poisoning, viz. 9.3 ppm Mn, the leaves were more spoonshaped and more erected, giving a resemblance to some features of the malformation after steaming (see Fig. 3).

The difficulty in the following experiments was to find the appropriate level for the high manganese series. A serious growth reduction by high Mn levels should be avoided. The high Mn level appeared to have indeed an unfavourable influence on heading of the lettuce (Table 5).

Table 5. The effect of Mn accumulation on heading of lettuce

| Experiment | High Mn - low Mn* | Statistical evaluation ||
|------------|------------------|-----------------|
|            | NH₄ NO₃ average  | Mn level        | Mn level x N form |
| Vp 674     | -0.5 +0.8 +0.1   | n.s.            | (+)              |
| Vp 737     | +3.9 +5.2 +4.5   | +++             | (+)              |
| Vp 758     | +3.3 +4.8 +4.1   | +++             | ++               |

Footnotes: see Table 3.
Only clear symptoms of Mn excess were found in the oldest leaves of the NO₃-supplied plants grown at a high Mn level (Fig. 4, VP 737). The phenomenon was transitory, but points to a higher sensitivity of NO₃-supplied plants towards high Mn levels.

The stimulation of bad heading by manganese was for the plants supplied with ammonium less pronounced than for the plants supplied with nitrate. For plants with a high manganese level the unfavourable influence of ammonium could hardly be perceived. The accumulation of ammonium and manganese together after steaming should not be considered as extra dangerous for a good performance of the crop in accordance to the results of these experiments; the degree of poor heading was even less than the additive unfavourable effect of these two factors separately.

Morphogenetic study of the leaf

Following the advice of Bensink (1958, 1962) we measured the length and breadth of the leaf, from the eldest leaf to the youngest, stopping at the 30-35th leaf. For a constant light intensity the length/breadth (1/b) ratio of the leaves reaches, after a certain number of leaves, a stationary level, as Bensink found. A decrease in light intensity is attended with an increase in the 1/b ratio of the leaves. The quality of heading with lettuce growing in late autumn can also be endangered by declining light conditions and consequently by an enhanced susceptibility to an unfavourable 1/b ratio. Only in the last of our experiments a constant 1/b ratio for a great number of leaves was shown, in the other ones the youngest leaves had again an increasing 1/b ratio. The leaves of plants of experiment Vp 737, growing in late autumn, showed the most irregular and also the highest 1/b ratio when arranged according to age, which indicates poor light conditions (Fig. 5).

The influence of the studied factors on the shape of the leaf is briefly represented by means of the lowest found 1/b ratio (Table 6).

Table 6. Influence of light, N form, and Mn level on the lowest length/breadth ratio of lettuce leaf

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Not shaded</th>
<th></th>
<th>Shaded</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>low Mn</td>
<td>high Mn</td>
<td>low Mn</td>
<td>high Mn</td>
</tr>
<tr>
<td></td>
<td>NH₄ NO₃</td>
<td>NH₄ NO₃</td>
<td>NH₄ NO₃</td>
<td>NH₄ NO₃</td>
</tr>
<tr>
<td>Vp 674</td>
<td>1.06 0.99</td>
<td>1.02 1.00</td>
<td>1.17 1.15</td>
<td>1.22 1.16</td>
</tr>
<tr>
<td>Vp 692</td>
<td>1.23 1.15</td>
<td>1.28 1.24</td>
<td>1.44 1.40</td>
<td>1.47 1.35</td>
</tr>
<tr>
<td>Vp 737</td>
<td>1.43 1.34</td>
<td>1.56 1.57</td>
<td>1.63 1.52</td>
<td>1.66 1.66</td>
</tr>
<tr>
<td>Vp 758</td>
<td>1.11 1.04</td>
<td>1.38 1.24</td>
<td>1.22 1.14</td>
<td>1.59 1.44</td>
</tr>
</tbody>
</table>
In agreement with the findings of Bensink (1958), shading caused an increase of the l/b ratio of the leaf. Generally nitrate nutrition favoured the breadth growth of the leaf and also the heading. High manganese levels also caused an increase of the l/b ratio. Especially in experiment Vp 737, performed in the late autumn a high Mn dosis under less favourable light conditions, did not give a constant l/b ratio for successively formed leaves, but a gradually increasing ratio (Fig. 5). These measurements confirmed the already mentioned influences on heading from the diverse objects.

