THE FORMATIVE EFFECT OF LIGHT INTENSITY IN LETTUCE PLANTS GROWN AT DIFFERENT NITRATE CONCENTRATIONS

by

J. BENSINK

Laboratory of Plant Physiological Research, Agricultural University, Wageningen Netherlands, 209th Communication.

(Received 22.12.'60)

INTRODUCTION

The object of the economic culture of lettuce is its vegetative stage of development. The market-gardener wants to grow plants that produce firm and heavy heads which are built up almost completely by leaves situated closely together along a thick and short stem. Typical for lettuce leaves is the strong development of mesophyll tissue in proportion to the nerve system, especially to the midrib. This leads to folding and crisping of the leaf blade which favours the formation of closed heads.

At low light intensities, a situation normally occurring during the winter months in the temperate zones, a good head formation is made difficult, first by the slow increase in weight owing to the low supply of light energy, but also by a formative growth reaction, *viz.*, lowering of the ratio mesophyll/midrib development. Especially the leaf base tends to elongate, and the growth in leaf width decreases, so that the relative leaf length continually increases with decreasing light intensity (1). This tendency holds on so that even the main stem may begin to elongate. Normally, with lettuce and most other rosette plants, stem elongation occurs only after flower initiation has taken place, and then is called shooting. Early shooting can also be a reason of incomplete head formation; this is mainly a matter of day length. If, however, stem elongation is induced by low light intensities, the growing point remains vegetative, and the moment of flower initiation is not speeded up. Moreover, as will be demonstrated later in this paper, the reproductive stem can be formed on top of a previously formed vegetative stem. There seems to be reason to consider both types of stem formation as two separate phenomena. In this connection, it is of interest that DE LINT (6) recently found indications that in the long day plant *Hyoscyamus niger*, in which flower initiation and stem formation appear as

closely connected phenomena, a separation can be made between a vegetative (formative) and a reproductive (photoperiodic) stimulus to stem elongation.

The vegetative stem elongation of lettuce increases with decreasing light intensity. At very low intensities, it reminds strongly of what generally is called etiolation. So far, there seems no reason to make a distinction in principle between this low-light-intensity-induced stem formation and dark etiolation. Apart from chlorophyll synthesis, the difference from complete dark etiolation seems to be only a gradual one, increasing with light intensity. Lettuce, however, requires rather high light intensities to suppress these etiolation phenomena. Moreover, a formative effect of light on leaf growth remains noticeable up to high light intensities (1), while a daily supplement of near-infrared radiation also results in strong etiolation (10). After IAA had been isolated as an endogenous growth substance, there has been a tendency in plant morphogenesis to ascribe all formative effects to a specific action of one or more, mostly hypothetical hormonal substances. Before this, morphogenetic effects were explained more by the nutritive state of the plant.

Light exerts a de-etiolation effect on dark grown plants already at very low light quantities, even if chlorophyll synthesis does not yet occur. In this case it is clear that the action is not due to photosynthetic activity of the light. With regard to the formative effect of light at high intensities, however, the question arises whether the production of essential growth substances or the total energy supply of the plant is the crucial fact.

This paper is concerned with the question whether the energy level of the plant may influence the formative reaction by affecting the relation between carbon and nitrogen supply. For this purpose plants were grown at different light intensities and nutrient solutions, differing in nitrate concentration.

MATERIAL AND METHODS

Lettuce plants of the variety "Meikoningin" were started in flats of soil in the greenhouse; at the stage of appearance of the 5th or 6th leaf they were selected for uniformity, and transplanted in glass jars of 1 l filled with fine gravel. An air volume of about 300 cc remained, and was filled several times a day with nutrient solution by sub-irrigation. Therefore, the jars had a hole in the bottom by which rubber tubing entered. The nutrient solution was in 10 l bottles, placed underneath the plants. Only six jars were connected simultaneously to one bottle, so that there was a great surplus of solution. The solution was renewed every fortnight. Different nutrient solutions were based on the four salt composition of HOAGLAND and SNIJDER. In most cases all solutions were given the same low concentration of potassium nitrate, while differentiation in nitrate concentration was achieved by adding calcium nitrate. The low-nitrate solutions received calcium chloride, equalizing the calcium ion concentration. Although the same composition was not used in all experiments—ammonium nitrate and sodium nitrate were also used as differentiating salts—in most cases solutions as specified in table 1 were applied. No obvious difference in effect has been noticed, comparing different nitrate sources. So far, ammonium alone has not been used as an N-source. The pH of the solutions was 6.7 to 6.9.

