

SOME ASPECTS OF MINERAL NUTRITION AND FLOWERING

WITH A SUMMARY IN DUTCH

ENIGE ASPECTEN VAN MINERALE VOEDING EN BLOEI

by (door)

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CONTENTS

I. General introduction	2
II. Review of literature	2
1. General effects of mineral nutrition on flowering	3
2. Effect of specific elements on flowering	3
2.1. Nitrogen	3
2.2. Potassium	5
2.3. Phosphorus	5
2.4. Calcium	6
2.5. Sulphur	6
III. General remarks on the experiments	7
IV. Effect of mineral deficiencies on the flowering responses and the growth of long and short-day plants	8
1. Mustard (<i>Sinapis alba</i> ; L.D.P.)	8
1.1. Experiment I: In water culture	8
1.2. Experiment II: In vermiculite	11
1.3. Discussion	15
2. Dill (<i>Anethum graveolens</i> ; L.D.P.) Experiment III:	15
3. <i>Perilla crispa</i> (S.D.P.) Experiment IV:	17
V. Effect of several nitrogen levels on the flowering responses and the growth of long and short-day plants	20
1. Introduction	20
2. Mustard (L.D.P.)	21
2.1. Experiment V: Orientation	21
2.2. Experiment VI: Four levels of nitrogen	21
2.3. Experiment VII: Seven levels of nitrogen	23
3. Dill (L.D.P.)	26
3.1. Experiment VIII: Orientation	26
3.2. Experiment IX: Three levels of nitrogen	26
4. Spinach (<i>Spinacea oleracea</i> ; L.D.P.) Experiment X:	28
5. <i>Perilla crispa</i> (S.D.P.)	29
5.1. Experiment XI: Three levels of nitrogen	29
5.2. Experiment XII: Five levels of nitrogen	32
6. <i>Kalanchoë blossfeldiana</i> (S.D.P.) Experiment XIII:	34

204 8863

VI. Effect of variation in relative concentration of ions in the nutrient solution, on the flowering responses and the growth of long and short-day plants	36
1. Mustard (L.D.P.) Experiment XIV:	36
2. <i>Perilla crispata</i> (S.D.P.) Experiment XV:	40
VII. General discussion	40
1. Introduction	40
2. Flower initiation, development and number of flowers	40
3. Growth	42
4. Auxin production	44
5. Conclusion	44
VIII. Summary	45
Samenvatting: Enige aspecten van minerale voeding en bloei	46
Literature references	47

CHAPTER I

GENERAL INTRODUCTION

The discovery of the important role of minerals in growth, flowering and fruiting of plants is one of the noteworthy achievements of science. The essential importance of minerals as a factor in plant growth has been repeatedly demonstrated. The occurrence of these inorganic substances as constituents of protoplasm and chlorophyll, and in the cell membranes and cell sap of plants is more or less fully discussed in most textbooks of plant physiology (MILLER 81, 1938*) As minerals have been shown to be active in so many physiological processes in plants, it is to be expected that their connection with the flowering process should have been considered. However, although there is a large amount of data scattered throughout the literature, on the effect of minerals on plant growth and fruitfulness, few papers deal with their influence on the flowering process. Undoubtedly minerals do affect the flowering behaviour, but their exact role in this process is still obscure.

The pioneer work of KLEBS (61, 1918) and GARNER and ALLARD (38, 1920; 39, 1923) was followed by many other investigators such as MURNEEK and WHYTE (84, 1948) and LANG (68, 1952), who have shown that flowering is conditioned by the environment and can be changed by modifying such factors as mineral nutrition, temperature and length of photoperiod. In recent years also some investigators have made an attempt to correlate the flowering behaviour of plants with changes in mineral nutrients: NEIDLE (86, 1938), NAYLOR (85, 1941), CAJLACHJAN (15, 1944), WITHROW (115, 1945) and others. These researches have yielded some information on this problem. However, in some cases different investigators have obtained opposing results. For this reason the present experiments have been conducted in the hope that they might throw some light on the relation between flowering and mineral nutrition.

CHAPTER II

REVIEW OF LITERATURE

The effect of minerals on the flowering process of plants will be discussed from two points of view, firstly, general effects of mineral nutrition on flowering, and secondly, the effect of specific elements on flowering. Each of these points

* First number refers to literature references on p.47-51, second number indicates the year of publication.

will be approached from three sides: effect on initiation and development of floral buds, effect on the time of flowering, and effect on the number of flowers produced.

1. GENERAL EFFECTS OF MINERAL NUTRITION ON FLOWERING

It is well known that minerals affect the growth of plants and thus as a result the flowering process is affected. LEOPOLD and THIMAN (71, 1949) stated that there is a strong correlation between the number of flower primordia and the weight of the plant, and emphasized that such a similarity between flowering and growth suggests that auxin may affect flower initiation in a manner parallel to its effect on growth. LEOPOLD (70, 1951) believed that growth itself may play a role in the flower initiation and in several instances flowering responses vary quantitatively with growth. SHANKS and LINK (102, 1951) showed that due to high phosphorus or low nitrogen or unfavourable ratio of the two elements, the rate of development of inflorescences was noticeably slower. LEOPOLD (70, 1951) recently stated that inorganic plant nutrients do not play a primary role in photoperiodism, and that mineral deficiencies seemed to have little effect on the flowering behaviour of plants. LANG (68, 1952) drew attention to the fact that the time of floral initiation depends on the rate of the preceding vegetative growth, and conditions which influence this rate may cause differences in the time of flower formation, without having affected initiation in a specific manner. FLINT and ASEN (36, 1953) found that the concentration of mineral nutrient has little or no effect on the initiation of flower primordia of snapdragons. Recently, THOMAS (107, 1955) suggested that the effects of mineral deficiencies on photosynthesis are indirect, by reducing the vigour of the leaves and interfering with the dark reaction of metabolism. YOUNIS (118, 1955) believed that the delay in the photoperiodic response of *Kalanchoë blossfeldiana* may be due to a deficiency of salt supply, and probably nitrogen in particular, or to a decrease in the water content of the plants. LAL and SUBBA (67, 1952) studied the effect of 21 ratios of N, P and K on growth and developmental characters of barley. They found that an increasing N/K ratio appeared favourable for vegetative growth, and an increasing N/P ratio was favourable for reproductive growth, whilst higher P/K ratios were not so effective. HAMNER, LYON and HAMNER (48, 1942) found that growth and fruitfulness in tomato are significantly affected by variation in nutrient composition. Also, SEELEY (99, 1950) with lilies found that mineral nutrient deficiencies had no significant effect on the flower production except for the minus calcium plants, which had many blasted buds. He also concluded that the nutrient treatments had little effect on the time of flowering.

From the above, it follows that mineral deficiencies affect the flowering behaviour only slightly. Various reductions in growth result when any one of the minerals is deficient. It may be that growth plays a role in flower initiation and that in many cases the flowering responses are correlated with growth.

2. EFFECT OF SPECIFIC ELEMENTS ON FLOWERING

2.1. *Nitrogen*. - Most of the earlier nutritional and chemical studies on photoperiodism were influenced by, or interpreted by means of the carbohydrate-nitrogen relationship concept, which was suggested by KLEBS (61, 1918) and re-emphasized by KRAUS and KRAYBILL (63, 1918), NIGHTINGALE (87,

1927; 88, 1937) and EGGERS (30, 1946). Recent studies on nitrogen nutrition in relation to photoperiodism, are those of NEIDLE (86, 1938) and NAYLOR (85, 1941) with *Xanthium pennsylvanicum*, who found that nitrogen does not affect the critical day length requirement, but that the development of the terminal inflorescences was slow in nitrogen-deficient plants. VON DENFFER (109, 1940) found that the effect of nitrogen withdrawal, was to accelerate the development of the long-day plants (summer wheat, barley and *Iberis amara*) and to inhibit the development of the short-day plants (*Tinantia fugax*, *Setaria*, *Kalanchoë blossfeldiana* and *Chrysanthemum mepo*). These results made VON DENFFER erroneously believe that an abnormal response of the plant to nitrogen withdrawal is connected with its type of photoperiodic reaction. MELCHERS (80, 1952) agreed with VON DENFFER that lack of nitrogen promotes, and excess of nitrogen delays flowering in long-day plants. In short-day plants the effects of nitrogen are smaller and in the opposite direction, that is nitrogen starvation slightly delays flowering. CAJLACHJAN (16, 1944) studied the effect of nitrogen upon the rate of blossoming in *Perilla* plants. He concluded that plants supplied with nitrogen compounds, become more susceptible to the effect of short-day and break into blossom sooner, than plants poor in nitrogen compounds. In another paper CAJLACHJAN (15, 1944) found that a diet rich in nitrogen, stimulates the accumulation of dry mass and the growth of all plants, inhibits flowering and fruiting in some of them (mustard and oat) speeds up flowering and fruiting of others (*Perilla*, millet, lupin and lettuce) and has no influence whatever upon the rate of these processes in others (buckwheat, soya and hemp). WITHROW (115, 1945) in her study of the interrelationship between nitrogen supply and photoperiod in their effect on the flowering of long-day plants *Scabiosa atropurpurea* and *Spinacia oleracea*, and short-day plants *Tithonia speciosa*, *Soya max*, *Salvia splendens* and *Xanthium pennsylvanicum*, obtained evidence that external nitrogen supply is not a determining factor in floral initiation, but that in some species it alters the time at which floral buds first become visible. HALL (45, 1949), in studying the effect of emasculation in relation to nitrogen supply during the ontogeny of the gherkin, found that nitrogen does not effect the flowering or the flower bud initiation. HACSKAYLO (43, 1953) found that the floral initiation was retarded in tomato plants treated with NH_4 , but not in plants treated with NO_3 . Recently HAUPT (52, 1954) conducted an experiment to study the effect of yeast application (to produce nitrogen) on *Pisum sativum* with and without cotyledons, and found that in plants without cotyledons the flower-inhibiting activity of yeast extract is caused by its nitrogen content, while the degree of flower inhibition is dependent on the nitrogen concentration and not on the type of nitrogen. The effect of nitrogen on the time of flowering in spinach was shown by KNOTT (62, 1950). He found that large quantities of nitrogen delay seedstalk initiation and development. SCULLY, PARKER and BORTHWICK (98, 1945) found that the position of the first flower primordia in soybean, did not vary with nitrogen treatment when the plants were grown under short photoperiods; with long photoperiods, however, the plants initiated their first flower primordia at higher nodes as the amount of nitrogen was increased. LAL and TYAGI (65, 1952) found that nitrogen application delays flowering in tomato and, when it is deficient, that flowering is inhibited. HEWITT and MILES (54, 1954) with tulip and daffodil found that the omission of nitrogen results in an extra length of flower stem and in delay in flowering.

The fact that nitrogen affects the number of flowers produced, has been brought forward by many investigators. EVANS and WILSIE (34, 1946) with bromegrass, SCULLY, PARKER and BORTHWICK (98, 1945) with soybean, SHANKS and LINK (102, 1951) with *Hydrangea*, GARDNER and LOOMIS (37, 1953) with orchard grass and SHANKS, LINK and PRESTON (103, 1955) with *Azalea* found that nitrogen supply increases the number of flowers in these plants and also increases the number of flower nodes in soybean. JENKINS (60, 1949) with *Narcissus* also found that nitrogen application affects the flowering, and that there must be available nitrogen at emergence if satisfactory flower and bulb production is to be maintained, and if early blooming is desired. ERGLE (32, 1953) showed that low nitrogen supply markedly limited the number of flower buds of cotton plants. On the other hand EASTWOOD (24, 1952) with lilies found that low concentration of soil nitrate produced better plants with a greater yield of flowers and high quality blooms, than did high levels of soil nitrate. POST and HOWLAND (92, 1946) concluded that light intensity controls flower production and that nitrate fertilization cannot overcome this effect.

From the above review of literature it follows that nitrogen is not a decisive factor in determining the type of flowering. Although nitrogen does not induce a plant to flower in an unfavourable condition, yet it accelerates or retards the flower initiation and development. Excessive quantities of nitrogen and also its deficiency delay the flowering of some plants. The number of flowers produced increases with increasing quantities of nitrogen, except in lilies, where low levels of nitrogen produce more flowers than when nitrogen is supplied in excess.

2.2. *Potassium*. - Within recent years some investigators have tried to correlate the flowering behaviour of plants with potassium nutrition. NAYLOR (85, 1941) with *Xanthium pennsylvanicum* found that plants supplied with low potassium, had the same critical day-length requirements as those amply supplied with this soil nutrient, but the rate of development was considerably affected. SHANKS and LINK (102, 1951) found that addition of potassium to *Hydrangea* had no effect on the flower formation. EATON (29, 1952) made a recent and very thorough study on the effect of potassium deficiency on growth and metabolism of sunflower plants, and obtained evidence that potassium was readily translocated in potassium-starved plants, as indicated by the fact that plants grown for 66 days with minus potassium solution developed small flower buds.

JENKINS (60, 1949) found that high potassium levels did not induce good flower production unless the nitrogen level was also high. SEELEY (100, 1950) with roses found that an insufficient supply of potassium produced shorter flowering shoots and flowers slightly smaller than normal. Recently SHANKS, LINK and PRESTON (103, 1955) showed that a low level of potassium was adequate for the production of flowers of *Azalea*, and increasing levels of this element resulted in fewer flowers per plant.

Hence, potassium did not effect the number of days for flower initiation, but the development and number of floral buds may be affected.

2.3. *Phosphorus*. - Phosphorus was considered by many investigators to effect the flowering behaviour of plants. The flower initiation is not affected by phosphorus salts. NAYLOR (85, 1941) found that *Xanthium pennsylvanicum* plants supplied with a low level of phosphorus, had the same critical day length requirement as those amply supplied with this soil nutrient, but that the rate

of floral development was considerably affected. EATON (28, 1952) has also made a recent study on the effect of phosphorus on growth and metabolism of black mustard, and found that the plants were suffering from extreme phosphorus deficiency during the experiment, but all the plants developed small flower buds. HOWELL (58, 1954) recently concluded that the phosphorus level had little effect on the number of days to flowering in soybeans, the principle effect being a slight retardation at the extremely low or extremely high phosphorus levels.

Thus phosphorus affects the time of flowering and the number of flowers produced. Although EATON (26, 1949) with sunflower plants, found that phosphorus did not affect flowering, and that all plants in minus phosphorus or plus phosphorus treatments had developed flower buds, WILLIAMS (114, 1955) with oat plants found that the plants receiving high levels of phosphorus quickly exhausted their nitrogen supply and this hastened flowering.

HILL, DAVIS and JOHANSON (55, 1934) with chrysanthemums found that reduced flower bud formation and reduction in flower size, are due to excessive phosphorus feeding, while SHANKS, LINK and PRESTON (103, 1955) stated that a low level of phosphorus was adequate for the production of flowers in *Azalea* plants, and increasing levels of this element resulted in a smaller number of flowers per plant.

Hence, phosphorus did not effect the flower initiation of these plants. However, initiation was slightly retarded in soybean, when phosphorus was deficient or when present at high levels. The time of flowering and the number of flowers produced were more affected by phosphorus than the flower initiation.

2.4. *Calcium*. - Calcium deficiency in most cases affected the terminal bud of the plants, and immediate death of the growing tips occurred. When a small amount of this element was supplied, the growth was normal. Most of the literature covers the effect of calcium on the growth responses of the plant, but few deal with its effect on flowering. KUSHMAN and BEATTIE (64, 1946) found that the amount of calcium supplied to the plant in the nutrient solutions, played a very important role in the flowering and fruitfulness of peanut plants, that is, the lower the calcium the fewer the pods produced and the fewer the nuts in the pods that developed. SEELEY (99, 1950) with lilies, found that calcium deficiency affects the number of flowers produced, because plants grown without calcium had many blasted buds.

Hence, calcium reduces the number of flowers and fruits when it is deficient.

2.5. *Sulphur*. - The studies of sulphur and its influence on the metabolism of plants have been summed up by WOOD (117, 1942) and ERGLE and EATON (33, 1951). A general review of sulphur as a plant nutrient has further been given by GILBERT (41, 1951). EATON (25, 1942) found that in black mustard, sulphur deficient plants developed flowers and fruits earlier than in complete nutrient solution. ERGLE (32, 1953) found that low sulphur supply to cotton plants, markedly limited the number of flower buds.

Hence, sulphur deficiency favours the development of the flower buds, but limits their number.

As far as the writer is aware, there is no literature on the effect of magnesium on flowering.

CHAPTER III

GENERAL REMARKS ON THE EXPERIMENTS

This work was started in 1953 to determine the effect of nitrogen on the flowering response and growth, because from the review of literature nitrogen seemed to be the most important mineral in this respect. The study continued by trying to determine the effect of the other major elements (Mg, S, K, P and Ca) on plants, and was concluded by studying the effect of the relative ion concentrations. These three studies will be discussed in this thesis as follows: First, the effect of the mineral deficiencies individually, followed by the effect of nitrogen, and finally the effect of the relative ion concentrations.