**Dry weight and heading**

Poor heading is associated with a smaller dry weight per plant. In Fig. 6 the mean values of each object for heading and dry weight are plotted. The objects showed the influences on dry weight of the plant listed in Table 7. Shortage of light gave a significant decrease of the dry weight of the plant. In our conditions the lettuce produced more dry matter if the same quantity of nitrogen was given as nitrate than as ammonium. In all five experiments the difference in production in favour of nitrate was more pronounced in case of shading, this interaction between light and form of nitrogen being, however, not significant per experiment. High Mn levels were injurious to the production of dry matter, especially under conditions of high air temperature (Vp 758). The decline in development caused by too high a manganese dose came forward more clearly with the better prospering plants on nitrate.

**Mineral composition of the plant**

After harvest the head of the lettuce was analysed for nitrogen and manganese. From these data also the total quantity of these elements in the head of the plant was calculated. The results of all five experiments were found not to be consistent, the effects of some ones, however, proved statistically significant. Part of the data is given in Table 8 and 9.
Table 7. Influence of light, N form and Mn level on dry weight (in g) of the plant

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>No. shading</th>
<th>Shading</th>
<th>NH₄ - NO₃</th>
<th>High Mn - low Mn</th>
<th>Statistical evaluation**</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>NH₄ NO₃ average</td>
<td></td>
<td>light N form Mn level Mn level x N form</td>
</tr>
<tr>
<td>Vp 597</td>
<td>5.16</td>
<td>3.83</td>
<td>-0.28</td>
<td>- - -</td>
<td>+++ n.s. - -</td>
</tr>
<tr>
<td>Vp 674</td>
<td>9.61</td>
<td>7.44</td>
<td>-0.25</td>
<td>+0.08 -0.51 -0.21</td>
<td>+++ n.s. n.s. n.s.</td>
</tr>
<tr>
<td>Vp 692</td>
<td>7.10</td>
<td>4.98</td>
<td>-0.45</td>
<td>+0.24 -0.66 -0.21</td>
<td>+++ +++ + +++</td>
</tr>
<tr>
<td>Vp 737</td>
<td>6.10</td>
<td>4.82</td>
<td>-0.21</td>
<td>-0.19 -1.44 -0.82</td>
<td>+++ n.s. +++ +</td>
</tr>
<tr>
<td>Vp 758</td>
<td>7.65</td>
<td>5.99</td>
<td>-1.11</td>
<td>-1.81 -3.70 -2.76</td>
<td>+++ +++ +++ +++</td>
</tr>
</tbody>
</table>

Footnote: see Table 3.
Table 8. Influence of light and N form on N content and N amount in the lettuce head

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Light</th>
<th>mg N per head</th>
<th>statistical evaluation</th>
<th>N form</th>
<th>statistical evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>N%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>no shading</td>
<td>shading</td>
<td>N%</td>
<td>mg N per head</td>
</tr>
<tr>
<td>Vp 597</td>
<td>4.04</td>
<td>4.28</td>
<td>216</td>
<td>165</td>
<td>+++</td>
</tr>
<tr>
<td>Vp 674</td>
<td>4.02</td>
<td>4.44</td>
<td>387</td>
<td>330</td>
<td>+++</td>
</tr>
<tr>
<td>Vp 692</td>
<td>5.00</td>
<td>4.94</td>
<td>355</td>
<td>245</td>
<td>n.s.+++</td>
</tr>
<tr>
<td>Vp 737</td>
<td>5.75</td>
<td>5.50</td>
<td>345</td>
<td>265</td>
<td>n.s.+++</td>
</tr>
<tr>
<td>Vp 753</td>
<td>4.91</td>
<td>5.01</td>
<td>372</td>
<td>300</td>
<td>+</td>
</tr>
</tbody>
</table>