The plants were given artificial light from PHILIPS 40 Watt TL 55 tubes during 12 hours per day. For higher intensities, water filtered HO 2000 high

TABLE 1. Molar composition of nutrient solutions, containing 1,6, and 11 m.eq NO_3.

Compound \ m. eq NO_3	1	6	11
KNO_3	.001	.001	.001
$Ca(NO_3)_2$	–	.0025	.005
$MgSO_4.7H_2O$	.002	.002	.002
KH_2PO_4	.001	.001	.001
$CaCl_2$	.005	.0025	–
Ferricitraat			
Micro-nutrients A-Z			

pressure mercury lamps were used. The light intensity was measured in ergs/ cm^2 sec. The temperature was about 20°C during the day and 17°C during the night.

The effects of differences in nitrate supply on leaf shape, stem elongation, top/root ratio, flower initiation, and subsequent shooting were studied.

RESULTS

Leaf shape

The ratio of total leaf length to greatest leaf width has been used as an index for leaf shape in previous work (1). With decreasing light intensity, this ratio increases, owing to elongation of the midrib, mainly at the base, and by reduction of leaf blade development. Both phenomena bring about an increase of the relative leaf length (L/W). Below a certain light intensity, however, leaf length shows no further elongation, because—as we may assume—the energy supply becomes a limiting factor. However, since leaf width is strongly reduced at these low light intensities, the decrease in L/W ratio goes on, yielding an exponential relation to light intensity (1).

By varying both light intensity and nitrate supply, the leaf shape reaction becomes more complicated as is demonstrated by table 2 and figs. 1a, b and 2a, b, so that, in general, the L/W ratio did not appear to be a very suitable criterion for the effect of nitrate on leaf growth.

TABLE 2. Mean leaf length, leaf width, and L/W ratio of plants grown at different light intensities and different nitrate concentrations.

m. eq NO_3	1		6		11		15	
Light Int. ergs/cm²sec.	L – W	L/W	L – W	L/W	L – W	L/W	L – W	L/W
7,500	142–69	2.06	156– 58	2.70				
	130–72	1.81	131– 54	2.42	119– 52	2.28		
15,000	140–83	1.69	158– 95	1.66	180–100	1.80		
20,000	114–86	1.33	148–107	1.38			151–103	1.46
28,000	85–78	1.10	134–113	1.18	165–120	1.37		

Fig. 1a shows that in the low light intensity region, from 7.5×10^3 to 15×10^3 ergs/cm² sec leaf length increases at all nitrate concentrations, and increasingly so from low to high concentrations. Above 15×10^3 erg/cm²sec the
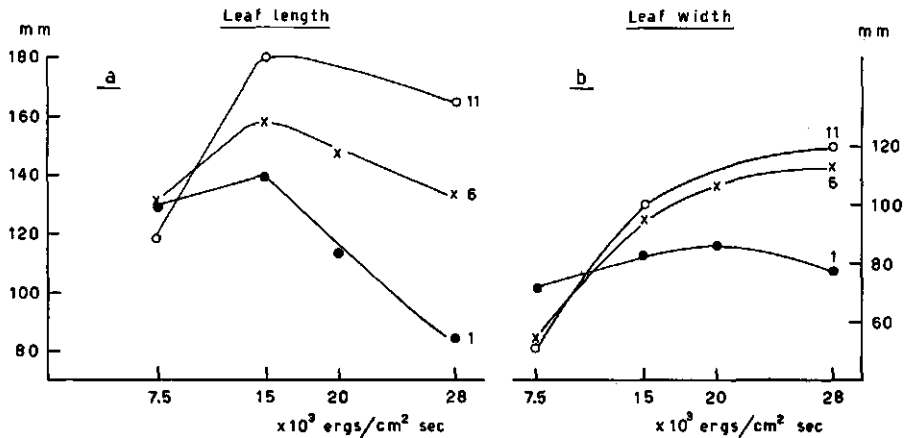
FIG. 1. Leaf length (a) and leaf width (b) in mm at different nitrate supply plotted against light intensity,