MATERIAL AND METHODS

Two types of plants differing in their photoperiodical reaction were chosen for this study:

Mustard (<i>Sinapis alba</i>)	} L.D. plants
Dill (<i>Anethum graveolens</i>)	
Spinach (<i>Spinacea oleracea</i>)	
<i>Perilla crispa</i>	} S.D. plants
<i>Kalanchoë blossfeldiana</i>	

Two media were used in growing the plants, water and vermiculite cultures. Vermiculite was found to be a good medium for absorbing the solutions and holding them for a long time, PACCINI (89, 1954). In the different experiments the plants mentioned above were sown and potted under an unfavourable photoperiod for flowering until they were large enough (with 4 leaves), and then transferred to water culture or to vermiculite after thoroughly washing their roots in water. In water culture after a few days (differing in each experiment) 12 plants were transferred to a favourable photoperiod, while 4 plants were left growing under the unfavourable photoperiod. During the growing period examination was made under the dissecting microscope to follow the flower bud appearance.

This was the general technique carried out in the different experiments, and any change in this method will be mentioned separately in each experiment.

The nutrient solutions used in the different experiments were those of HOAGLAND and ARNON (56, 1950) and of HAMNER (46, 1940). A supplementary solution supplying the minor elements was added. Also 0.5 g/l solution of iron citrate was added every 15 days, at a rate of 1 cc per litre of nutrient solution, to prevent iron deficiency. The pH of the nutrient solutions used in the different experiments ranged between 5.5 and 6. Pots of 37 cl capacity were used to grow the plants.

In water culture, the solutions were replenished every 15 days. When the pots were filled with the nutrient solutions only ± 30 cl were put in each pot. This was done to lower the level of the nutrient solutions in the pots in order to increase the oxygen supply to the roots (ARNON and HOAGLAND, 3, 1944), while in mustard (because it is a high oxygen requiring plant) compressed air was bubbled through the solution to obtain good growth, ALLISON (1, 1921), DURELL (23, 1941) and HOPKINS *et al.* (57, 1950). The technique carried out in the water culture or in the vermiculite culture was adopted from SHIVE and

ROBBINS (104, 1938), DUNLAP (22, 1939), ROBBINS (94, 1946), ELLIS and SWANEY (31, 1938), WITHROW, R. B. and WITHROW, A. P. (116, 1948), GERICKE (40, 1950) and HEWITT (53, 1952).

In every experiment 20 plants were kept growing in soil, to compare them with the other plants in the different treatments.

Because growth may interfere with the flowering process, growth responses of the plants were determined as well as the flowering responses. In each experiment data on the time of formation of floral buds, height of plants and number of leaves and floral buds, diameter of stem and fresh and dry weights were recorded. The plant material was dried for some days (differing in every experiment) in an electric oven thermostatically controlled at 80 °C. The height of the plants was measured from the cotyledon node to the tip of the terminal bud. The diameter of stem, in millimeters, was determined at a point approximately one cm above the cotyledon node. The leaf areas in cm² were determined by means of a planimeter just prior to inductive treatment (in some experiments) and after the flower bud appearance (in others). The top/root ratio was calculated as dry weight of stem, plus leaves, plus flowers (if present) to dry weight of roots. The dry matter percentage = the weight of dry material as % of the fresh weight. The leaf efficiency = the dry weight of stems and roots produced per unit weight of leaf.

CHAPTER IV

EFFECT OF MINERAL DEFICIENCIES ON THE FLOWERING RESPONSES AND THE GROWTH OF LONG AND SHORT-DAY PLANTS

1. MUSTARD (*SINAPIS ALBA*; L.D.P.)

1.1. *Experiment I: In water culture*

Material and methods. – According to CAJLACHJAN (15, 1944) mustard is a long-day plant which flowers sooner in low levels of nitrogen.

Seeds of mustard were sown on 18/1/1955 and were potted on 25/1/1955. When the plants had four leaves (22/2/1955), the roots were thoroughly washed in water and grown in culture solution with forced aeration. Compressed air was bubbled through the nutrient solutions for half an hour each day. Seven nutrient solutions according to HOAGLAND and ARNON (56) were used in this experiment: a complete solution (N), and -N, -P, -S, -Mg, -K and -Ca solutions respectively.

Each treatment mentioned above contained 16 plants, left under short day until 11/3/1955. On this date 12 plants of each treatment received an inductive period of long-day with supplementary light of high intensity (450 watt), while 4 plants of each treatment remained under short-day.

During the growing period, observations were made on the type of growth of the plants in the different treatments and the time of appearance and rate of development of any symptoms of abnormal nutrition. In addition, quantitative characters of the plants were measured under both long and short day conditions.

Results. – During the period in which the plants were growing in the various nutrient solutions, decided differences in size and growth became apparent and different symptoms were produced. The plants in the various solutions were not similar in colour to ordinary plants grown in soil.

Leaf symptoms – 1. Nitrogen deficiency: The most clear evidence of N-deficiency shown by the leaves was the general yellow colour, which started first in the old leaves and spread gradually to the young ones. The other evidence was the reduced leaf size. No particular necrotic areas developed in the leaves and a marked dropping of the older leaves occurred.

2. Magnesium deficiency: There was a progressive development of a light green chlorotic area from the tip to the base of the leaf. The most affected leaves were the younger ones. A marked inhibition of growth occurred and in many cases the plants terminal bud died.

3. Sulphur deficiency: The upper foliage was the first to be affected by the lack of sulphur. A light red colour was seen in the different parts of the plant especially in the stem. The stems and leaves of the plant were stiff.

4. Phosphorus deficiency: The colour of the leaves was very dark green especially along the veins. The leaves were reduced in size and there was a pronounced dropping of the old leaves. The margin of the leaves was light green.

5. Potassium deficiency: First a light green colour developed at the tip and along the edges of the leaves, followed by the occurrence of necrotic areas with a fairly sharp break between normal and necrotic leaf tissue.

6. Calcium deficiency: The calcium deficiency was seen in the terminal bud and top leaves. The leaves became wrinkled and were reduced in size. The terminal bud died and sometimes the whole tops died. Little dropping of the older leaves occurred.

Floral responses: According to table 1, row 1, the effect on the flower bud appearance of the different mineral deficiencies was generally of little significance. The -N and -P plants were the first to show their flower primordia, followed by -S and -Ca, (N) and -K, while the -Mg plants were the last.

The development of floral buds was more affected by mineral deficiencies (table 1, row 3). Plants growing in -N solution open their flowers in 16 days with long-day treatment, the plants growing in -P solution in 30 days with long-day treatment, and plants growing in -S solution in 40 days. The floral buds of the plants growing in -Ca, -Mg, or -K failed to develop and the flowers did not open. Photo 1 at the end shows the accelerating effect of nitrogen deficiency on the development of the floral buds. The lowest number of floral buds occurred in plants grown in -N solution.

Growth responses: Plants in -N solution were significantly taller than the others (table 1, row 7, column 8) and generally plants grown in the different solutions under L.D. were taller than those under S.D. (rows 7 and 8). The last conclusion also holds true for stem diameter (rows 11 and 12).

The lack of minerals reduced the diameter of the stems under S.D. more than under L.D.

Under both long and short-day conditions, P-deficiency increased the internode length (rows 9 and 10, column 5), but N-deficiency increased it to a marked degree (rows 9 and 10, column 8), while K-, Mg- and S-deficiencies reduced internode length.

There were no significant differences in the number of leaves in the different treatments (row 13 and 14), but leaf drop was caused mainly by N- and P-deficiencies (rows 15 and 16, columns 5 and 8). The number of leaves that dropped decreased in the other treatments. Leaf size (rows 17 and 18) was lowest in the -N treatment. The largest leaves were produced when N was

TABLE 1. Experiment I. Effect of mineral deficiencies on the flowering responses and the growth of mustard

1		2	3	4	5	6	7	8
Treatment		(N)	-Mg	-S	-P	-K	-Ca	-N
(mean) Character								
1. Days to flower bud	L.D.	9	15	8	6	9	8	6
2. Days to flower bud	S.D.	∞ ¹	∞	∞	∞	∞	∞	∞
3. Days to open flowers	L.D.	∞	∞	40	30	∞	∞	16
4. Days to open flowers	S.D.	∞	∞	∞	∞	∞	∞	∞
5. Number of floral buds	L.D.	∞	∞	28	26	∞	∞	20
6. Number of floral buds	S.D.	∞	∞	∞	∞	∞	∞	∞
7. Height in cm	L.D.	16.0	11.7	13.9	15.5	11.5	11.2	38.0
8. Height in cm	S.D.	12.0	11.5	11.5	13.5	9.5	8.7	21.5
9. Length of internodes in mm	L.D.	7.6	6.8	6.3	8.6	6.3	7.0	14.0
10. Length of internodes in mm	S.D.	5.7	5.2	5.5	6.4	5.0	5.1	10.0
11. Diameter in mm	L.D.	3.8	3.9	3.4	3.4	3.4	2.7	2.9
12. Diameter in mm	S.D.	3.4	2.9	3.2	2.3	2.3	2.1	2.6
13. Number of leaves	L.D.	19.0	17.5	19.0	13.0	17.0	13.0	13.0
14. Number of leaves	S.D.	19.0	22.0	21.0	15.5	17.0	13.5	13.0
15. Number of dropped leaves	L.D.	2.0	0	3.5	5.0	1.0	3.5	7.5
16. Number of dropped leaves	S.D.	2.0	0	0	6.0	1.0	3.5	7.0
17. Area of two median leaves	L.D.	17.8	17.2	17.8	12.9	11.4	8.9	3.9
18. Area of two median leaves	S.D.	13.1	14.0	13.4	9.0	7.7	7.0	3.8
19. Dry weight of leaves in g	L.D.	0.283	0.493	0.270	0.149	0.175	0.101	0.025
20. Dry weight of leaves in g	S.D.	0.195	0.219	0.185	0.114	0.053	0.049	0.030
21. Stem + root dry weight in g	L.D.	0.377	0.204	0.271	0.282	0.153	0.127	0.242
22. Stem + root dry weight in g	S.D.	0.229	0.123	0.190	0.187	0.126	0.051	0.184
23. Leaf efficiency	L.D.	1.332	0.413	1.003	1.898	0.659	1.257	9.680
24. Leaf efficiency	S.D.	1.174	0.561	1.027	1.255	0.874	1.040	6.133
25. Dry weight per plant in g	L.D.	0.660	0.697	0.541	0.431	0.328	0.228	0.267
26. Dry weight per plant in g	S.D.	0.424	0.342	0.375	0.301	0.179	0.100	0.214
27. Top/root ratio	L.D.	6.1	6.3	4.5	3.3	5.6	9.3	3.7
28. Top/root ratio	S.D.	6.2	6.6	3.8	3.0	7.9	19.0	4.6

¹ In this and following tables ∞ means that no data could be collected, because the plants did not flower.

supplied, and when Mg and S were lacking in the nutrient solution. P-, K- and Ca-deficiencies decreased the leaf size slightly, but N-deficiency decreased it to a marked degree. Leaf size increased under L.D. more than under S.D.

Dry weight: The dry weight of the leaves was affected largely by -Mg (rows 19 and 20). A large dry weight was obtained, under both long and short-day conditions, when Mg was lacking from the solution (rows 19 and 20, column 3), while Ca- or N-deficiencies decreased the dry weight to a marked degree (rows 19 and 20, columns 7 and 8). The greatest leaf efficiency was obtained when the plants were supplied with -N solution (rows 23 and 24, column 8). Leaf efficiency was considerably less when Mg or K were lacking from the culture solution (rows 23 and 24, columns 3 and 6). The total dry weight of stem plus roots was large under both long and short-day when S and P were lacking (rows 21 and 22, columns 4 and 5). N-, K- or Mg-deficiencies decreased the dry weight slightly, but Ca- deficiency reduced it to a marked degree.

The total dry weight of plants was affected largely by the Ca-deficiency; a smaller dry weight was obtained when Ca was lacking from the nutrient solution under both long and short-day (rows 25 and 26, column 7).

The top/root ratio was high in plants grown in -Ca solution (rows 27 and 28, column 7), because the roots failed to develop and were dying especially under short-day, while in N-, P- and S-deficiencies the root system was well developed, and the top/root ratio was low. Because lack of calcium curtailed root development, a higher ratio of leaves and stalk to total dry weight of roots was obtained. In this experiment it was the lack of Ca, N or P that gave the greatest extremes in the ratio of tops to roots. Ca-deficiency produced the smallest, and N- and P-deficiencies the greatest amount of roots in relation to leaves and stalks.

Additional remarks. - From the data obtained it follows that the different mineral deficiencies have little effect on the time of flower bud appearance. Lack of nitrogen accelerated the flower bud initiation, while magnesium retarded it.

Some plants in the -P solution under L.D. were still in the vegetative state after the 8 days which other plants need for their flower initiation, but one should keep in mind the fact, so aptly stated by LOEWING (73, 1942), that at any given time similar organs of a plant may be in various stages of development. Parts of the tissue on the same plant may range from juvenile to senescent stages, and through all stages of reproductive type of growth. According to this fact P-deficiency may be considered to accelerate the flower initiation to a small degree, unlike the N-deficiency which definitely affects the flower bud appearance.

At the end of the experiment all the plants in the different treatments grown under short day, were still in the vegetative stage. This indicates that mineral deficiencies did not alter the photoperiodical reaction of mustard.

The development of the floral buds was greatly affected by mineral deficiencies. The flowers opened much earlier when N was lacking, while it was retarded when S or P were lacking.

In -Ca, -K and -Mg plants none of the floral buds developed. From table 1, row 19, column 3 it follows that the cause of the bud retardation in the Mg-deficient plants, was that the leaves kept a large quantity of carbohydrates and prevented it from being translocated to the stem and roots, and as a result the floral bud appearance was delayed.

1.2. *Experiment II: In vermiculite*

Material and methods. - In the first experiment it was found that mustard did not grow well in water culture unless oxygen was supplied to the roots. In order that the roots may obtain the oxygen required for their growth, a well-aerated medium must be used, so that the plants develop normally and react to mineral deficiency. For this reason vermiculite was chosen as a medium for growing the plants in the present experiment.

Seeds of mustard were sown on 25/6/1955 under S.D. On 6/7/1955 the small plants were transplanted to asbestos boxes filled with vermiculite and watered with different nutrient solutions. Fourteen asbestos boxes (50 × 50 × 20 cm) were used. Each was filled with vermiculite to a depth of four inches. A small pot to subirrigate with nutrient solution when required, was placed in the centre. In each box 3 litres of the nutrient solution were supplied and 25 plants were grown. The same seven nutrient solutions which were used in the former experiment were used here. Every 15 days the boxes were watered with the different solutions, while distilled water was given to the plants when they needed it. The 14 boxes were put under S.D. until 21/7/1955. On this date 7 boxes were transferred to L.D., while 7 remained in S.D. During the growing

period examination under the dissecting microscope was made every two days to follow the initiation of the flower buds. At the end of the experiment the same quantitative measurements as in the first experiment were made, in the present case with 15 plants. The rate of development of the floral buds was also studied by daily recording the number of plants with opened flowers.

Results. -- In the course of the experiment decided differences in size and growth became apparent, but the symptoms produced by the lack of minerals in the different treatments were not as pronounced as in water culture.

Flowering responses: Mineral deficiencies had an effect on the flower bud appearance. Table 2, row 1 shows that the group of plants which was supplied with -N solution was the first to initiate their flower primordia (8 long days). Plants watered with -P, -K, -Ca or -S solutions were second in producing their flower primordia (12, 12, 12, 11 long-days respectively), this second group needed the same period as the control (plants supplied with full nutrient solution) (12 long-days). The last to initiate flower primordia was the group of plants supplied with -Mg solution (14 long-days).

Figure 1 shows that the development of the floral buds of plants supplied

TABLE 2. Experiment II. Effect of mineral deficiencies on the flowering responses and the growth of mustard

(mean) Character	Treatment						
	(N)	-Mg	-S	-P	-K	-Ca	-N
1. Days to flower bud L.D.	12	14	11	12	12	12	8
2. Days to flower bud S.D.	∞	∞	∞	∞	∞	∞	∞
3. Number of floral buds . . . L.D.	70.0	69.0	64.0	44.0	62.0	31.0	52.0
4. Number of floral buds . . . S.D.	∞	∞	∞	∞	∞	∞	∞
5. Plants with open flowers % . L.D.	60.0	60.0	100.0	6.6	100.0	13.3	100.0
6. Plants with open flowers % . S.D.	∞	∞	∞	∞	∞	∞	∞
7. Number of days to open flowers L.D.	70	70	55	66	59	66	38
8. Number of days to open flowers S.D.	∞	∞	∞	∞	∞	∞	∞
9. Height cm L.D.	86.0	74.0	55.0	29.0	65.0	40.0	62.0
10. Height cm S.D.	91.0	78.0	66.0	50.0	52.0	46.0	30.0
11. Length of internodes in mm L.D.	3.9	3.2	2.5	1.6	3.0	2.0	3.1
12. Length of internodes in mm S.D.	2.3	2.0	1.9	1.3	1.6	1.3	1.2
13. Diameter in mm L.D.	7.42	7.92	4.95	3.20	4.97	4.10	3.30
14. Diameter in mm S.D.	10.15	9.72	6.80	4.02	5.10	5.52	3.75
15. Number of leaves L.D.	16	19	12	8	10	13	8
16. Number of leaves S.D.	29	31	27	15	18	21	13
17. Number of dropped leaves L.D.	7	4	8	10	13	8	13
18. Number of dropped leaves S.D.	11	9	8	14	14	14	11
19. Area two median leaves . . L.D.	130.0	129.0	64.0	14.0	53.0	26.0	14.0
20. Area two median leaves . . S.D.	104.0	94.0	61.0	17.0	30.0	27.0	16.0
21. Dry weight of leaves in g . . L.D.	2.076	2.046	0.518	0.722	0.185	0.149	0.484
22. Dry weight of leaves in g . . S.D.	2.637	3.075	0.513	1.440	0.828	0.247	0.805
23. Dry weight of stem in g . . L.D.	1.629	1.525	0.744	0.737	0.178	0.386	0.277
24. Dry weight of stem in g . . S.D.	2.962	2.985	0.775	1.613	1.440	0.218	0.809
25. Dry weight of flowers in g . L.D.	0.057	0.057	0.042	0.035	0.006	0.071	0.009
26. Dry weight of flowers in g . S.D.	∞	∞	∞	∞	∞	∞	∞
27. Dry weight per plant in g . L.D.	3.762	3.628	1.304	1.494	0.369	0.606	0.770
28. Dry weight per plant in g . S.D.	5.599	6.060	1.288	3.053	2.263	0.465	1.614

with $-N$ solution was faster than in the other treatments, while the opening of the flowers was retarded in $-Mg$ plants, or when supplied with the full nutrient solutions. The different mineral deficiencies generally had a great influence on the number of floral buds produced. P-, Ca- or N-deficiencies decreased the number of floral buds to 44, 31, 52 respectively (table 2, row 3, columns 5, 7 and 8). The (N), $-Mg$, $-S$ and $-K$ solutions increased the number of the floral bud produced to 70, 69, 64, 62 respectively (row 3, columns 2, 3, 4 and 6).