Footnote: see Table 3.
Table 9. Influence of light and Mn level, dependent on N form or not, on the Mn content and Mn amount of the lettuce head

<table>
<thead>
<tr>
<th>Exp. No.</th>
<th>Light</th>
<th>Mn, ppm</th>
<th>Mn, mg per plant</th>
<th>statistical evaluation</th>
<th>Mn level</th>
<th>statistical evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>no shading</td>
<td>no shading</td>
<td>Mn, Mn, ppm</td>
<td>high low high Mn - low Mn</td>
<td>high Mn - low Mn</td>
</tr>
<tr>
<td>Vp 587</td>
<td>63</td>
<td>71</td>
<td>0.31</td>
<td>0.26</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Vp 674</td>
<td>165</td>
<td>157</td>
<td>1.57</td>
<td>1.17</td>
<td>n.s.</td>
<td>***</td>
</tr>
<tr>
<td>Vp 692</td>
<td>287</td>
<td>187</td>
<td>1.46</td>
<td>0.92</td>
<td>n.s.</td>
<td>***</td>
</tr>
<tr>
<td>Vp 737</td>
<td>495</td>
<td>506</td>
<td>2.79</td>
<td>2.26</td>
<td>n.s.</td>
<td>***</td>
</tr>
<tr>
<td>Vp 758</td>
<td>495</td>
<td>489</td>
<td>3.20</td>
<td>2.13</td>
<td>n.s.</td>
<td>***</td>
</tr>
</tbody>
</table>

Note: The table shows the influence of light and Mn level, dependent on N form or not, on the Mn content and Mn amount of the lettuce head. The statistical evaluation is indicated by symbols: * for significance at the 0.05 level, ** for significance at the 0.01 level, and *** for significance at the 0.001 level. N-form shading level x Mn level x light.
Growth reduction by shading was, as may be expected, sometimes attended with a higher N content in the leaf and a lower nitrogen quantity in the head. The quantities of nitrogen in the nutrient solutions being the same, the lettuce has taken up more nitrogen from the ammonium solution. If this is the same for the lettuce growing on soil, the greater susceptibility of the plant for poor heading can be caused by a disturbed balance between carbohydrates and organic nitrogen in the plant under light conditions which become gradually unfavourable. A high dose of ammonium-nitrogen increased the nitrogen content of the leaf more than a high amount of nitrate (Vp 597). Generally, the nitrogen quantity in the plant decreased stronger at the high manganese level in the nitrate objects than in the ammonium objects (all four experiments showing the same trend, two interactions of Mn level x N form did so significantly).

Shading did not clearly influence the manganese content of the leaf. On account of the growth reduction the total Mn amount of the head was lower. The form of nitrogen had a varied effect on the manganese content of the plant, in one experiment a significant increase with ammonium and in another a significant decrease. When NH₄ was given the Mn content and the Mn amount of the plant tended to increase more in the cases of a high Mn supply, than when NO₃ was administered. (This occurred in three of four cases, two interactions Mn level x N form were significant.) This would thus be an indication of an unfavourable interaction between manganese and nitrogen form for the plant. The unfavourable influence of a high manganese level in the soil after steaming would be strengthened from ammonium accumulation, giving a greater uptake of manganese. For heading and dry weight such an interaction was, however, not found, as already mentioned.

With regard to the Mn amount there was a significant interaction between Mn level and light. In the four experiments the increase of the manganese amount in the head at the high Mn level was significantly larger when shading was not carried out. Growth reduction from shading was not accompanied by an undesired increase of manganese in the plant, so the unfavourable effect of steaming presumably cannot be ascribed to an uncontrolled Mn absorption under less favourable light conditions.