●————● 1 m. eq NO$_3$ ×————× 6 m. eq NO$_3$ O————O 11 m. eq NO$_3$
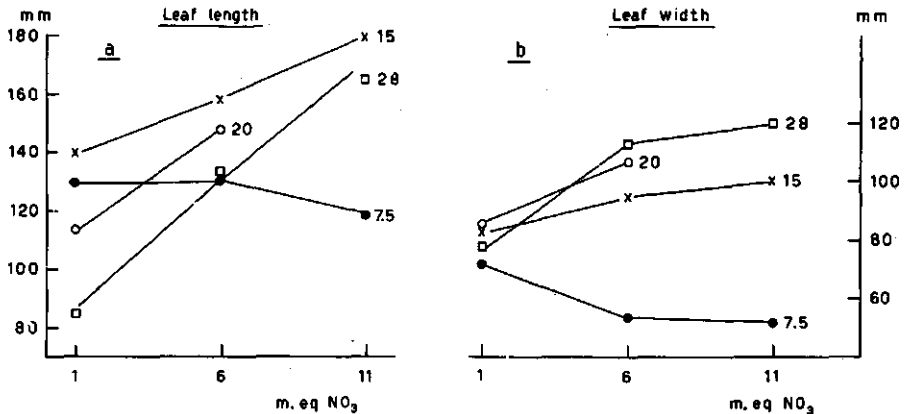

FIG. 2. Leaf length (a) and leaf width (b) in mm at different light intensities plotted against nitrate supply:

●————● 7500 ergs/cm²sec,   ×————× 15000 ergs/cm²sec,
O————O 20000 ergs/cm²sec,   □————□ 28000 ergs/cm²sec.

reaction is reversed in two respects: leaf length decreases at all nitrate concentration, and decreasingly so from low to high concentrations.

Fig. 1b demonstrates that leaf width also shows a reversal between 7.5 and 15 × 10³ ergs/cm²sec. in a way comparable to the reaction of leaf length in this intensity region. However, contrary to leaf length, leaf width shows hardly any reaction upon light intensity at the lowest nitrate supply.

The same data plotted against nitrate supply are shown in Fig. 2a, b. They reveal a fairly linear increase in leaf length with nitrate supply in the high light intensity region. At low light intensity, there is hardly any reaction of leaf length to increase in nitrate supply; in relation to the higher light intensities the type of reaction appears fairly reversed.

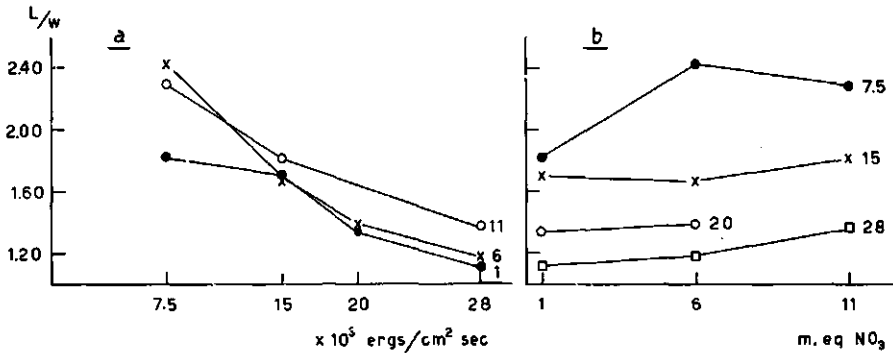4   *Meded. Landbouwhogeschool, Wageningen* **60** *(19), 1–12 (1960)*

FIG. 3. Changes in leaf shape, represented as length/width ratio, at different light intensities (a) and different nitrate supply (b).

Leaf width hardly reacts upon increase in nitrate concentration from 6 to 11 m.eq. at any light intensity. In the lower region of nitrate supply, however, there is a pronounced reaction which, again, is reversed between 7.5 and 15 × 10^3 ergs/cm²sec.