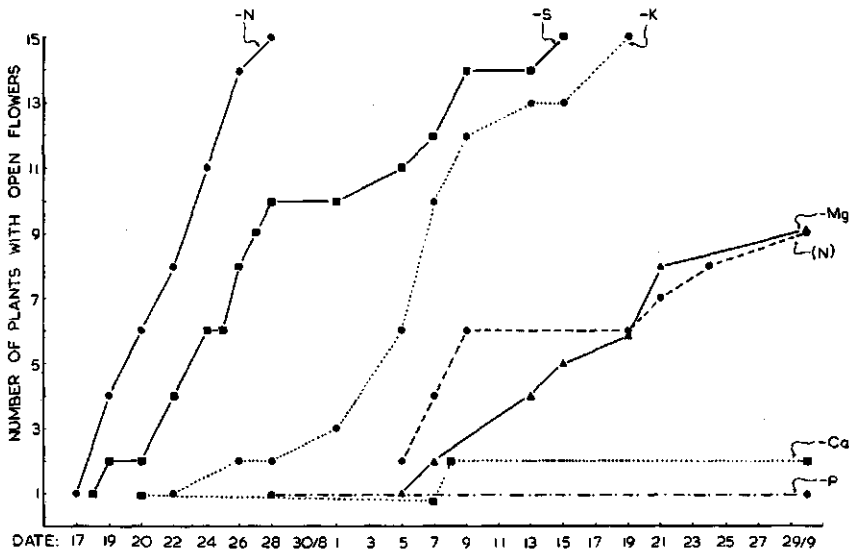


FIG. 1. Experiment II: Effect of mineral deficiencies on flowering of mustard in long-day.

The percentage of plants with opened flowers was also greatly affected. A high percentage was obtained when S, K or N was lacking (row 5, columns 4, 6 and 8), the percentage decreased in plants supplied with (N) solution or with $-Mg$ (row 5, columns 2 and 3), the percentage decreased to a marked degree when P or Ca were lacking (row 5, columns 5 and 7).

In the different treatments the number of days needed by the plants to produce these percentages of opened flowers was significantly different. In plants supplied with $-S$, $-K$ or $-N$ a high percentage of plants with opened flowers was obtained (100%), but the number of days needed in these three treatments was 55, 59 and 38 days respectively (row 7, columns 4, 6 and 8). From rows 3, 5 and 7 and figures 1 and 2 it is clear that N-deficiency accelerated the flower bud development, while the other mineral deficiencies and the (N) solutions retarded it. Ca- and P-deficiencies decreased the rate of development to a marked degree.

Vegetative responses: Under both long and short-day plants supplied with (N) solution or with $-Mg$ solution were clearly taller than the others (rows 9 and 10, columns 2 and 3). The (N) solution and $-Mg$ solution increased the diameter of the plants, while N- and P-deficiencies reduced it. Generally the diameter of plants in the different treatments under L.D. was smaller than under S.D. (rows 13 and 14). Plants supplied with (N) solution and $-Mg$ solu-

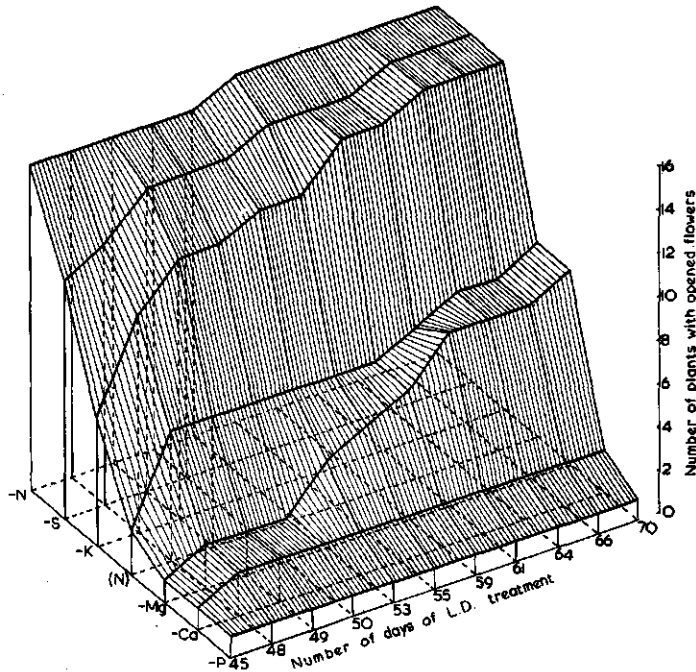


FIG. 2. Experiment II: Effect of mineral deficiencies on flowering of mustard in long - day.

tion produced long internodes (rows 11 and 12, columns 2 and 3) while plants supplied with $-P$ solution had short internodes. Generally the internodes of the plants in the different treatments under L.D., were longer than under S.D. (rows 11 and 12). The (N) solution and $-Mg$ solution increased the number of leaves produced under both long and short-day and at the same time reduced the number of dropped leaves (rows 15, 16, 17 and 18, columns 2 and 3). Leaf drop was mostly greater under S.D. than under L.D. (rows 17 and 18) and it was also greater in N-, Ca-, K- and P-deficiencies than in S- and Mg-deficiencies.

Leaf size, and the number of leaves were increased mainly by (N) and also by Mg- deficiency (rows 19 and 20, columns 2 and 3). S-, K- and Ca-deficiencies decreased the leaf size to different degrees, but N- and P-deficiencies decreased it to a marked degree. These results hold true under both long and short-day conditions (rows 19 and 20).

Dry weight: The dry weight of leaves was large under both long and short-day, when nitrogen was supplied and when Mg was deficient (rows 21 and 22, columns 2 and 3). The other mineral deficiencies reduced the dry weight of leaves to different degrees.

Summary of results: The data obtained in this experiment showed that lack of N accelerated the flower bud appearance, while Mg-deficiency and N supply retarded it. The various mineral deficiencies affected the time of flower bud appearance of mustard only slightly. It is natural that the minerals, active in so many growth processes in plants, have also been important in connection with flowering. Undoubtedly they do affect flowering behaviour, and play an important part in the physiological process of flowering.

Although mineral deficiencies did not alter the habit of flowering of mustard under unfavourable photoperiod, yet they interfered in the process of flowering under a favourable photoperiod by modifying the rapidity of flower bud formation. The average number of floral buds produced, the rate of development of the floral buds, and the percentage of opened flowers, were affected by mineral deficiencies. From figures 1 and 2 it is clear that N-deficiency played an important role in accelerating these three processes.

In vigorously growing plants there is no effect on the initiation and development of floral buds. Plants with reduced growth and small dry weight, flowered sooner than plants with good growth and high dry weight.

Among the minerals used in this experiment N- or Mg-deficiencies gave the greatest extremes in the floral responses of mustard; N-deficiency accelerated the initiation and development of the floral buds, while Mg-deficiency retarded these processes.

1.3. *Discussion.* - The two experiments with mustard, showed that the flower bud appearance was accelerated by the lack of N. In water culture, mustard plants were poorly developed and many of the plants in the different treatments did not develop their flowers, while in vermiculite the plants grew normally, developed their floral buds and opened their flowers.

The growth of plants in vermiculite, under both long and short-day, was greater than in water culture. This is demonstrated for instance by the figures for height and dry weight shown in tables 1 and 2. In both water and vermiculite, N-deficiency accelerates the flower bud appearance and the development of mustard, but the effect is clearer in vermiculite than in water culture.

With regard to the growth in general, our experiments demonstrated that plants in (N) solution were more vigorous than the other treatments, where one of the mineral elements was lacking. This is in agreement with the literature (31, 79, 93). However, flowering response in mustard is not positively correlated with growth, as found by some authors (68, 70, 71), but negatively. Our results in tables 1 and 2 show positively that poor growth and low dry weight are accompanied by early flower bud appearance and rapid development. With plants of good growth and high dry weight the reverse occurs. The top/root ratio is lowered by P- or N-deficiency, which is in agreement with the literature (25, 27, 58, 91). With the exception of -P our vegetative plants had a larger top/root ratio than the flowering ones. This result is in opposition to WITHROW (115) and ROBERTS and STRUCKMEYER (95) who worked with other plants. Generally, when the plants are flowering, the dry weight accumulation is decreased by deficiency of K, Ca or N. This result is in accordance with several authors (48, 96, 105, 107).

The general conclusion is that mineral deficiencies affect the flower bud appearance, the flowering and the growth behaviour of mustard. The most typical reaction is that the time of flower bud appearance is negatively correlated with vigour.

2. DILL (*ANETHUM GRAVEOLENS* L.D.P.)

Experiment III:

Material and methods. - Dill is a plant specifically requiring L.D. treatment to induce flowering (47). Roots of plants with 4 leaves were thoroughly washed in water and grown in culture solution under S.D. The nutrient

solutions which were used in the former experiments were also used here, thus having seven treatments each with 16 plants. After nearly one month (on 16/9/1955) 12 plants from each treatment received an inductive period of L.D. (sun light, supplemented by ordinary light bulbs to reach a total of 16 hours photo-period), while 4 plants of each treatment remained growing under S.D. During the induction period, examination under the dissecting microscope was made at regular intervals, to follow the floral bud development.

At the end of the experiment, quantitative measurements were made of the plants under L.D., and the data obtained in the different treatments were recorded in table 3.

Results. - Flowering responses: From table 3, row 1 we conclude that the flower bud appearance of dill was effected by mineral deficiencies. (N) accelerated the flower initiation of the plants. Mg- or S-deficiencies retarded it 5 days compared with the former group, while N-, P- or K-deficiencies retarded it 20 days.

TABLE 3. Experiment III. Effect of mineral deficiencies on the flowering responses and the growth of dill under L.D.

	1	2	3	4	5	6	7
	Treatment	(N)	-Mg	-S	-K	-P	-N
(mean) Character							
1. Days to flower bud		17	22	22	37	37	37
2. Number of inflorescences		42	20	10	10	4	10
3. Height cm		118.0	32.0	14.0	12.0	9.0	12.0
4. Diameter mm		5.55	3.10	2.95	2.35	2.10	2.13
5. Number of nodes		17.0	17.0	12.0	15.0	13.0	12.0
6. Length of internodes cm		6.9	1.9	1.1	0.8	0.7	1.0
7. Number of leaves		15.0	11.0	9.0	10.0	8.0	8.0
8. Number of dropped leaves		3.0	6.0	5.0	5.0	5.0	5.0
9. Number of branches		7.0	4.0	-	-	-	-
10. Fresh weight of roots in g		5.25	1.10	0.60	0.97	0.55	0.46
11. Dry weight of roots in g		0.38	0.05	0.03	0.06	0.02	0.03
12. Dry weight % of roots		7.03	5.0	5.68	6.12	4.82	6.62
13. Fresh weight of leaves in g		7.44	1.33	0.92	1.31	0.27	0.24
14. Dry weight of leaves in g		1.08	0.27	0.16	0.58	0.10	0.08
15. Dry weight % of leaves		14.47	20.36	19.83	21.38	38.58	31.72
16. Fresh weight of stems in g		13.31	1.37	0.37	0.52	0.13	0.17
17. Dry weight of stems in g		1.77	0.10	0.06	0.06	0.01	0.03
18. Dry weight % of stems		13.09	8.22	16.86	11.83	12.09	16.70
19. Fresh weight per plant in g		26.0	3.80	1.89	2.80	0.95	0.87
20. Dry weight per plant in g		3.23	0.42	0.25	0.70	0.13	0.14
21. Dry weight % per plant		12.3	11.0	13.2	25.0	13.6	16.0
22. Percentage water content		87.7	89.0	86.8	75.0	86.4	84.0
23. Leaf efficiency		2.064	0.555	0.562	0.206	0.300	0.750
24. Top/root ratio		7.5	7.4	7.3	10.7	2.5	3.7

Plants grown in -Ca solution died prematurely, so this treatment was omitted from table 3. The number of inflorescences produced in the treatments were significantly different. The ratio between the different treatments was 10.5 in (N) solution: 5 in -Mg: 2.5 in -N, -K and -S plants: 1 in -P (row 2).

Growth responses.: The plants in the various nutrient solutions were not equivalent in size and growth to those grown in soil. From the data recorded in table 3 (rows 3 and 4) it is clear that the (N) solution produced considerably

taller plants with large stem diameter, while the five mineral deficient treatments produced small stunted plants with reduced diameters. There were no big differences in the number of nodes in the different treatments, but the length of the internodes was more affected (rows 5 and 6). Mg-deficiency decreased internode length slightly (row 6, column 3), while the other mineral deficiencies decreased it to a marked degree (row 6, columns 4, 5, 6 and 7).

There were no big differences in the number of leaves produced in the different treatments, but the number of dropped leaves was large in -Mg (row 8, column 3) and slightly smaller in the other treatments (row 8, columns 4, 5, 6 and 7), while it was least in plants supplied with full nutrient (row 8, column 2). The number of branches produced in -Mg plants was nearly half of that of plants supplied with full nutrient (row 9, columns 2 and 3), while in the other deficient solutions the development of lateral buds was inhibited.

Fresh and dry weight: The fresh and dry weight reflected how much the mineral deficiencies affected the growth of dill plants. (N) solution increased the growth, while the other mineral deficiencies reduced it to a marked degree (rows 10, 11, 13, 14, 16 and 17). The total percentage of dry weight and percentage of water content were slightly affected by mineral deficiencies. Mg-deficiency produced the lowest total dry weight percentage (row 21, column 3) and the highest water content percentage (row 22, column 3), while -K produced the reverse: a high percentage of dry weight (row 21, column 5) and a low percentage of water content (row 22, column 5).

The greatest leaf efficiency was obtained in (N) (row 23, column 2) and was decreased by mineral deficiencies especially by K- and P-deficiencies (row 23, columns 5 and 6).

The top/root ratio was high with K-deficiency (row 24, column 5), because the roots failed to develop, while in -P or -N treatments the ratio was low (row 24, columns 6 and 7) because the vegetative parts were more affected than the roots.

Conclusion. - The data obtained in this experiment show that the time of flower bud appearance was effected by the mineral deficiencies. Plants develop flowers normally in the full nutrient solution, while the growth was greatly reduced by the different mineral deficiencies and this interferes with the flowering process.

3. *PERILLA CRISPA* (S.D.P.)

Experiment IV:

Material and methods. - *Perilla* is a qualitative S.D. plant which under optimum conditions has visible flower buds about 20 cycles of 8 hours light and 16 hours darkness (112). The technique and the seven nutrient solutions in the present experiment, are the same as those used in the former experiment, except that the plants grew under L.D. until 23/5/1955. On this date 12 plants per treatment received an inductive period of S.D., while 4 plants remained under L.D.

Results. - The effect of the different mineral deficiencies was clearly reflected in the leaves. The lack of each element produced characteristic changes which were accompanied by the appearance of certain symptoms. -N produced small plants with a comparatively long root system. The leaves were small, light in colour, with stiff blades and the old leaves soon dropped. -Mg affected more the

upperpart of the plant. The leaves dropped when they were still young and the plants appeared defoliated and in most cases the terminal bud died. -K produced necrotic areas in the leaves which then dropped. The effect of -S was reflected in the upper leaves of the plants. The new leaves were small and light red in colour. Plants generally failed to develop to normal size. -P produced small plants and a marked inhibition of growth. The leaves were dark red and easily dropped when they were touched. The root system was poorly developed and longer than usual. -Ca produced wrinkled cup-shaped leaves. The terminal bud died and generally the whole plant died prematurely. The root system was poorly developed and very weak.

Floral responses: Table 4 row 2 shows that the time of flower bud appearance was only slightly affected by the different mineral deficiencies. Plants grown in (N) were the first to initiate their flower primordia (20 short days), immediately followed by the plants grown in -Mg and in -S (21 short days). The third was the group of plants grown in -K (22 short days). The last were the plants grown in -N and -P (26 short days). The plants in -Ca died prematurely, but when traces of calcium (20 ml/g litre) were supplied, the plants grew and developed normally and initiated their flower primordia after the same number of days as the standard (plants in soil).