DISCUSSION

Light - dry weight and heading

In each of our experiments plotted in Fig. 6 a positive correlation exists between the dry weights of the plants and the heading. The dry weight of a plant is the result of photosynthesis and is thus governed by production factors as light intensity,
day length, carbon dioxide concentration and consumption factors like respiration (increasing with rising temperature).

For lettuce we know from the work of Bensink (1958) and Dulforce (1963) that light intensity and day length should not be below certain temperature-dependent limits for a good head to be formed (see Dulforce, 1963, table I). Factors causing an extra conversion of products of photosynthesis or diminishing their formation, unfavourably influence heading and thus have to be compensated by better conditions for photosynthesis should heading be equivalent.

Bensink (1958) observed that the 1/b ratio of the successive leaves of a lettuce plant depends on the conditions for photosynthesis during growth. Under good conditions the 1/b ratio is low and it is larger when the conditions for photosynthesis are unfavourable (low light intensity, short days, a too low CO₂ concentration or a partly elimination of the outer leaves). It is also known from Bensink's work (1958) that plants bearing leaves with too high a 1/b ratio don't form a head.

**Nitrogen form - dry weight and heading**

A relatively high 1/b ratio is not only induced by unfavourable conditions for photosynthesis such, as shading, as we could confirm in our experiments, but ammonium nutrition and high manganese levels also cause higher 1/b ratios than nitrate or a normal low manganese level (Fig. 5, Table 6).

The growth of lettuce on steamed soil thus has a greater change to fail than growth on fresh soil, due to the high amounts of ammonium and manganese accumulated in the former. In autumn the declining light intensity and the curtailed daylength as such are already limiting for heading.

With respect to growth and dry-matter production nitrate is mostly reported to be superior to ammonium as a nitrogen source (Bareket, 1968). The occurrence of differences in growth and development between plants grown with nitrate or ammonium depends on some factors:

a. **The plant species.** Lettuce belongs to the large group of ammonium-sensitive plants (Davidson and Thiegs, 1966) adversely affected by high concentrations of ammonium (Grogan and Zink, 1956).

b. **The composition, pH and aeration of the nutrient medium** is of great importance with regard to the ionic balance of the plant. A normal ionic balance of the plant, from which the C-A content (organic acids) is an expression, is one condition for a good growth (De Wit et al., 1963). C-A is strongly influenced by the type of ion in which the nitrogen of the fertilizer is present. NH₄ competes with other cations during uptake and promotes the uptake of anions, while it itself is lost in the plant by assimilation,
thus giving easily a too low C-A value. NO\textsubscript{3} does the reverse and consequently is a much more favourable nitrogen source, leading to a normal C-A value and a normal yield. Competition of other anions which are readily taken up, as chloride, influences C-A and yield in an unfavourable way if present in about the same quantity as the nitrate (De Wit et al., 1963). The type of cations in the nutrient solution is of importance for the quantitative uptake of nitrate and cations and thus for C-A. De Wit et al. (1963, fig. 19) for barley and Van Tuyl (1965, fig. 13) for perennial ryegrass found a higher C-A and dry-matter production with KNO\textsubscript{3} than with Ca(NO\textsubscript{3})\textsubscript{2}. This may be an explanation for the fact that Sonneveld (1968 a, b) only found minute differences in the weight of the heads of ammonium sulphate and calcium nitrate fertilized lettuce on steamed soil in favour of nitrate.

The pH range for a reasonable growth of plants with ammonium seems to be higher and narrower than with nitrate.

The nutrient solutions used by the different investigators differ in composition and in pH and comparisons of the results gained with different plants grown in different seasons are hardly possible (Pirschle, 1931; Tiedjens and Robbins, 1931; Tiedjens, 1934; Clark, 1936; Arnon, 1937; Evans and Weeks, 1947; Bennett et al., 1964; Klemm, 1966; Barker et al., 1966; Kirkby, 1968).

A good aeration of the nutrient solution or the soil is a greater necessity for plants growing with ammonium, as nitrate can serve as a source of oxygen (Vladimirow, 1945; Barker et al., 1965). Conditions as a good aeration and a pH of about 7, which improve plant growth also improve nitrification. Contamination of the ammonium containing nutrient medium with nitrifying bacteria soon occurs and nitrification will proceed rapidly if no specific inhibitors are used.

c. Light. Under sub-optimal light conditions the need for light is higher for plants grown with ammonium. NH\textsubscript{4} - N in the plant is converted rapidly and in an uncontrolled way into organic nitrogen compounds and tends to deplete the available carbohydrates, especially if the light conditions are marginal (Nightingale, 1948; Ferguson, 1957; Barker et al., 1965). The assimilation of NO\textsubscript{3} - N to organic nitrogen on the contrary is controlled by an energy requiring enzymatic reduction and never leads to a depletion of carbohydrates. In the leaves the reduction is strongly promoted by illumination. Ammonium plants show a higher nitrogen content than nitrate plants, but a lower content of cellulose, lignin, starch, soluble sugars and organic acids (Clark, 1936; Vladimirow, 1945; Evans and Weeks, 1947; De Wit et al., 1963).
The difference in shape and upright position of the leaves between lettuce plants grown with ammonium and those grown with nitrate also may be of influence on the total photosynthesis of the plant due to reduction of active leaf area by overlap. Brouwer and Huyskes (1968) compared the growth of two lettuce varieties and found that the variety showing the greatest overlap made the slowest growth. In both varieties the rate of photosynthesis per unit of leaf area was the same, which probably is not the case for lettuce plants grown with either ammonium or nitrate; a higher 1/b ratio for leaves of ammonium supplied plants points to this already. Barker et al. (1963) observed, for instance, in the leaves of bean plants (Phaseolus) grown with ammonium a lower rate of photosynthesis per unit of leaf area than in leaves of plants grown with nitrate.

### Mn accumulation - dry weight

Increasing amounts of available manganese negatively influenced the weight of the lettuce. Sonneveld (1966) also found a depression of yield, not only as a result of growth disturbance, but also by an earlier harvest time in consequence of yellowing of the older leaves. The unfavourable effects appeared at a Mn level over 300 ppm. According to Messing (1965a, b) values of 1000 - 1500 ppm, however, need not be injurious for crop production. Harward et al., (1955) found a significant decrease in yield for lettuce, if the Mn content of the young leaves was 350 ppm and that of the old leaves 930 ppm. Growth depression was preceded by foliar symptoms of manganese excess.