The flowers of the plants growing in (N) solution were also the first to open (30 short days) (row 4, column 2) and those of the plants growing in -P and -N solutions were the last to open (41 short days) (row 4, columns 6 and 7).

Row 6 shows that the number of floral buds produced by plants in the different solutions varied enormously. The average number produced by plants grown in (N) solution was nearly 5 times that of the plants grown in -Mg, -S or -K solutions, and more than 12 times as much as those produced by plants grown in -P or -N solutions.

From the data obtained we conclude that the various mineral deficiencies had little effect on the flower bud appearance in *Perilla*. (N) accelerated the flower bud initiation, while -P or -N retarded it.

Growth responses: Rows 7 and 8 show that the plants grown in (N) were much taller than the others under both L.D. and S.D. Plants in -Ca solution were the smallest (rows 7 and 8, column 8).

The diameter of the stem was affected in a similar way as was the height of plant. The lack of N, P or Ca in the solution reduced the diameter of the stems to a marked degree under both L.D. and S.D. (rows 9 and 10, columns 6, 7 and 8). Plants had long internodes under both L.D. and S.D. in (N) solution (rows 13 and 14, column 2). Plants supplied with solutions -P, -N or -Ca had short internodes (rows 13 and 14, columns 6, 7 and 8).

A large leaf drop is caused mainly by -Mg or -K under S.D. (row 18, columns 3 and 4). The number of dropped leaves was lower in the other treatments.

The number of leaves on the whole plant, was largest in the plants grown in the (N) solution (rows 19 and 20, column 2), and the number decreased to a marked degree in the various deficient solutions. The ratio between the different treatments under L.D. was 21 (N):14 -Mg:8 -K:6 -S:3 -P:3 -N:1 -Ca, and under S.D.: 10 (N):5 -Mg:7 -K:6 -S:2 -P:3 -N:1 -Ca.

Especially the lack of P, N or Ca from the solution reduced the number of branches (rows 21 and 22, columns 6, 7 and 8).

Rows 23 and 24 show that the leaf area was largest in the (N) solution,

TABLE 4. Experiment IV. Effect of mineral deficiencies on the flowering responses and the growth of *Perilla*

1	2	3	4	5	6	7	8
(mean) Character	Treatment						
	(N)	-Mg	-K	-S	-P	-N	-Ca
1. Days to flower bud	L.D.	∞	∞	∞	∞	∞	∞
2. Days to flower bud	S.D.	20	21	22	21	26	26
3. Days to open flowers	L.D.	∞	∞	∞	∞	∞	∞
4. Days to open flowers (from short day treatment) .	S.D.	30	32	35	34	41	41
5. Number of floral buds per plant							
	L.D.	∞	∞	∞	∞	∞	∞
6. Number of floral buds per plant							
	S.D.	370	70	80	84	30	29
7. Height cm	L.D.	40.5	16	16.5	17	7.5	8.2
8. Height cm	S.D.	50.5	16.5	17.7	28.0	9.1	9.0
9. Diameter mm	L.D.	6.41	3.87	3.41	3.82	2.64	2.90
10. Diameter mm	S.D.	5.46	2.97	3.20	3.62	2.46	2.46
11. Number of nodes	L.D.	10.5	8.0	9.0	7.0	6.0	6.0
12. Number of nodes	S.D.	9.5	8.0	8.0	8.0	7.0	6.0
13. Length of internodes cm . . .	L.D.	3.8	2.0	1.8	2.4	1.2	1.3
14. Length of internodes cm . .	S.D.	5.3	1.9	2.2	3.5	1.3	1.5
15. Number of leaves on the main stem	L.D.	21.0	14.0	11.0	14.0	6.0	7.0
16. Number of leaves on the main stem	S.D.	19.0	8.0	6.0	14.0	8.0	7.0
17. Number of dropped leaves on the main stem	L.D.	0.0	4.0	6.5	1.0	6.0	4.0
18. Number of dropped leaves on the main stem	S.D.	0.0	8.0	10.0	1.0	6.0	5.0
19. Number of leaves on the whole plant	L.D.	84.0	54.0	32.5	23.0	11.0	12.0
20. Number of leaves on the whole plant	S.D.	60.0	28.0	40.0	34.0	13.0	15.0
21. Number of branches	L.D.	16.0	11.5	12.0	5.0	3.0	3.0
22. Number of branches	S.D.	16.0	14.0	15.0	14.0	6.0	7.0
23. Leaf area cm ² of each plant before transferred to S.D.		173.2	135.0	134.5	112.1	64.3	48.3
24. Differences of leaf area in % of the plants grown in soil		+55%	+21%	+21%	+0.9%	-42%	-56%
							-67%
25. Dry weight of leaves in g . . .	L.D.	3.88	0.90	0.74	0.89	0.23	0.16
26. Dry weight of leaves in g . . .	S.D.	2.85	0.29	0.29	1.02	0.29	0.14
27. Stem + root dry weight in g . .	L.D.	3.23	0.46	0.48	0.72	0.26	0.17
28. Stem + root dry weight in g . .	S.D.	3.12	0.31	0.49	0.97	0.28	0.15
29. Leaf efficiency	L.D.	0.832	0.511	0.648	0.820	1.130	1.062
30. Leaf efficiency	S.D.	1.095	1.068	1.690	0.950	0.965	1.071
31. Dry weight per plant in g . . .	L.D.	7.11	1.36	1.22	1.61	0.49	0.33
32. Dry weight per plant in g . . .	S.D.	5.97	0.60	0.78	1.99	0.58	0.29
33. Top/root ratio	L.D.	3.3	4.4	3.5	2.5	1.3	2.0
34. Top/root ratio	S.D.	3.4	3.0	2.1	2.9	1.7	2.0

followed by -Mg, -K and -S solutions, while -P, -N and -Ca decreased it to a marked degree.

Dry weight: Rows 25 and 26 show that the dry weight of leaves was most affected by nitrogen. The other mineral deficiencies decreased the dry weight production of leaves to different degrees. In the case of -P and -Mg the dry

weight of leaves produced was small, because a large number of leaves dropped, especially under S.D.

The dry weight of stem + roots + flowers under S.D. was large in -S solution (row 28, column 5). -Mg and -K (row 28, columns 3 and 4) decreased it slightly, while -P, -N and -Ca decreased it to a marked degree (row 28, columns 6, 7 and 8).

In general the dry weight was decreased when any element was lacking (rows 31 and 32).

Growth as measured by the increase in dry weight of the plants, was rapid when N was supplied. The decrease in the growth under L.D. amounted to about 81%, 83%, 77%, 93%, 96%, 95% respectively. When Mg, K, S, P, N or Ca was lacking from the solution, there was an overall decrease in growth amounting to about 90%, 88%, 67%, 90%, 95%, 95% respectively of the total dry weight under S.D.

Because lack of P curtailed the growth of plants, while the roots were normally developed, a low top/root ratio was obtained. This result was found under both L.D. and S.D. (rows 33 and 34, column 6). Leaf efficiency was generally larger under S.D. than under L.D. (rows 29 and 30), except in -P, where it was high under L.D. (row 29, column 6).

At the end of the experiment, all the plants in the different treatments grown under L.D. were still vegetative. This indicates that mineral deficiencies did not induce the plant to flower under an unfavourable photoperiod.

Summary of results: The floral bud development was affected by mineral deficiencies more than the flower initiation.

In general the mineral deficiencies reduced the growth of leaves and stems, interfered with the dry weight production, and as a result the flowering was affected.

Among the minerals used in this experiment, -N and -P had the greatest effect in retarding flowering.

CHAPTER V

EFFECT OF SEVERAL NITROGEN LEVELS ON THE FLOWERING RESPONSES AND THE GROWTH OF LONG AND SHORT-DAY PLANTS

1. INTRODUCTION

The relation of nitrogen to growth, flowering and fruitfulness of plants, has been extensively studied by many investigators. There is a considerable volume of data scattered throughout the literature on this subject, but the various experiments show that plants do not all respond in the same manner.

Considering the literature and the work carried out in the first part of this study, nitrogen may be considered as the most effective mineral in the flowering of plants, and as a crucial nutrient in the process of flowering. The purpose of the work undertaken in this chapter, is to determine what effect various levels of nitrogen may have upon the flower initiation and the further development of some long-day plants, namely mustard, dill and spinach, and short-day plants, namely *Perilla* and *Kalanchoë*.

2. MUSTARD (L.D.P.)

2.1. Experiment V: Orientation

This experiment was carried out to find the best nutrient solution for the growth of mustard. The roots of small plants with 4 leaves were thoroughly washed in water and grown in water culture. The nutrient solutions are given in table 5.

TABLE 5. Experiment V. Nutrient solution Formulac in g/l

Nutrient solution Salts	Complete Pfeffer	Complete-N Pfeffer	Knop	Complete Hoagland and Arnon	Complete-N Hoagland and Arnon
Ca(NO ₃) ₂	1.30	—	0.80	0.80	—
KNO ₃	0.33	—	0.20	0.50	—
Ca(H ₂ PO ₄) ₂	—	—	—	—	0.11
KH ₂ PO ₄	0.33	0.33	0.20	0.13	—
FePO ₄	—	—	0.10	—	—
CaSO ₄ ·2H ₂ O	—	1.30	—	—	0.27
K ₂ SO ₄	—	—	—	—	0.43
MgSO ₄ ·7H ₂ O	0.33	0.33	0.20	0.24	0.24
KCL	0.16	0.49	—	—	—
FeCl ₂	0.002	0.002	—	—	—

The plants grew for nearly one month in these solutions under S.D., then were transferred to L.D. During the experiment differences in size and vigour became apparent. After close observation, it was found that the nutrient solution of HOAGLAND and ARNON (56) was the most suitable. Also, the different solutions containing various N concentrations could be easily prepared from a stock solution. Therefore, the further experiments were made with HOAGLAND and ARNON solution.

2.2. Experiment VI: Four levels of nitrogen

Introduction. — In an experiment carried out by CAJLACHJAN (15, 1944), he found that mustard is a long-day plant, which begins to flower much sooner when mineral food poor in nitrogen is given. In sand culture he found that $\frac{1}{4}$ of the normal ration of nitrogen is the best level to induce the plants to flower soonest. When he supplied the plants with double the normal ration the plants failed to flower.

In a preliminary experiment by the present author it was found that continuous light in itself favoured the root development. In the present experiment continuous light was studied in its combined effect with different N levels.

Material and methods. — Roots of plants with 4 leaves were washed in water and grown in solutions with different N concentrations under S.D. Four solutions were used (N), $\frac{1}{2}$ N, $\frac{1}{4}$ N and -N solution. After two weeks the plants were divided into two groups of sixteen. The first group was transferred to L.D. and the second group to continuous light (L.D. + 9 hours light of incandescent lamps).

Results. — Flowering responses: Table 6 row 1 and 2 show that plants growing in -N were the first group to initiate their flowers under both L.D. and C.L.* (8 days).

Plants growing in $\frac{1}{2}$ N and $\frac{1}{4}$ N solutions were the second group to initiate

*) C.L. = continuous light.

their flower primordia (13 days), but plants under C.L. were (3 days) sooner in their flowering than the others under L.D.

TABLE 6. Experiment VI. Effect of four levels of nitrogen on the flowering responses and the growth of mustard under long-day (= L.D.) and continuous light (= C.L.)

1	2	3	4	5	6
Treatment	(N)	$\frac{1}{2}$ N	$\frac{1}{4}$ N	-N	Plants in soil
(mean) Character					
1. Days to flower bud . . . L.D.	25	13	13	8	10
2. Days to flower bud . . . C.L.	17	10	10	8	9
3. Number of unopened flowers L.D.	55	35	33	7	50
4. Number of unopened flowers C.L.	42	34	29	4	27
5. Number of opened flowers L.D.	∞	∞	∞	3	14
6. Number of opened flowers C.L.	∞	∞	∞	5	22
7. Height cm L.D.	13	14	14	34	105
8. Height cm C.L.	16	22	34	36	113
9. Diameter mm L.D.	3.6	3.0	3.0	2.3	10.0
10. Diameter mm C.L.	3.3	3.0	3.0	2.8	5.3
11. Number of leaves . . . L.D.	11	12	13	8	20
12. Number of leaves . . . C.L.	12	10	13	8	18
13. Number of dropped leaves L.D.	3	3	3	7	0
14. Number of dropped leaves C.L.	7	7	7	10	4

Plants growing in (N) (row 1, column 2) were the last to initiate their flower primordia (25 days). Plants under C.L. (row 2, column 2) were 8 days sooner in their flowering than the others under L.D.

The development of the floral buds was generally faster in plants under C.L. than those under L.D., and also the development of the floral buds was quicker in plants growing in -N solution than plants growing in $\frac{1}{2}$ N and $\frac{1}{4}$ N solutions under both L.D. and C.L.

The number of floral buds produced was greatly affected by the N level, while in L.D. the number of floral buds was larger than in C.L. (rows 3 and 4).

Growth responses: Rows 7 and 8 show that the height of the plants was negatively correlated with the amount of N supplied under both L.D. and C.L. photo 2. The height of plants also increased under C.L. as the N decreased (row 8), especially in plants growing in $\frac{1}{2}$ N and $\frac{1}{4}$ N solution (row 8, columns 3 and 4).

No big differences in the diameter of the plants were found, except in the plants grown in soil. The diameter was bigger under L.D. (row 9) than under C.L. (row 10). N supply increased the diameter.

The number of leaves produced (number of leaves on the plants plus the dropped leaves) is more under C.L. (rows 12 and 14) than under L.D. (rows 11 and 13).

The root system of the plants in -N solution developed normally and was longer than that in the (N), which failed to develop and became brown in colour and then died. The root system of plants in $\frac{1}{2}$ N and $\frac{1}{4}$ N solutions showed a length between those of plants growing in the (N) and in -N solution photo 3.

Summary of results: C.L. affected the growth behaviour of mustard more than its flowering behaviour, and it was more effective when N was supplied than when it was lacking.

2.3. Experiment VII: Seven levels of nitrogen

Material and methods. - Roots of plants with 4 leaves were thoroughly washed in water and put in culture solutions with various levels of N and with forced aeration. Seven N levels (see table 7) were used. The plants stayed under S.D. for nearly one month, then were transferred to L.D. with high intensity of light: a mercury lamp of 450 watt. At the end of the experiment, data on the growth and flowering responses were recorded.

TABLE 7. Experiment VII. Composition of nutrient solutions. Cubic centimeters of stock solution required to make one litre of culture solution

	1	2	3	4	5	6	7	8
Stock solutions	1 KNO ₃ 101.12	1 Ca(NO ₃) ₂ 164.08	1 KH ₂ PO ₄ 136.12	1 MgSO ₄ 7H ₂ O 120.36	0.5 K ₂ SO ₄ 87.12	0.05 Ca(H ₂ PO ₄) ₂ 11.70	0.01 CaSO ₄ 1.96	
Concentration of N								
1. (N) 202.0 mg/l	5.00 cc	5.00 cc	1.0 cc	2.0 cc	-	-	-	
2. ½ N 101.0 mg/l	2.50 cc	2.50 cc	1.0 cc	2.0 cc	-	-	-	
3. ¼ N 50.50 mg/l	1.25 cc	1.25 cc	1.0 cc	2.0 cc	-	-	-	
4. ⅓ N 25.22 mg/l	0.62 cc	0.62 cc	1.0 cc	2.0 cc	-	-	-	
5. ⅕ N 16.83 mg/l	0.41 cc	0.41 cc	1.0 cc	2.0 cc	-	-	-	
6. ⅙ N 12.62 mg/l	0.31 cc	0.31 cc	1.0 cc	2.0 cc	-	-	-	
7. O 0.0	-	-	-	2.0 cc	5.0 cc	10.0 cc	200.0 cc	

In columns 2-8 under "stock solutions" the figure at the top means the volume molecule concentration of stock solution. The figure below the chemical substance indicates grams per litre stock solution.

Results. - Flowering responses: From the data presented in table 8 it is clear that plants grown in -N solution (row 1, column 8), and plants grown

TABLE 8. Experiment VII. Influence of nitrogen supply on the flowering responses and the growth of mustard

	1	2	3	4	5	6	7	8
Treatment	(N)	½ N	¼ N	⅓ N	⅕ N	⅙ N	-N	
(mean) Character								
1. Number of days to flower bud	14	14	13	13	13	12	12	
2. Number of days to open the first flower	41	41	36	37	34	34	37	
3. Number of floral buds and opened flowers	55.5	44.6	43.0	34.3	29.0	25.3	11.3	
4. Height cm	46.0	44.0	48.0	46.0	48.0	40.0	25.0	
5. Diameter mm	4.95	4.22	2.73	2.14	1.97	1.95	1.19	
6. Leaf area in cm ² of each plant	188.3	124.0	120.7	41.0	24.7	18.2	4.4	
7. Number of leaves per plant	18.0	15.0	15.3	13.0	11.3	10.3	9.0	
8. Number of dropped leaves	∞	2.0	3.3	6.3	7.0	8.3	6.6	

in the lowest level of nitrogen ($1/16$ N) (row 1, column 7) initiated their flower primordia 1 or 2 days sooner than the other treatments.