The relation between yield and manganese content of the plant is not consistent, but dependent of the growing season (Heslep, 1951). In general, the harmful effect of manganese excess is less pronounced under restricted light conditions. The Mn content is also decreased (McCooil, 1935; Löhnis, 1951; Dey, 1964). This does, however, not agree with the results of the experiments of Sonneveld (1965). In winter conditions the lettuce showed symptoms of Mn toxicity, but the following crop in spring was apparently sound. Besides, a greater depression in weight of lettuce heads was caused by Mn-excess under light than under restricted light conditions; but the relative depression of Mn excess was stronger under restricted light. We did not find, however, an interaction of Mn supply and light conditions on the weight of plant. Löhnis (1951) found an increased toleration for Mn by high temperature. In that case the slow decrease of temperature in autumn might make the lettuce more susceptible for Mn excess. The influence of the nitrogen source on the appearance of manganese toxicity is not clear from literature. In culture solutions the nitrate is stimulating the toxicity of Mn (Mulder and Gerretsen, 1952; Millikan, 1950). Dey (1964), however, could not confirm this. In our experiments the manganese excess decreased the dry matter production with nitrate stronger than with ammonium, absolutely and relatively (Table 7).
Symptoms of manganese toxicity are distinctive, but varying for different crops (Hewitt, 1948). The tolerance is dependent on the amount of manganese taken up, and on the relative ability to endure large amounts within the plant (Morris and Pierre, 1949). There are great differences in susceptibility for Mn excess between species and varieties (Morris and Pierre, 1949; Williams and Vlamis, 1957a, b; Ozaki, 1959; Messing, 1965a, b) and characteristics of toxicity symptoms are different for various plant parts (Ouellette and Généreux, 1965). Symptoms of manganese excess are first observed in the older tissues and in marginal or distal interveinal tissues of leaves (Millikan, 1951; Bussler, 1958). Lettuce is moderately susceptible of manganese excess (Hewitt, 1948; Löhnis, 1951; Williams and Vlamis, 1957a, b). The common characteristic is a pale foliage with a dull yellow around the leaf margin (Sherman and Fujimoto, 1946; Hewitt, 1948) or marginal paling (Heslep, 1951; Vlamis, 1953) and in a later stage browning and darkening of the veins (Löhnis, 1951; Sonneveld, 1967) and necrosis of the leaf disc. Only Sonneveld (1966) described the malformation of the head. That other authors did not signalize this growth deviation, may be due to the use of other varieties or to the fact that the test plants were not grown out to adulthood in their experiments.

The fact that Mn toxicity symptoms are appearing to a more serious degree under conditions of much light than under poor light conditions (McCool, 1935; Löhnis, 1951), combined with a lower manganese content of the plant tissue, is contrary to the frequent appearance of poor heading in the autumn. This seems to indicate that the unfavourable effect of Mn accumulation on the heading of lettuce is not a direct toxicity symptom. The unfavourable effect of manganese excess may be ascribed to its contribution to an increased l/b ratio of the leaves, endangering a good head formation in this way (Table 6). Lettuce on steamed acid light soils, however, yet showed typical Mn toxicity symptoms.

The relationship between manganese toxicity symptoms and the manganese content of the plant is not simple (Hewitt, 1948; Heslep, 1951). Older leaves have higher Mn contents than new leaves. The values of the minimum levels at which Mn toxicity symptoms in lettuce are recorded diverge. Harward et al. (1955) mentioned 180 ppm for young and 550 ppm for old leaves; Sonneveld (1968a, b) reported 240 and 330 ppm, respectively. Mild and more marked toxicity symptoms are reported at contents of 200–500 and over 500 ppm (Messing, 1965a, b) or at 750 and 1650 ppm, respectively (Heslep, 1951); Löhnis (1951) reported slight symptoms at 1638–2023 ppm. Sherman and Fujimoto (1946) mentioned 3000 ppm Mn, but considered the Mn/Fe ratio more important.
Schmehl et al. (1950) found for the appearance of toxicity symptoms in alfalfa the Ca/Mn ratio a better measure. The manganese contents found in our experiments mentioned in Table 9, are to be considered as slightly toxic to toxic, when we compare these with the data of Messing (1965a, b) and of Sonneveld (1968a, b).

In our work with a range of manganese contents 252–929 ppm manganese stimulated poor heading in three of four experiments, but did not in one with fast-growing lettuce under good light conditions.

For the growth of well-headed winter lettuce it is favourable to avoid or at least to reduce the excessive formation of \( \text{NH}_4^- \), available Mn and soluble inhibitory organic material. A reduction can be achieved by steaming the soil in a relatively dry condition and by restricting the temperature and the duration of the treatment to a minimum. Leaching directly after steaming, although of benefit (Van der Hoeven, 1967), has the drawback to enhance the amount of available Mn. Reinfection of the sterilized soil with saprophytic micro-organisms together with the addition of a well-decomposable nitrogen-poor sub-stratum - for instance straw chaff (Hartman, 1961; Wiebe, 1968) - brought into the soil soon after steaming, will lead to immobilization of \( \text{NH}_4^- \) by the developing microflora, will reduce the amounts of available Mn sooner by biological oxidation, will stimulate the decomposition of inhibiting organic compounds and will lead to a sooner start of the nitrification. A quick expansion of a saprophytic microflora is of benefit to control parasitic members which somehow survived (subsoil) or were introduced. Nitrogen fertilization, if necessary, should be given as nitrate (Wiebe, 1968). The release of Mn during steaming is restricted when the soil has a neutral \( \text{pH} \); liming of a too acid soil before steaming, however, stimulates \( \text{NH}_4^- \)-accumulation. Factors governing photosynthesis should be kept as best as possible (light and \( \text{CO}_2 \) supply).