The development of the floral buds was more affected by the N level. From figures 3 and 4 it is clear that the rate of development was accelerated by the low levels of N. The level $1/12$ of the normal ration (16.83 mg/l) was the best one for flowering. In general the normal ration of N, the $1/2$ N and $1/4$ N retarded the development, while $-N$, $1/8$ N, $1/12$ N and $1/16$ N accelerated the development.

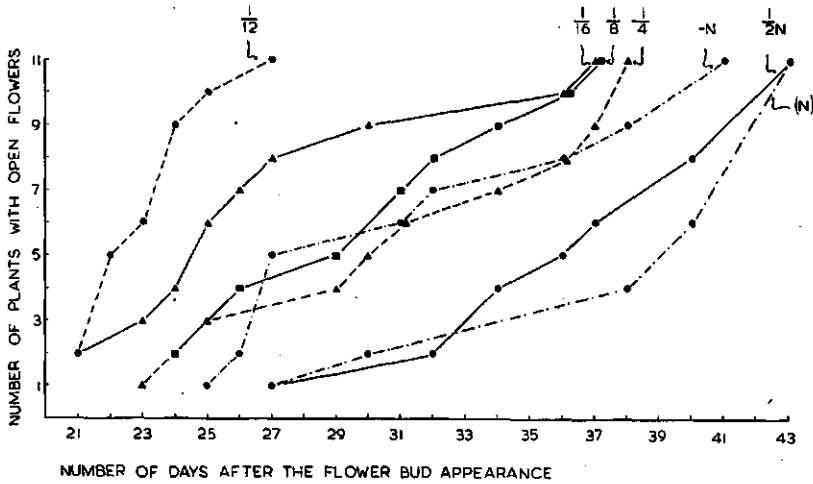


FIG. 3. Experiment VII: Effect of nitrogen on flower development of mustard in long day.

The number of floral buds produced was positively correlated with the quantity of N supplied (table 8, row 3), low levels and $-N$ decreased the number of floral buds (row 3, columns 7 and 8), while high levels increased it (row 3, columns 2, 3 and 4).

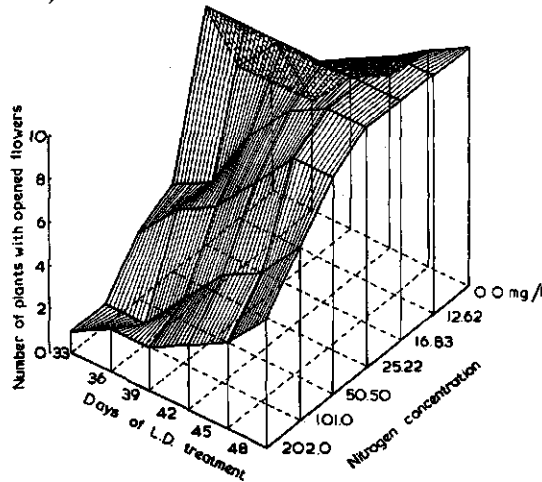


FIG. 4. Experiment VII: Effect of nitrogen flower development of mustard in long day. The N concentrations refer to: 202.0 = N; 101.0 = $1/2$ N; 50.50 = $1/4$ N; 25.22 = $1/8$ N; 16.83 = $1/12$ N; 12.62 = $1/16$ N and 0.0 = $-N$

Growth responses: The high intensity of light favoured the development of the root system in the different treatments. The height, the diameter and the rate and the extent of growth of the leaves, varied with the relative amount of N supplied. Plants grown in high N levels had more vigorous growth than the others grown in low N levels. The average diameter of the plants (row 5) and the average leaf area of plants (row 6) were positively correlated with the quantity of N in the solution, high levels increased them, while low levels decreased them. The number of leaves produced per plant (row 7) was also positively correlated with the quantity of N supplied, but the number of dropped leaves per plant (row 8) was negatively correlated with the quantity of N in the solution. Leaves from plants grown in -N solution (especially at the bottom of the stem) became yellow and died first, and those supplied with low N levels followed.

Dry weight: (table 9). The greatest production of dry material was found in the plants grown in high N levels. Generally the dry weight of root, stem and leaves before the floral buds open was less than after the opening of the flower buds.

TABLE 9. Experiment VII. Influence of nitrogen supply on the dry weight material of mustard

1	2	3	4	5	6	7	8
Treatment	(N)	$\frac{1}{2}$ N	$\frac{1}{4}$ N	$\frac{1}{8}$ N	$\frac{1}{12}$ N	$\frac{1}{16}$ N	-N
(mean) Character							
A. Before the flowers open							
1. Dry weight of buds in g	0.0077	0.0057	0.0138	0.0144	0.0052	0.0084	0.0014
2. Dry weight of leaves in g	0.2415	0.2973	0.1848	0.1073	0.0675	0.1076	0.0091
3. Dry weight of stems in g	0.2002	0.2287	0.2153	0.1456	0.0928	0.0529	0.0156
4. Dry weight of top in g	0.4494	0.5317	0.4139	0.2675	0.1655	0.1689	0.0261
5. Dry weight of roots in g	0.0256	0.0447	0.0333	0.0253	0.0219	0.0195	0.0073
6. Dry weight of plant in g	0.4750	0.5764	0.4472	0.2926	0.1874	0.1884	0.0334
7. Top/root ratio	17.5	11.9	12.4	10.5	7.6	8.7	3.6
8. Dry matter %	39.5	42.9	42.6	47.4	50.5	49.2	66.6
B. After the flowers open							
9. Dry weight of buds in g	0.2159	0.1367	0.0887	0.0538	0.0326	0.0282	0.0068
10. Dry weight of leaves in g	0.4585	0.3643	0.2085	0.0639	0.0412	0.0398	0.0100
11. Dry weight of stems in g	0.6858	0.4913	0.2705	0.1685	0.1191	0.1108	0.0278
12. Dry weight of top in g	1.3602	0.9923	0.5677	0.2862	0.1929	0.1788	0.0446
13. Dry weight of roots in g	0.1058	0.0516	0.0408	0.0260	0.0174	0.0187	0.0140
14. Dry weight of plant in g	1.4670	1.0539	0.6085	0.3165	0.2103	0.1975	0.0586
15. Top/root ratio	12.7	16.1	13.9	11.0	11.0	9.6	3.2
16. Dry matter %	42.8	42.6	45.2	47.1	49.3	47.7	48.4

The top/root ratio of the plants grown in -N solution was small (rows 7 and 15, column 8) and increased with increasing amount of N.

The dry matter percentage was high in the plants grown in -N solution (rows 8 and 16, column 8) and decreased when the quantity of N increased.

Summary of results: The data obtained in this experiment showed that the time of flower bud appearance was only slightly affected by the N concentration, while the rate of development of floral buds and the number of flowers produced were greatly affected. Much earlier flowering occurred when the N was supplied in low levels ($1/12$ N, $1/16$ N) to the plants or when the N was lacking.

The rate and extent of growth varied with the amount of N supplied, more growth being found as the N levels increased.

The data obtained in this experiment confirmed the results obtained in the first part, that in mustard the vigour had no influence on the flower bud appearance and the development of the floral buds, for the plants supplied with -N solution and also plants supplied with low N levels flowered sooner than the others supplied with high N levels.

3. DILL (L.D.P.)

3.1. *Experiment VIII: Orientation*

Introduction. - This experiment was conducted to study the effect of the number of leaves and of growth, on the flower bud appearance and the number of inflorescences produced.

Experimental. - Seeds of dill were sown and potted under S.D. When the plants had 6 leaves, they were transferred to L.D. and divided into 3 groups:

1. plants with only *one* leaf (all the leaves were removed continuously from the plant except the youngest leaf at the top of the stem);
2. plants with only *three* leaves (all the leaves were removed continuously except the three apical ones);
3. normal plants with all the leaves (control).

After 10 days from this treatment, plants were dissected under the microscope every 2 days to follow the flower bud appearance.

Results and discussion. - From the data presented in table 10 it is clear that plants with only one leaf (column 2) possess little growth when compared with the other two groups (columns 3 and 4). The time of flower bud appearance is slightly affected by growth. Plants with only 3 leaves (row 1, column 2) showed their flower primordia on the same date as the normal plants (row 1, column 3) despite the big difference in the number of leaves between these two groups. Plants with only one leaf (row 1, column 2) initiated their flower primordia 4 days later than the other two groups. The development and the number of inflorescences produced were more affected by the number of leaves. The development was quicker and the number of inflorescences was bigger as the number of leaves increased (row 2).

Conclusion. - Flower bud appearance of dill is slightly positively affected by the growth, while the development and number of inflorescences are considerably positively affected.

3.2. *Experiment IX: Three levels of nitrogen*

Introduction. - The present experiment has been carried out to study the effect of three N levels on the flowering responses and growth.

TABLE 10. Experiment VIII. Effect of number of leaves and growth vigour on the flowering responses of dill

	1	2	3	4
	Treatment			
(mean) Character	One leaf	Three leaves	All leaves	
1. Days to flower bud	20	16	16	
2. Number of inflorescences	22	31	38	
3. Height cm	50	109	142	
4. Diameter mm	4.03	4.93	5.75	
5. Number of leaves on the stem	1	3	13	

Experimental. - The roots of plants with 6 leaves were washed and grown in nutrient solutions under S.D. Three nutrient solutions were used, a double ration of nitrogen 2 N, a solution with normal ration of nitrogen (N) and the third solution without nitrogen -N. After 60 days 6 plants from each treatment were transferred to L.D., while 4 plants from each treatment stayed under S.D. At the end of the experiment data on the growth and flowering responses were recorded.

Results and discussion. - Flowering responses: From the data presented in table 11, we see that plants grown in 2 N solution and plants grown in (N) solution, showed their flower primordia after 17 days (row 1, columns 2 and 3). Plants grown in -N solution (row 1, column 4) were 20 days later than the former two groups to initiate their flower primordia. Plants of the three groups under S.D. were in the vegetative state till the end of the experiment.

The development of the inflorescences was faster in plants supplied with the two different levels of N, while it was very slow in plants lacking N. Plants

TABLE 11. Experiment IX. Effect of three levels of nitrogen on the flowering responses and the growth of dill under long-day

	1	2	3	4
	Treatment			
(mean) Character	2 N	(N)	-N	
1. Days to flower bud	17	17	37	
2. Number of inflorescences	30	35	∞	
3. Height cm	106	116	10	
4. Diameter mm	3.87	5.35	2.30	
5. Number of nodes	15	15	11	
6. Length of internodes cm	7.0	7.7	0.9	
7. Number of leaves	14	14	7	
8. Number of dropped leaves	2	1	4	
9. Number of branches	5	5	∞	
10. Dry weight of leaves in g	0.49	1.12	0.05	
11. Dry weight stem + root in g	1.44	2.80	0.06	
12. Dry weight per plant in g	1.93	3.92	0.11	
13. Leaf efficiency	2.93	2.50	1.50	
14. Top/root ratio	8.2	7.7	1.2	
15. Dry weight % of root	11.04	10.51	8.44	
16. Dry weight % of leaf	17.60	14.39	28.03	
17. Dry weight % of stem	20.47	14.93	12.46	
18. Dry weight % of flowers	20.03	16.12	∞	
19. Total dry weight %	69.14	55.95	48.93	

grown in 2 N or (N) produced large numbers of inflorescences (row 2, columns 2 and 3), while in -N solution the inflorescences failed to develop.

Growth responses: Plants supplied either with 2 N or with (N) solution were large and normal as compared with those grown in the soil. There was a small difference in the heights of plants between these two groups (row 3, columns 2 and 3), but the difference was considerable between plants supplied with N and the others grown in -N solution (row 3, column 4).

The number of nodes per plant (row 5) and the length of internodes (row 6) react in the same manner as the height of plants (row 3). Plants supplied with N possessed more nodes and longer internodes than those grown in -N solution.

The number of leaves is much larger with N (row 7, columns 2 and 3) and the dropped leaves are few (row 8, columns 2 and 3). The lateral buds in -N solution failed to develop (row 9, column 4).

Dry weight: (table 11). From the top/root ratios (row 14) and from the leaf efficiencies (row 13) it is clear that early flowering (row 1) of plants and an abundant number of inflorescences (row 2) were associated with a large quantity of dry matter in the different parts of the plants. The cause of the retardation of flowering in -N plants, is that the leaves keep a large percentage of dry matter and prevent the translocation to the meristematic parts.

The dry weight percentage of leaves (row 16) was high in -N and decreased when N was supplied.

The dry weight percentage of roots (row 15), stem (row 17) and the total dry weight percentage (row 19) were low when N was lacking, and these percentages increased relatively with the increasing amount of N.

Conclusion. - Dill is a plant requiring long days for flowering and affected considerably by N. N-application speeds up the flower bud appearance and the development of the inflorescences, while these characters are retarded when N is lacking. N does not induce the plants to flower under an unfavourable photoperiod, but it accelerates the flowering in a favourable photoperiod.

4. SPINACH (L.D.P.)

Experiment X:

Introduction. - Spinach (*Spinacea oleracea*) is a plant requiring long days for its flowering. It was chosen as material to study the effect of three different levels of N on its flowering and growth behaviour.

Experimental. - Seeds of spinach were sown and potted under S.D. After 50 days roots were washed and grown in nutrient solutions. The methods and the solutions were the same as of experiment IX, page 26.

Results. - Flowering responses (table 12): N effected the flower bud appearance of spinach only slightly. Four days retardation occurred when N was lacking (row 1, column 4). 2 N solution had the same effect as the (N) solution. Plants under S.D. were in the vegetative stage at the end of the experiment.

Growth responses: It is evident from the data presented in table 12 that the dominant effect of N application was the increase in growth. The average height (row 2), diameter (row 3), number of nodes (row 4), length of internodes (row 5), number of leaves (row 6), area of the two median leaves (row 8) increased relatively with increasing quantities of N. Leaf drop increased slightly, when N was lacking (row 7, column 4).

TABLE 12. Experiment X. Effect of three levels of nitrogen on the flowering responses and the growth of spinach

	1	2	3	4
	Treatment	2 N	(N)	-N
(mean) Character				
1. Days to flower bud		10	10	14
2. Height cm		25.5	20.0	9.5
3. Diameter mm		4.60	4.50	1.70
4. Number of nodes		46.0	43.0	27.0
5. Length of internodes in cm		5.5	4.6	3.5
6. Number of leaves		43	38	20
7. Number of dropped leaves		5	4	7
8. Area of two median leaves		20.8	16.8	2.6
9. Dry weight of leaves in g		0.964	0.958	0.189
10. Dry weight of stem + roots in g		0.625	0.440	0.097
11. Dry weight per plant in g		1.589	1.398	0.286
12. Leaf efficiency		0.648	0.459	0.315
13. Top/root ratio		7.2	5.9	4.5
14. Dry weight % of root		9.69	8.83	10.34
15. Dry weight % of leaf		13.90	11.08	23.77
16. Dry weight % of stem		14.61	11.62	16.27
17. Total dry weight %		38.20	31.53	49.52

Dry weight: The growth as represented by dry weight increased with increasing N concentration, and N starvation resulted in loss of vegetative vigour. The total dry weight of leaves produced (row 9) and also of stem plus roots (row 10) were considerably larger in plants supplied with N than in plants without N.

Leaf efficiency (row 12) and top/root ratio (row 13) also showed that the growth of both shoots and roots were promoted by increasing N concentrations. The total dry weight percentage (row 17) and also the separate dry weight percentages of root (row 14), leaf (row 15) and stem (row 16) increased when N was lacking.

Conclusion. - N application has only a slight effect on the flowering response of spinach. The flower bud appearance is delayed for a few days when N is lacking. The growth is more affected and it increases with increasing amounts of N.

5. *PERILLA CRISPA* (S.D.P.)

5.1. Experiment XI. Three levels of nitrogen

Material and methods. - The roots of plants with 6 leaves were thoroughly washed in water and grown in the nutrient solutions under L.D. The three solutions which were used in experiment X were also used here. After 50 days, 12 plants from each treatment were given an induction period of S.D., while 4 plants from each treatment stayed under L.D. At the end of the experiment the characters of the plants were recorded. The dry weight of roots, leaves and stems were recorded during three periods of plant development, one week before visible flower bud (12 days of S.D. treatment), on the day of flower bud appearance (19 days of S.D. treatment), and at the end of the experiment (37 days of S.D. treatment).

Results. – Flowering responses (table 13): Plants growing in 2 N or (N) solutions had visible flower buds at the same time, after 18 S.D., while the plants growing in –N solution initiated their flower primordia 6 days later (row 1, column 4).

TABLE 13. Experiment XI. Effect of three levels of nitrogen on the flowering responses and the growth of *Perilla*

	1	2	3	4
	Treatment			
(mean) Character	2 N	(N)	–N	
1. Days to flower bud	18	18	24	
2. Number of flowers	690	651	17	
3. Height cm	64	67	9	
4. Length of internodes cm	2.9	3.0	0.8	
5. Number of leaves on the main stem	22	22	11	

There was no striking difference in the number of floral buds produced in the two groups of plants supplied with N (row 2, columns 2 and 3), but the number of floral buds was very much less when N was lacking (row 2, column 4).

Growth responses: From the data presented in table 13 it is clear that N application increased height (row 3), length of internodes (row 4), and number of leaves (row 5). In the absence of N these characters were much lower (rows 3, 4 and 5, column 4). There was no big difference in the growth between 2 N and (N) solutions.

At the end of the experiment all the plants in the different treatments growing under L.D. were still vegetative. This indicates that N concentration did not induce the flowering of *Perilla* under an unfavourable photoperiod.

The root system in –N solution was longer than in (N) or 2 N photo 4.

TABLE 14. Experiment XI. Effect of three levels of nitrogen on the dry matter in grams of roots, leaves and stems in different periods of development of *Perilla*

	1	2	3	4
	Treatment			
(mean) Character	2 N	(N)	–N	
<i>after 12 S.D.</i>				
1. Roots	0.93	0.98	0.04	
2. Leaves	3.0	2.98	0.05	
3. Stems	1.80	2.03	0.02	
4. Top/root ratio	5.1	5.1	1.7	
<i>after 19 S.D.</i>				
5. Roots	1.0	1.21	0.04	
6. Leaves	3.51	3.54	0.06	
7. Stems	2.19	2.27	0.02	
8. Top/root ratio	5.7	4.8	2.0	
<i>after 37 S.D.</i>				
9. Roots	1.49	1.51	0.05	
10. Leaves	5.12	4.44	0.08	
11. Stems	3.92	3.81	0.05	
12. Top/root ratio	6.0	5.4	2.6	

Dry weight: Table 14 and fig. 5, 6 and 7, show the variation in growth of roots, leaves and stems of *Perilla* during its inductive S.D. treatment. The growth of the different parts of the plants in the various treatments increased with the increase in age. The increase in dry weight of the different parts of the plant was greater in the plants supplied with N (columns 2 and 3) than in those without N (column 4). The top/root ratio was also large in plants supplied with N (columns 2 and 3) and it decreased to a marked degree in plants without N (column 4).

Summary of results: N slightly affected the flower bud formation of *Perilla*. It made the plants react quicker to the short-day, while in its absence the flower bud initiation was retarded for a few days. Evidently this is due to the strong growth which is the result of nitrogen application.

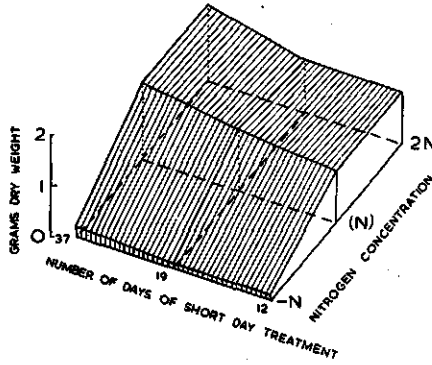


FIG. 5 ROOTS

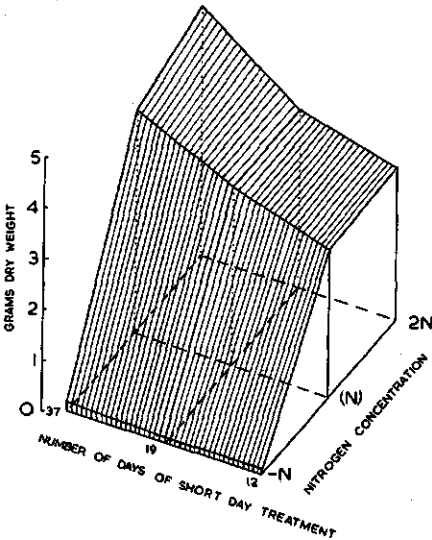


FIG. 6 LEAVES

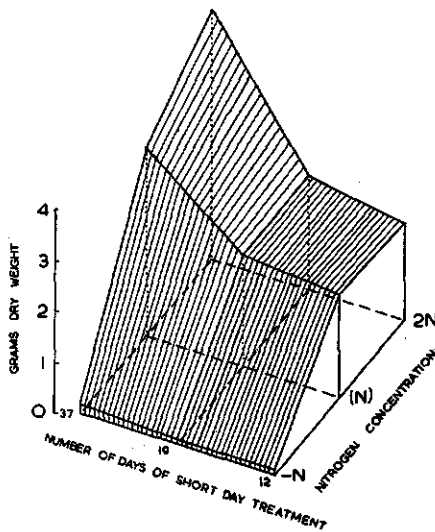


FIG. 7 STEMS

FIG. 5-7. Experiment XI: Effect of three levels of nitrogen on dry weight of roots, leaves and stems in different stages of development of *Perilla*.

5.2. Experiment XII. Five levels of nitrogen

Introduction. – In the former experiment three N levels were used. To study the effect of nitrogen in more details more nitrogen concentrations were used in the present experiment, namely five.

Material and methods. – The roots of plants with 6 leaves were washed in water and put in culture solutions under L.D. Five N levels were used, namely those indicated in table 7 (p. 23) in rows 1, 2, 3 and 7 plus 2 N with a double quantity of KNO_3 and $\text{Ca}(\text{NO}_3)_2$. After 50 days 12 plants from each group received an inductive photoperiod of S.D., while 4 plants from each group stayed under L.D. At the end of the experiment the characters of the plants were recorded.

Results. – See table 15. Flowering responses: The differences between the 4 concentrations 2 N, (N), $\frac{1}{2}$ N, $\frac{1}{4}$ N, on the flower bud appearance were generally slight, but there was a big difference of 7–9 days between these groups and the other group without N (row 1).

The number of floral buds decreased with decreasing amounts of N, except in 2 N which reduced the number (row 2). The leaf area was positively correlated with the number of flower buds (rows 2, 8 and 9).

TABLE 15. Experiment XII. Effect of five levels of nitrogen on the flowering responses and the growth of *Perilla*

	1	2	3	4	5	6
	Treatment					
(mean) Character	2 N	(N)	$\frac{1}{2}$ N	$\frac{1}{4}$ N	–N	
1. Days to flower bud	23	23	24	25	32	
2. Number of flowers	250	360	283	183	23	
3. Height cm	46.3	54.0	44.6	38.0	10.3	
4. Diameter mm	4.43	4.86	4.60	3.86	1.63	
5. Number of nodes	9	9	9	8	6	
6. Length of internodes cm	5.1	6.0	4.9	4.7	1.7	
7. Number of leaves	18	18	18	16	12	
8. Leaf area in cm^2 before flower initiation	163.6	195.1	206.7	161.7	47.9	
9. Leaf area in cm^2 after flower initiation	480.4	535.6	474.3	321.5	54.9	
<i>Total dry matter %</i>						
10. On the day of budding	34.1	36.2	38.3	41.9	49.8	
11. At the end of experiment	61.9	62.9	64.1	65.6	66.3	
12. Under long-day	36.5	39.8	40.9	45.5	54.4	
<i>Top/root ratio</i>						
13. On the day of budding	5.3	5.6	7.7	7.4	2.0	
14. At the end of experiment	4.8	5.4	5.7	6.8	2.5	
15. Under long-day	5.0	5.0	6.9	4.6	2.2	

Growth responses: The wide differences in the five levels of N supplied during the three months of the experiment, produced big differences in the growth responses and the development of the plants. Where the nutrient was in proper balance (complete nutrient solution), large, excellent plants, normal in all aspects, were produced that compared favourably with those grown in soil under similar conditions of light and temperature.

Table 15 shows that there were small differences in height between the plants supplied with solutions containing different N levels (row 3, columns 2, 3, 4 and 5), but the differences were big as compared with the plants growing in -N solution (row 3, column 6). The number of nodes (row 5) and leaves (row 7) tended to increase with increasing N. The diameter of stem (row 4), the length of internodes (row 6), leaf area (rows 8 and 9) and the number of floral buds (row 2) also increased with increasing N quantities, but the excessive N (column 2) reduced these values when compared with the plants supplied with (N) (column 3). The rate of increase in the leaf area (the difference between the leaf area before flower bud appearance and after flower bud appearance) increased in plants supplied with high N levels (315 cm² in 2 N and 340 cm² in (N)) and was less in the low N levels and in -N solution (268 cm² in $\frac{1}{2}$ N, 160 cm² in $\frac{1}{4}$ N and 7 cm² in -N).

Dry weight: The total dry matter % at the end of the experiment for plants grown in -N solution was 66.3% (row 11, column 6); and this percentage decreased when the quantity of N increased in the solution until it reached 61.9% in 2 N (row 11, column 2). On the day of budding the total dry weight % stayed the same as before. The plants in -N solution had a high dry weight % of 49.8 (row 10, column 6), and this percentage decreased to 34.1 in the highest N solution (row 10, column 2). The difference in the total dry matter % of the plants during the period of flowering, the period between the day of flower bud appearance (row 10) and the end of the experiment (row 11), was high (24%-27%) in the plants supplied with N, and low (17%) in plants in -N solution.

The top/root ratio of plants supplied with $\frac{1}{2}$ N or $\frac{1}{4}$ N solutions was high, both on the date of budding (row 13, columns 4 and 5) and at the end of the experiment (row 14, columns 4 and 5), and this ratio decreased when the quantity of N in the nutrient solution increased. Plants in a solution containing different quantities of N had a high top/root ratio, compared with the plants in -N solution. The top/root ratio of plants supplied with N was high on the day of budding and decreased at the end of the experiment, while the top/root ratio was nearly constant (or increased slightly) in plants grown in -N solution (rows 13 and 14).

At the end of the experiment, the total dry matter percentage of the plants grown in L.D. (row 12) was smaller than that of the plants grown in S.D. (row 11).

The dry matter percentage of leaves was high in plants in -N solution despite their small area, while the dry matter percentage was low and the average leaf area was big in plants supplied with different N levels. There was some relation between the total dry weight percentage and the times of flower bud appearance and opening of the flowers. Macroscopic floral primordia occurred much earlier when plants had a small production of dry matter; flowering was also earlier.

Summary of results: The data obtained from this experiment show that N affected the flower bud appearance only slightly. This was due to the reduction in growth in -N solution, resulting in a retardation of flower bud appearance. N was not a decisive factor in the flowering in *Perilla* and it did not induce flowering under an unfavourable photoperiod. However, the development of the floral buds was considerably affected by the N concentration.

With the exception of 2 N, the vegetative growth, the earliness of flower bud

formation, and the abundance of flowers produced were positively correlated with the quantity of N supplied.

6. *KALANCHOË BLOSSFELDIANA* (S.D.P.)

Experiment XIII

Material and methods. – *Kalanchoë blossfeldiana* is a S.D. plant. HARDER (49, 1948) found that days of 18 and 24 hours markedly delay the flower bud initiation in comparison with days of 12 hours. The roots of the three months old plants were thoroughly washed in water and grown in nutrient solutions. The three nutrient solutions (2 N, (N), and -N) which were used in experiment IX were used also in the present experiment. After two months, 12 plants from each treatment received an inductive photoperiod of S.D., while 4 plants from each treatment stayed under L.D. The lateral buds of 2 N and (N) plants were removed except those in the axils of the upper five pairs of leaves. At the end of the experiment, data on the flowering and growth responses were recorded. The dry weight of roots, leaves and stems were determined.

Results. – See table 16. Flowering responses: Plants in S.D. and grown in 2 N and (N) solutions formed macroscopic floral buds after 17 days (row 1, columns 2 and 3) and opened their flowers in 125 days from S.D. treatment (row 2, columns 2 and 3). Plants in -N solution formed macroscopic flower buds 15 days later than the former groups (row 1, column 4). Their flower buds opened in 150 days (row 2, column 4). The plants grown in -N solution had few floral buds (row 4, column 4), because all the lateral buds in the axils of the leaves failed to develop and only the terminal bud of the plant formed flowers. The abundance of flowers appearing when the plants were supplied with N, was largely associated with the vigorous vegetative development prevalent with this treatment, as contrasted with the poor vegetative development occurring in the -N, see photo 5. When the quantity of N was doubled, no significant increase in the number of flowers occurred. Plants grown in the different N levels under L.D. remained in the vegetative state.

Growth responses: Plants grown either in the (N) solution or in 2 N solution were large and normal as compared with those grown in the soil. There was a small difference in height between plants supplied with the two N levels (row 7, columns 2 and 3), but the difference was very considerable between plants supplied with N and those lacking N (row 7, column 4). The number of leaves in 2 N and (N) was $4\frac{1}{2}$ times as much as in the -N solution. From the data presented in table 16 it is clear that the growth of plants supplied with N was greater than that of plants grown in soil. This greater growth was reflected in their increased height, diameter and their abundance of leaves (rows 8, 11 and 14, columns 2 and 3). These characters decreased markedly in -N plants (rows 8, 11 and 14, column 4).

Dry weight: The dry weight percentage of the roots (row 15), leaves (row 16), stems (row 17) and also the total dry weight of the plants (row 18) was high when N was lacking in the nutrient solution, and these percentages decreased relatively with the relative amount of N supplied. Data on the vegetative and flowering responses, and on the dry matter percentage clearly indicate that the vigorous vegetative growth and the large number of floral buds were associated with small dry matter percentages.

TABLE 16. Experiment XIII. Effect of three levels of nitrogen on the flowering responses and the growth of *Kalanchoë blossfeldiana*

	1	2	3	4	5
	Treatment				
(mean)Character	2 N	(N)	-N	Standard	
1. Days to flower bud	17	17	32	-	
2. Days to open flowers . . .	125	125	150	-	
<i>Number of flowers</i>					
3. Potted plants (standard) . .				151	
4. Treated plants	210	217	12		
5. Differences in % of the standard	+39 %	+43 %	-92 %		
<i>Height cm</i>					
6. Potted plants (standard) . .				18.3	
7. Treated plants	20.6	18.6	6.0		
8. Differences in % of the standard	+12 %	+2 %	-67 %		
<i>Diameter mm</i>					
9. Potted plants (standard) . .				4.37	
10. Treated plants	5.17	5.17	2.31		
11. Differences in % of the standard	+16 %	+16 %	-47 %		
<i>Number of leaves</i>					
12. Potted plants (standard) . .				23.3	
13. Treated plants					
14. Differences in % of the standard	36.0 +54 %	36.6 +57 %	8.0 -65 %		
<i>Dry weight % to the fresh weight</i>					
15. Root	5.90	6.01	8.05	-	
16. Leaf	4.13	4.50	5.50	-	
17. Stem	12.85	13.28	21.16	-	
18. Total dry weight %	22.88	23.79	34.71	-	

There was a correlation between the total dry weight percentage and the times of flower bud appearance and flowering. Much earlier flowering occurred when the plants possessed a small dry matter percentage (row 18, columns 2 and 3).

Summary of results: Nitrogen affects the growth and flower responses of *Kalanchoë*. N application accelerates the flower bud appearance and the development of the flowers, and these two processes are retarded when it is lacking.

N does not alter the habit of flowering, but it is intimately related to its growth and flowering behaviour.

N does not induce the flowering of plants under L.D., but it interferes in the S.D. reaction and speeds up the plants development towards the generative state.

CHAPTER VI

EFFECT OF VARIATION IN RELATIVE CONCENTRATION OF IONS IN THE NUTRIENT SOLUTION, ON THE FLOWERING RESPONSES AND THE GROWTH OF LONG AND SHORT-DAY PLANTS

1. Mustard

Experiment XIV:

1.1. Methods. – It is a well known fact that the concentration of a certain element in the nutrient solution may affect the rate of absorption of other ions, some elements being antagonistic, others synergistic (81). The purpose of the present experiments, was to determine the effects of relative concentrations of three anions and three cations on the flowering responses, the growth rate and the accumulation of dry matter.

In one set of treatments, the concentration of the anions NO_3^- , SO_4^{2-} and PO_4^{3-} was varied, while the relative concentration of the cations was kept constant. In the second set of treatments, the anions were kept constant, while the cations K^+ , Mg^{++} and Ca^{++} were varied. The stock solutions used to make the different combinations are represented in table 17.

TABLE 17. Experiment XIV. Concentration of salts in the six stock nutrient solutions used in making up the 26 combinations

Molar concentration		Salt content g/l	Molar concentration		Salt content g/l	Molar concentration		Salt content g/l
Anion Varied								
SO ₄ solution			NO ₃ solution			PO ₄ solution		
K ₂ SO ₄	0.0045	0.78	KNO ₃	0.0045	0.45	KH ₂ PO ₄	0.0045	0.61
MgSO ₄	0.0045	1.10	Mg(NO ₃) ₂	0.0045	0.66	MgHPO ₄	0.0045	0.54
CaSO ₄	0.0060	1.03	Ca(NO ₃) ₂	0.0060	1.42	Ca(H ₂ PO ₄) ₂	0.0060	1.40
Cation Varied								
Mg solution			K solution			Ca solution		
Mg(NO ₃) ₂	0.0045	0.66	KNO ₃	0.0045	0.45	Ca(NO ₃) ₂	0.0060	1.42
MgSO ₄	0.0045	1.10	K ₂ SO ₄	0.0045	0.78	CaSO ₄	0.0060	1.03
MgHPH ₄	0.0045	0.5	KH ₂ PO ₄	0.0045	0.61	Ca(H ₂ PO ₄) ₂	0.0060	1.40

To each solution was added 0.5 ppm H₃BO₃; 0.5 ppm MnCl₂; 0.05 ppm ZnSO₄; 0.02 ppm CuSO₄; 0.01 ppm H₂MOO₄ and also iron citrate 0.5 % at a rate of lcc per litre.