The method of soil pasteurization with a steam-air mixture, as described by Baker and Olsen (1964) and by Dawson et al. (1965) seems much promising. The rise in available Mn is low and lasts only a relatively short time. The parasites would be damaged severely and are kept within acceptable limits as the saprophytes, which survive the treatment in sufficient large numbers, develop again. However, an enhanced formation of ammonia and a nitrification lag still occur. This method seems, however, not yet suitable for practice because of certain technical difficulties.
SUMMARY

A study was made of the influence of ammonium and manganese on heading of winter lettuce. Both factors can be present in excess after steaming of soil. Conditions of restricted light were included in the experiments.

Lettuce (variety Proeftuin's Blackpool) was grown in autumn and winter in a glasshouse in plastic pots with sand under trickle irrigation. Four groups of pots got a different nutrient solution each. These solutions differed with regard to the nitrogen form (NO\textsubscript{3} or NH\textsubscript{4}) and the manganese content. A number of plants was shaded.

Shading resulted in a significant decrease in dry weight and a significant increase in bad heading. Shaded plants had a higher N content, but a lower N amount. The Mn content of the plants was not clearly influenced by shading. It decreased, however, the total Mn amount in the plants significantly.

Nitrogen form. The dry-matter production was unfavourably influenced by NH\textsubscript{4} nutrition; NH\textsubscript{4} proved also significantly inferior to NO\textsubscript{3} with regard to heading. NH\textsubscript{4} plants had higher N contents and mostly higher N amounts than NO\textsubscript{3} plants.

Manganese. High Mn levels proved injurious to dry-matter production and heading. NO\textsubscript{3} supplied plants were more injured by high Mn levels than the less well growing NH\textsubscript{4} supplied plants. High Mn gifts tended to cause higher Mn contents, and higher Mn amounts in NH\textsubscript{4} than in NO\textsubscript{3} plants.

With regard to the morphogenesis of the leaf it was observed that shading, NH\textsubscript{4} nutrition and a high level of Mn caused a higher length/breadth ratio than no shading, NO\textsubscript{3} nutrition and a low Mn level. A high 1/b ratio of the leaves must be looked upon as an unfavourable condition for the formation of a good head.

Heading of winter lettuce is thus endangered by poor light conditions and by ammonium- and manganese accumulations as consequence of the steaming of the soil. Soil steaming can be better postponed to the spring after the winter lettuce or should be carried out carefully, under certain conditions or with counter-measures.
LITERATURE


Fig. 1. Poor heading of lettuce on steamed soil in practice (photo Dr. L.S. Spithorst).

Fig. 4. Necrotic spots of Mn excess in NO₃-N plants.
Fig. 2. Influence of NH$_4^+$- and NO$_3^-$-N on habitus of lettuce in pot experiment. Intact (above) and exposed (below) plants.
Fig. 5
Length/breadth ratios of leaves, arranged from base to top, as influenced by light, N-form and Mn. Contrast is given of: NO₃ + low Mn; NH₄ + high Mn under light and shade conditions.

--- shaded
- not shaded

• NO₃ - N, low Mn
• NH₄ - N, high Mn

l/b ratios

1.20
1.40
1.60
1.80
2.00
2.20

number of the leaf

1 5 10 15 20 25 30

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