The method of combining these stock solutions was adapted from HAMNER (46, 1940), HAMNER, LYON and HAMNER (48, 1942) and VOTH (110, 1941) and is represented in fig. 8 in general and in fig. 9 in detail for anions. In the last figure the 13 solutions which were actually used, are indicated by squares.

Seeds of mustard were sown on 26/10/55 and transplanted on 11/11/55 into 26 small wooden boxes covered with plastic on the inside and filled to a height of 10 cm with vermiculite. In each box 24 plants were grown. On the day of planting 6 litres of nutrient solution were applied to each box.

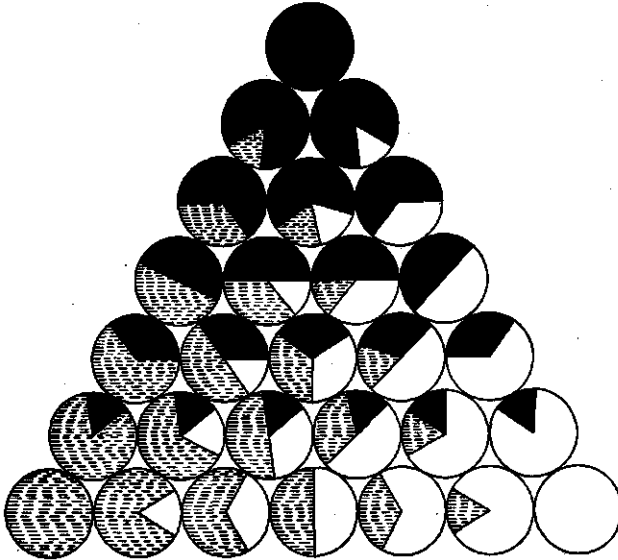


FIG. 8. Experiment XIV. Triangle diagram representing the relative proportions used to produce the 28 combinations. The combining stock solutions on the basis of sixths. (Simplified after HAMNER, LYON and HAMNER, Lit. 48). ●, ⊗ and ○ indicate different anions or different cations.

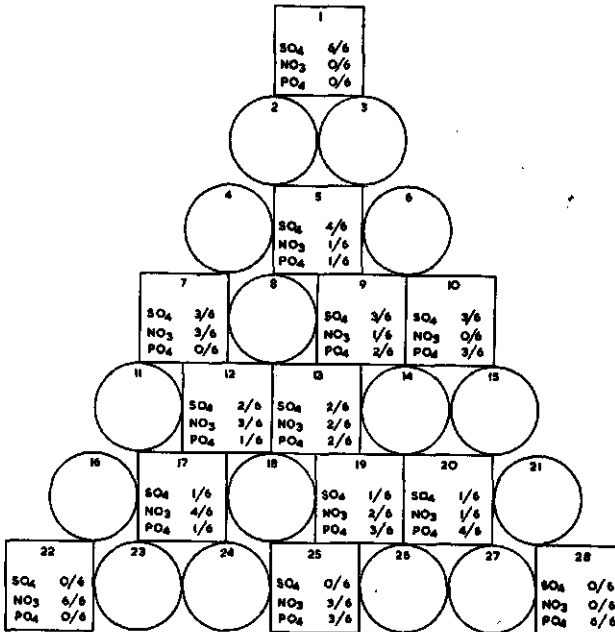


FIG. 9. Experiment XIV. Anion triangle showing method of combining stock solutions, on basis of sixths, to secure a range of 28 solutions varying in anions and constant for cations. A similar triangle for varying cation combination was employed: Mg at top K at lower left and Ca at lower right (Simplified after VOHN, Lit. 110).

TABLE 18. Experiment XIV. Effect of 13 different solutions in which the cations remained constant and the anions varied on the flowering responses and the growth of mustard

Square (see fig. 9)	1	5	7	9	10	12	13	17	19	20	22	25	28
Relative concentration of ions	SO ₄	6	4	3	3	2	2	1	1	1	0	0	0
	NO ₃	0	1	3	1	3	2	4	2	1	6	3	0
	PO ₄	0	1	0	2	1	2	1	3	4	0	3	6
(mean) Character													
1. Days to flower bud	† ¹	†	†	†	20	32	13	41	20	32	†	†	32
2. Number of flowers	†	†	†	23	10	32	34	25	5	5	†	†	8
3. Height cm	†	†	†	30.5	20.0	40.0	48.5	31.5	13.5	8.0	†	†	12.5
4. Number of nodes	†	†	†	17.0	14.0	21.5	20.5	19.0	16.0	11.5	†	†	14.0
5. Length of internodes cm	†	†	†	1.8	1.4	1.9	2.4	1.7	0.8	0.7	†	†	0.9
6. Total number of leaves produced	†	†	†	17.0	14.0	21.5	20.5	19.0	16.0	11.5	†	†	14.0
7. Fresh weight per plant in g	†	†	†	2.381	0.284	3.519	4.855	3.498	0.326	0.277	†	†	0.159
8. Dry weight per plant in g	†	†	†	1.893	0.029	0.279	0.374	0.247	0.030	0.025	†	†	0.008
9. Dry weight %	†	†	†	7.95	10.12	8.09	7.71	7.06	9.64	9.21	†	†	5.28

† † = dead

TABLE 19. Experiment XIV. Effect of 13 different solutions in which the anions remained constant and the cations varied on the flowering responses and the growth of mustard

Square (see fig. 9)	1	5	7	9	10	12	13	17	19	20	22	25	28
Relative concentration of ions	Mg	6	4	3	3	2	2	1	1	1	0	0	0
	K	0	1	3	1	3	2	4	2	1	6	3	0
	Ca	0	1	0	2	1	2	1	3	4	0	3	6
(mean) Character													
1. Days to flower bud	†	†	†	†	30	†	41	†	30	30	41	30	30
2. Number of flowers	†	†	†	†	19	†	25	†	27	40	4	12	19
3. Height cm	†	†	†	†	24.5	†	21.5	†	41.5	44.0	10.0	15.0	31.0
4. Number of nodes	†	†	†	†	19.0	†	18.5	†	21.0	20.5	15.5	17.0	19.5
5. Length of internodes cm	†	†	†	†	1.3	†	1.2	†	2.0	2.1	0.6	0.9	1.5
6. Total number of leaves produced	†	†	†	†	19.0	†	18.5	†	21.0	20.5	14.5	17.0	19.5
7. Fresh weight per plant in g	†	†	†	†	2.417	†	2.062	†	4.897	4.113	0.196	0.855	2.207
8. Dry weight per plant in g	†	†	†	†	0.163	†	0.153	†	0.357	0.316	0.021	0.060	0.180
9. Dry weight %	†	†	†	†	6.78	†	7.36	†	7.32	7.64	11.02	7.16	8.15

1.2. Results and discussion. - Flowering responses: The effects of variations in relative anion concentrations on flowering, are represented in table 18. These data confirm previous results with mustard, viz. low N levels accelerate flower development. The flower primordia developed soonest when the anions were present in equivalent quantities or when only N was deficient (row 1, squares 13 and 10). When any of the other anions was deficient flower bud appearance was delayed (squares 12, 17, 20 and 28) or the plants died (squares 1, 5, 7, 22 and 25).

The number of flowers was highest when the anions were present in equivalent concentrations (row 2, square 13), and was also high in squares 12 and 17 (high levels of N) and in square 9. When little or no N was present, the number of buds was small (squares 10, 20 and 28).

The number of days to flower bud appearance when the cations were varied is shown in table 19. Plants grown in solutions containing high Ca levels were normal in their appearance and produced their flower primordia sooner than those grown in low Ca levels. High levels of Mg were toxic especially at low Ca levels; in solutions with a high Mg/Ca ratio many plants died (squares 1, 5, 7, also in 9). The number of flower buds (row 2) was highest at high Ca levels and low Mg levels; it decreased markedly when Ca was lacking.

Growth responses: The relative concentration of ions in the nutrient solution markedly affected the growth. In tables 18 and 19 the values are given for height of the plants, and number and length of internodes after 90 days. Table 18 shows that the height, the number of nodes and the length of internodes increased mainly when N was at high levels (rows 3, 4, 5, squares 12, 13 and 17). High concentrations of P reduced these values, and also when P was in high concentration and both SO_4 and NO_3 in low concentration (squares 20 and 28). Table 19 shows that these factors also increased when Ca was in high concentration in relation to K and Mg (rows 3, 4, 5, squares 19 and 20), while they were reduced when Ca was lacking (square 22).

There was no big difference in the total number of leaves produced. Generally the lack of N and also low N concentrations with high P concentration, slightly reduced the number of leaves (table 18, row 6, squares 10, 20 and 28). However, during the growing period a number of leaves died, and this number differed in the various solutions.

Dry weight.: Another indication of the growth is the amount of vegetative mass produced. Data on the fresh and dry weight of plants grown in the different nutrient solutions are given in tables 18 and 19. Again N and Ca are the ions that have the most pronounced effect. The highest amount of dry weight in the anion triangle was obtained in square 13, see table 18, where the three anions were present in equivalent quantities. At higher N levels the fresh and the dry weight were lower (rows 7, 8, squares 12 and 17), but when less N was present they decreased very markedly (squares 10, 19, 20 and 28).

In the cation triangle the highest fresh and dry weight were obtained where Ca was high and Mg was low, table 19, rows 7, 8, square 19, and also when Ca was high and both Mg and K were low, square 20.

The percentage of dry weight was highest when N was deficient (table 18, row 9, square 10) and in plants that were lacking both Ca and Mg (table 19, row 9, square 22).

1.3. Conclusion. - The data obtained in these experiments confirm that in mustard the ion concentration affects flowering. The minerals N and Ca have

the most pronounced effect on this process. A low level of N hastens the appearance of flower buds, but reduces their number. High levels of Ca produce plants that flower sooner than those at low Ca levels, but the effect of this element is not as pronounced as that of N.

2. *PERILLA CRISPA*

Experiment XV

For the experiment with *Perilla* the same solutions were used as for mustard (table 17), but the plants were grown in water culture according to the method described on page 7. The data obtained from the present experiment confirm the results of former experiments with *Perilla*, and it is unnecessary to report them in detail. They again show that the flowering behaviour of *Perilla* is affected by N and P. A deficiency of either one of these ions reduces the growth rate of the plants and thereby retards flower bud appearance.

The cation concentration had no marked effect on the flowering of *Perilla*. Ca-deficiency may retard flowering for a few days owing to the very poor growth which in most cases leads to a premature death of the plants.

CHAPTER VII

GENERAL DISCUSSION

1. INTRODUCTION

In the experimental part the flowering and growth responses were studied in relation to mineral deficiencies, several nitrogen levels and relative ion concentrations. We shall now discuss the experimental results from three points of view: the initiation, development and number of flowers, the growth, and the production of auxin, because mineral nutrition strongly affects all these processes.

2. FLOWER INITIATION, DEVELOPMENT AND NUMBER OF FLOWERS

The experiments with mustard, dill (L.D.P.) and *Perilla* (S.D.P.) showed that mineral deficiencies affected the flower bud appearance, the development and the number of flowers. In mustard, the flower bud appearance was definitely accelerated by N-deficiency. The other minerals affected the flowering behaviour by accelerating or retarding the flower bud formation for a few days. According to the literature, as discussed before (p. 5), *nitrogen* seems to be the most effective mineral in the flowering of plants. The present experiments confirm this fact and partly substantiate the finding of CAJLACHIAN (15, 1944) and WITHROW (115, 1945) that N-application made the plants more susceptible to the inductive period and caused them to break into blossom sooner than plants poor in N. This holds true for dill, spinach, *Perilla* and *Kalanchoë*. KNOTT (62, 1950) found that a large quantity of N applied to spinach, delays seed stalk initiation and development. Our results show that spinach plants were not affected in their flowering when the quantity of N was doubled in the solution. Mustard is affected in a reverse manner to our other experimental plants: the initiation and the development of the floral buds were accelerated by low levels of N or when it was lacking.

From the review of literature (43, 45, 52, 54, 66, 98) it follows that plants vary widely in their mineral requirement. The initiation and development of thy

floral buds are accelerated or retarded according to the quantity of nitrogen supplied. The results of this present study are in accordance with this fact. VON DENFFER (109, 1940) and MELCHERS (80, 1952) concluded that lack of nitrogen promotes flowering, while excess of N delays flowering in L.D. plants, while the effect is in the contrary sense in S.D. plants. These findings hold true for the L.D. plant mustard and for the S.D. plants *Perilla* and *Kalanchoë*, but do not agree with the results obtained with the L.D. plants dill and spinach. From our results it is clear that high N-concentration favoured the flowering of these two L.D. plants.

The number of flowers produced is greatly affected by mineral nutrition. The addition of N produced more flowers than plants receiving a N-deficient solution (24, 32, 34, 37, 60, 98, 102, 103). The results obtained in the present work are in accordance with these findings.

According to several authors *potassium* did not effect the initiation of flower buds, but the development and the number of flowers were considerably affected (29, 60, 85, 100, 102, 103). However, both the flower initiation and development in dill and *Perilla* were affected by K-deficiency. The flower initiation in dill and *Perilla* was retarded and the number of inflorescences and flowers were small.

The results obtained with *phosphorus* deficiency in the present work are in accordance with the literature (26, 28, 55, 58, 85, 102, 103, 114). The flower initiation was not affected, but the development and the number of flowers were decreased. In mustard only 6.6% of the plants opened their flowers and the number of flowers was also greatly reduced. In dill the number of inflorescences was also reduced. In *Perilla* the development of the floral buds was delayed and the number of flowers was less, in the P-deficient plants.

The effect of P-deficiency on the flowering behaviour may be due to the reduced growth which is reflected in the low top/root ratio of the different plants. These results are in accordance with the literature (26, 28, 58, 91). According to PIRSON (91, 1955) this is due to the lowering of the auxin level in P-deficient plants.

Calcium deficiency affected the terminal bud of the plants, causing an immediate death of the growing tips.

The review of literature (p. 6) indicated that the flowering of plants was slightly affected by Ca-deficiency. The results obtained in the present work show that in dill and *Perilla* Ca-deficiency caused the premature death of the plants. In mustard the plants tolerated the Ca-deficiency, but the development of the floral buds and the number of flowers were greatly reduced.

The present study shows that the flower initiation and development were retarded in mustard by *magnesium* deficiency. The number of flowers was not affected. In dill the flower bud appearance was slightly retarded and the number of inflorescences was reduced. In *Perilla* only the number of flowers was markedly decreased when Mg was deficient.

Mustard was affected by *sulphur* deficiency. The number of floral buds which opened was 100%, while in (N) solution it was only 60%. This result agrees with the finding of EGGLE (32, 1953). The number of flowers produced in mustard was not affected. In dill the flower bud appearance was slightly retarded, while the number of inflorescences was markedly reduced by S-deficiency. In *Perilla* the development of the floral buds was slightly retarded, while the number of flowers was markedly reduced by S-deficiency.

Relative ion concentration also effects the flowering behaviour of mustard and *Perilla*. The foregoing results (p. 39) bring out the fact that plants are markedly different in their nutrient requirements and tolerance. The anion that most affected the flowering of mustard was the nitrate. Its high concentration favoured the vegetative growth and retarded the flowering, while the reverse was true when it was at low levels or when it was deficient. However, high N-concentration favours both the growth and the flowering of *Perilla*. Mustard plants could not tolerate the deficiency of any of the anions and most of the plants died prematurely, while in *Perilla* the plants overcame this malnutrition and developed flowers. In mustard, a high PO_4 concentration was decidedly toxic, but when SO_4 or NO_3 were added the plants tolerated the toxicity of phosphate. Also high SO_4 concentration was toxic, when PO_4 was in low concentration or deficient. However, high PO_4 concentration was not toxic for *Perilla*, but on the contrary favoured both its growth and flowering.

The cation that most affects the flowering of mustard is calcium. All plants in high Ca-concentration flowered normally (but later than the plants in N-deficiency), especially when Mg was lacking or when it was in low concentrations. When Mg or K were in high concentration and Ca in low concentration, the plants died.

In the light of literature and from our experimental results it follows that minerals affect the flowering behaviour of plants to different degrees. Each plant differs from the other in its response to mineral food. According to HARDER and GÜMMER (50, 1952) this may be due to their interference in the metabolic process.

Minerals did not alter the photoperiodical reaction of plants under unfavourable photoperiod, but they make the plants more sensitive to the reaction of light under a favourable photoperiod. Mineral deficiencies impede or prevent differentiation or development of flower primordia, even under proper photoperiod (59, 108). In trying to answer the question as to what is the function of minerals in flower bud production, it seems rather evident that firstly minerals react with products of photosynthesis to form material for the building up of flower buds. This idea is supported in the literature, e.g. HARDER and GÜMMER (50, 1952) emphasize the interference of minerals in the metabolic process. HOWLETT (59, 1936) and TIBEAU (108, 1936) obtained evidence that mineral deficiencies impede or prevent differentiation or development of flower primordia even under proper photoperiod and temperature. Our results point to the special importance of N, P and Ca, while the other elements studied seem to be of incidental or no importance.

3. GROWTH

The present experiments show that minerals affect the growth of plants and that various reductions in growth result, when any of the mineral elements are deficient. There is a relationship between growth and flower bud appearance (except in mustard). In many cases the flowering responses are positively correlated with growth. When any mineral was deficient, specific symptoms appeared. These symptoms have been fully described in many textbooks and papers (12, 28, 44, 54, 79, 82, 111). *Nitrogen* favours the growth of plants and may be employed to decrease or increase the vegetative growth under many environmental conditions (30, 61, 63, 87, 88). N-application increases growth (8, 20, 72), internode length (48), and height, number of leaves and leaf area of

plants (66, 101). On the other hand MASKOVCEV and PSAREVA (77, 1954) showed that large quantities of N retard the growth of very young tobacco seedlings. The results obtained in the present experiments showed that the growth of the plants was greatly affected by N concentration. Generally, the height, the diameter, number of nodes and number of leaves in all experimental plants increased with N-supply. These characters were reduced when N was deficient with the exception of mustard (see below).

The present study clearly showed that the dry weight of plants increased when N was supplied. This result was obtained with mustard, dill and spinach and is in accordance with the literature (14, 15, 105). On the other hand low levels of N retard the dry weight production (74). Plants with abundant N supply had a lower percentage of dry matter than those to which the supply was limited. This is in accordance with the literature (45, 115).

The complete nutrient solution slightly depressed the rooting of *Phaseolus vulgaris* (106) and also high levels of N produced a poor root system. The same results were found in mustard. The root system was depressed in the complete nutrient solution (when there was no aeration in the solution), while it was promoted in low N concentrations and also when it was lacking. In *Perilla* the root system was normally developed in both (N) and 2 N solutions, while few but long roots were obtained in -N solution. These results show that the root system of plants varies with N concentration. Generally when N was deficient, few but long roots were produced, while many short ones developed when N was supplied.

Potassium deficiency affects the growth of plants in different ways. This effect has been studied by many investigators (13, 14, 48, 51, 75, 105). The results of these investigators holds true with our experiments. The most pronounced effect of K-deficiency is the premature defoliation of plants in most cases. *Phosphorus* deficiency delays the growth and causes depression in the dry weight (48, 101). This fact was confirmed in the present work with all experimental plants.

Calcium deficiency resulted in most cases in small stunted plants and caused the immediate death of the growing tips (79, 110). The number of leaves produced and the leaf area of *Perilla* were greatly reduced by Ca-deficiency. In dill premature death occurred. The root system in all plants deficient in Ca was more depressed than the shoots, and it seems as if the bad effect of Ca-deficiency on the shoots was due to the depression of the roots. The depression of the roots resulted in a high top/root ratio of some plants.

Magnesium deficiency affected the growth of some plants and a premature defoliation occurred (76). This case was found in *Perilla*, especially under short day. In other plants Mg-deficiency produced much more growth (48). This was found in mustard. Plants deficient in Mg showed vigorous growth which was reflected in their relatively high number of leaves, their large leaf area and dry weight of leaves, stems and total dry weight.

Sulphur deficiency caused reduction in growth of shoots and in dry weight. These results are in accordance with KYLIN (65). The total dry weight of plants was decreased by S-deficiency.

According to LEOPOLD and THIMAN (71, 1949) there is a correlation between the number of flower primordia and the weight of the plants, suggesting that auxin may affect flower initiation in a manner parallel to its effect on growth. In the light of literature and the results obtained in this study it is clear that the

growth of plants is reduced in different degrees by mineral deficiencies. This effect may be due to the low auxin level in such plants, as will be discussed under the next point.

4. AUXIN PRODUCTION

There is plenty of evidence that minerals and especially nitrogen play a part in auxin production. The growth hormone is most abundant in shoot tips of *Helianthus* and *Nicotiana* grown with high N concentrations, while the osmotic pressure of the nutrient solutions does not affect the growth hormone (AVERY *et al.* 4, 1936; 5, 1937). The same investigators also found that in *Nicotiana*, the growth hormone concentration varies with vigour and that both may be controlled by varying the N supply: no nitrogen, no growth hormone and no growth. Auxin is scarcely detectable in the stem tips of N-starved plants, and increasing N concentration resulted in increased auxin content (6, 7). Auxin production in plants is influenced by nitrates of mineral salts and the absence of nitrate in the nutrient solution causes a remarkable decrease in the production of auxin (42). In a recent paper PIRSON (91, 1955) suggested that the lowering of the shoot/root ratio may be considered as a general characteristic common to N-deficiency and this phenomenon is a result of the sinking of the auxin level in the whole plant.

From the foregoing literature it follows that growth and top/root ratio may be considered as a true picture reflecting the quantity of auxin produced in the plants. Vigorous plants with high top/root ratio indicate a high auxin concentration and vice versa. In plants supplied with N the growth is strong and the top/root ratio high, while they are less in -N plants, compare tables 9, 11, 12, 15. This might well be due to auxin concentration.

The relation between auxin and flowering has been extensively studied by many investigators. Some of them deny the influence of auxin in the flowering process (17, 18), while others emphasize that auxin plays a role in the flowering (9, 10, 11, 21, 35, 68, 69, 70, 113). It seems as if auxin definitely influences flower bud formation, but the true action of auxin in this process is not known in all cases.

From this evidence it appears as if mineral nutrients are factors in the production of growth substances, which in their turn may act as factors in differentiation and development (2, 78, 83).

5. CONCLUSION

Photoperiod is the primary factor in flower initiation, but its effect may be modified by mineral nutrition. Mineral deficiencies reduce the growth of plants to different degrees which may be due to the lowering of auxin level of the plants. This effect may also lead to the retardation of flowering. The accelerating effect of minerals (especially nitrogen) on the flowering process may be explained by their effect on auxin production. Also, minerals react with products of photosynthesis to supply the plants with material for the formation of building up of flower buds.

Mustard forms an exception. It seems as if in this plant low auxin levels, resulting from N-deficiency, favour flower initiation. In this case there is a negative correlation between growth and flower bud formation.

The general conclusion is that the effect of minerals on the flowering process

of long and short-day plants is indirect, through their effect on the synthesis of material to build up both flower buds and auxin.

CHAPTER VIII

SUMMARY

1. This work was carried out to determine the relationship between mineral nutrition and the flowering of some long and short-day plants.
2. The literature concerning the effect of mineral nutrition on flower initiation, time of flowering and number of flowers is discussed.
3. Mustard, dill and spinach were chosen as long-day plants, *Perilla crispa* and *Kalanchoë blossfeldiana* as short-day plants. Both water and vermiculite cultures were used for growing the plants. The nutrient solutions of HOAGLAND and ARNON (56) and of HAMNER (46) were chosen.
4. Mineral deficiencies affected the flower bud appearance, the development and the number of flowers in mustard, dill and *Perilla*.

Mustard. – Vermiculite was a more suitable medium for growing mustard than water. The flower bud appearance was definitely accelerated by N-deficiency. The other minerals also affected the flowering behaviour by accelerating or retarding the flower bud appearance for a few days. The rate of development of the floral buds and the percentage of opened flowers were greatly affected by mineral deficiencies. It was definitely shown that N-deficiency favours the flowering of mustard.

Dill. – The mineral deficiencies retarded the initiation and development and reduced the number of inflorescences.

Perilla. – The deficiency of both N or P had the greatest effect in retarding the initiation, the development and the number of floral buds. It was shown that N affected the flowering behaviour of plants more than the other elements used in this study.

Minerals did not alter the photoperiodical reaction, but they made the plants more sensitive to the reaction of light under a favourable photoperiod.

5. Nitrogen level affected the flowering behaviour of plants very considerably. **Mustard.** – The flower initiation was only slightly affected by the N concentration, but the rate of development of floral buds and the number of flowers were greatly affected. Much earlier flowering occurred when N was supplied in low levels ($\frac{1}{12}$ N, $\frac{1}{16}$ N) or when it was lacking.

Dill. – The normal concentration (N) and excessive nitrogen 2 N, speeded up the flower bud appearance and the development and produced large numbers of inflorescences, while these characters were retarded when N was lacking.

Spinach. – N level had only a slight effect on the flowering responses of spinach. The flower bud appearance was delayed for a few days, when N was lacking.

Perilla. – With the exception of 2 N, the earliness of flower bud appearance, the development and the abundance of flowers produced were positively correlated with the quantity of N supplied.

Kalanchoë. – High N levels accelerated the flower bud initiation and development and a large number of flowers were produced.

6. Relative ion concentration affected the flowering behaviour of mustard and *Perilla*. The ions that most affected the flowering of mustard were N and Ca, while in *Perilla* these were N and P.
7. It is concluded that the effect of minerals on the flowering process of long and short-day plants are indirect, through their effect on the production of material for flower bud formation, and on the production of auxin and hence on the growth.

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SAMENVATTING

ENIGE ASPECTEN VAN MINERALE VOEDING EN BLOEI

1. De hier beschreven studie werd ondernomen om enig inzicht te verkrijgen in de invloed van de minerale voeding op bloemaanleg, tijdstip van bloei en aantal bloemen.
2. Er werd een overzicht gegeven van de betreffende literatuur.
3. Er werden experimenten verricht met de lange-dag-planten witte mosterd, dille en spinazie, en de korte-dag-planten *Perilla crispa* en *Kalanchoë blossfeldiana*. Deze werden geteeld in water en in vermiculiet, waarbij voedingsoplossingen volgens HOAGLAND EN ARNON (56) en volgens HAMNER (46) werden gebruikt.
4. Bij witte mosterd was de aanleg doch vooral de ontwikkeling van de bloemknoppen zeer versneld wanneer N ontbrak of in zeer geringe concentratie ($1/12$ N, $1/16$ N) aanwezig was. Bij overmaat N was de bloei vertraagd, doch het aantal bloemen was groter. Van de andere elementen beïnvloedde vooral Ca de bloei; het effect van P, S, K en Mg was gering.
5. Bij dille was de ontwikkeling van de bloemen het snelst bij normale of hoge hoeveelheden N; N-gebrek vertraagde de bloei, terwijl ook het aantal bloeiwijzen gering was.
6. Bij spinazie was de invloed van de mineralen gering. Wanneer N ontbrak, verschenen de bloemknoppen enkele dagen later.
7. *Perilla crispa* reageerde vooral op N en P. Behalve wanneer stikstof in overmaat aanwezig was (2 N), bleek de tijd nodig voor verschijnen en ontwikkeling van de bloemknoppen omgekeerd evenredig met de N-concentratie, terwijl het aantal bloemen er recht evenredig mee was. Van de andere elementen had vooral P invloed; P-gebrek vertraagde de bloei en verminderde het aantal bloemen.
8. Ook bij *Kalanchoë blossfeldiana* werd het aantal bloemen door N verhoogd, terwijl de planten iets sneller tot bloei kwamen.

9. Afgezien van de genoemde kwantitatieve beïnvloeding, had de minerale voeding geen invloed op het fotoperiodiek gedrag van de bestudeerde gewassen.
10. Er wordt geconcludeerd, dat de minerale voedingsstoffen een indirecte invloed op de bloei uitoefenen, en wel via (a) de productie van de voor bloemknopontwikkeling noodzakelijke voedingsstoffen, en (b) de productie van auxine. Zij oefenen dus een invloed uit via de groeiprocessen.

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PLATE I

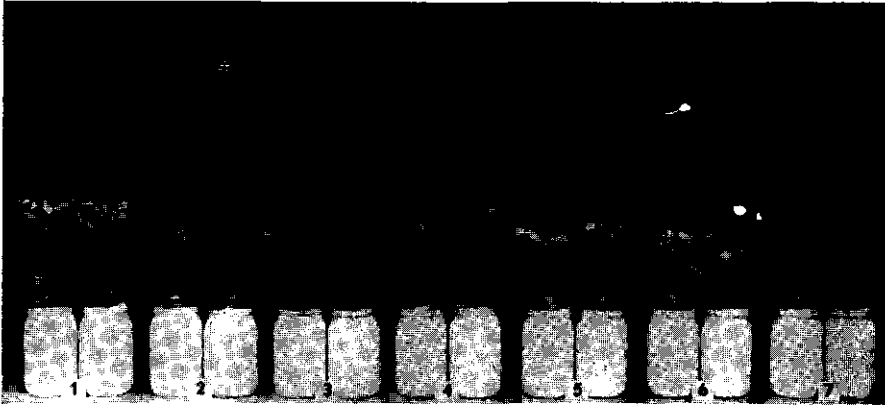


PHOTO 1. Experiment I, see p. 9: Mustard plants in water culture, showing the accelerating effect of nitrogen deficiency on flower development: 1. complete nutrient solution, 2. minus N, 3. -P, 4. -S, 5. -Mg, 6. -K, 7. -Ca.

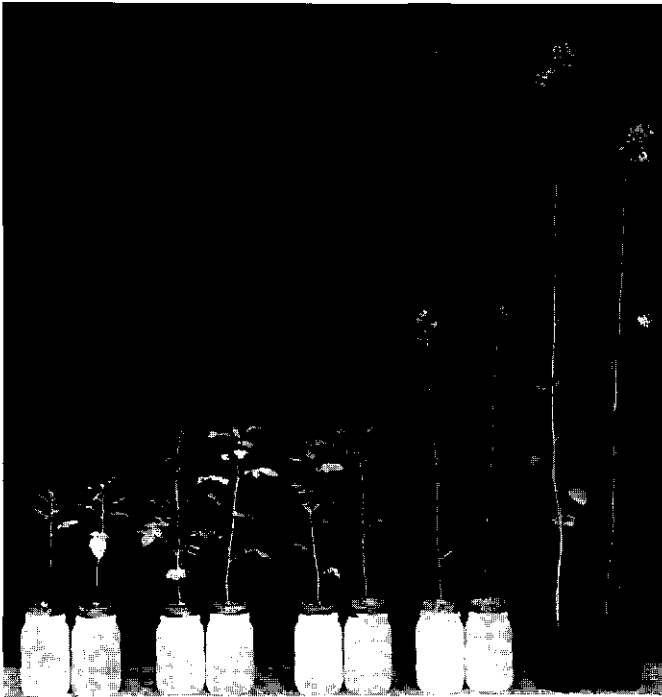


PHOTO 2. Experiment VI, see p. 22: Effect of nitrogen supply on mustard. From left to right: plants grown in complete nutrient solution, $\frac{1}{2}$ N, $\frac{1}{4}$ N, -N and in soil.

PLATE II

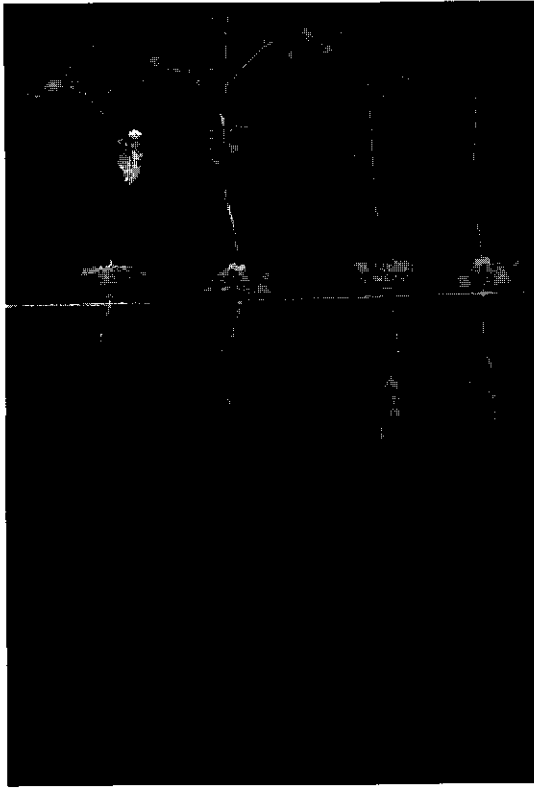


PHOTO 3. Experiment VI, see p. 22: Effect of nitrogen supply on the root system of mustard. From left to right; plants grown in complete nutrient solution, $\frac{1}{2}$ N, $\frac{1}{4}$ N, and -N.

PLATE III



PHOTO 4. Experiment XI, see p. 30: Effect of nitrogen supply on the root system of *Perilla* grown in, from left to right, 2 N, -N, (N). Two plants of each treatment are shown.

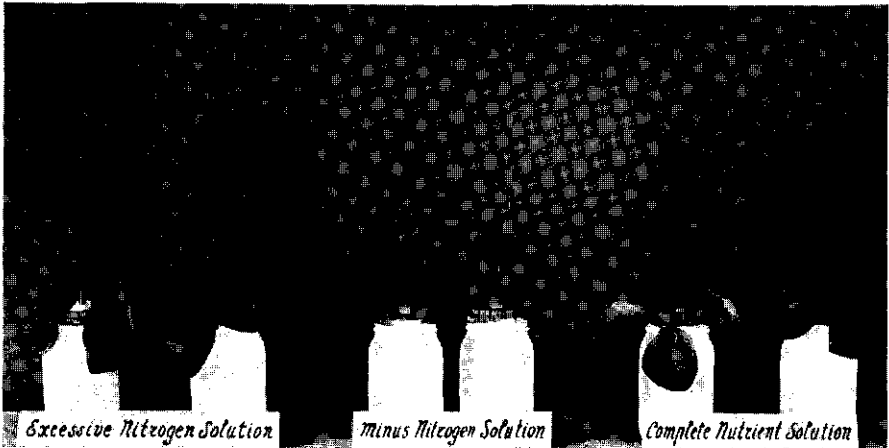


PHOTO 5. Experiment XIII, see p. 34: Effect of nitrogen supply on *Kalanchoë blossfeldiana*.