It will be evident that changes in leaf shape as represented by the L/W ratio (shown in fig. 3a, b) are the result of a rather complicated set of reactions, shown separately in fig. 1a, b and 2a, b.

At low nitrate supply, the rate of leaf production is slightly lower. However, as can be seen on plate IIa, the leaves of plants at higher nitrate concentrations die off sooner. Thus, the total active leaf area of the low nitrate plants at low light intensity will be greater in the end. This may have consequences in morphogenesis, especially at conditions of low energy supply.

As low nitrate supply suppresses the reduction of leaf blade development, normally occurring at low light intensities, while also leaf color is darker green, the entire growth of the low nitrate plants at low light intensities appears better balanced. Prelimenary determinations showed that total nitrogen in leaf blade tissue of low nitrate plants is about half that in high nitrate plants. It is likely, therefore, that the balance of nutrient salts and available photosynthates as such has important consequences with regard to formative processes.

Stem elongation

Vegetative elongation of stems, normally occurring at low light intensities can be fully suppressed by decreasing the nitrate supply (see table 3, and the plates

TABLE 3. Mean stem length in mm of plants grown at different light intensities and nitrate concentrations. Plants at the lowest nitrate concentration in the end formed reproductive stems.

m. eq NO₃ Light Int. ergs/cm²sec.	1	6	11
7,500	70–530 [1]	450	
15,000	54	142	152
28,000	35–290 [1]	50	59

[1] Shooting plants.

Ib and IIa). The vegetative stems show little differentiation, no cambium activity, and no secondary xylem. Therefore, these stems have to be given artificial support at greater lengths (see plate II).

Flower initiation and shooting

Not all experiments have lasted sufficiently long for flower initiation to take place. But if flowering was waited for, it appeared that plants at the lowest nitrate concentration showed earlier flower initiation and earlier subsequent shooting (see table 4 and plates Ia and IIb).

TABLE 4. Days to macroscopical visible flower initiation of plants grown at different light intensities and different nitrate concentrations.

Light Int. ergs/cm²sec. \ m. eq NO₃	1	6	11
7,500	133	170	170 (see plate IIb)
20,000	120	>120	>120
35,000	87	120	120 (see plate Ia)

The anatomy of shooting stems differs from that of the above mentioned vegetative stems in showing more differentiation. There is cambium activity and formation of secondary xylem, giving the stems a sufficient rigidity to stand upright. They show a violet colour, owing to anthocyanin formation. As can be seen from plates Ia and IIb, shooting plants attain greater lengths at low light intensities than at high ones, mainly by formation of longer internodes. Thus, the elongation of a reproductive stem may be influenced by the intensity of light as a formative effect. This may be denoted as etiolation of the reproductive stem at low light intensities if the maintenance of differentiated tissue is not in contradiction with the concept of etiolation.

Plants at low light intensities and high nitrate concentrations which form long etiolated vegetative stems, in the end also enter the reproductive state. It is of special interest that in this case shooting takes place at the top of the previously formed vegetative stem. The shooting stem now bears the anatomical characteristics of a reproductive stem so that, obviously, both types of stems may be present in the same plant. This strongly suggests that, in lettuce, the formation of reproductive and vegetative stems can be considered as unrelated phenomena.

Root/top ratio

In all experiments, root development was promoted by low nitrate concentration. As may be seen from table 5, the production of roots at 1 m.eq NO₃ has been 1.5 to 2 times greater than that at 7.5 and 12.5 m.eq NO₃. This seems to be independent of light intensity. At very low light intensities, no dry weight figures are available, but the greater root production at low nitrate concentrations can be seen from plate IIc. One may suggest that differences in top/root ratio are effected primarily by a still unknown formative mechanism in the plant that distributes dry matter production over shoot and root system.

TABLE 5. Dry weights of roots, shoots, total plant, and root weight percentage of 5 experiments. Plants grown at different nitrate concentrations. Weights are given in relative units, the weights at the lowest nitrate concentration has been given weight 100. Light int. exp. 1,2: 20,000 ergs/cm²sec; exp. 3,4: 25,000 ergs/cm²sec; exp. 5: 60,000 ergs/cm²sec.

Exp. no. m. eq NO₃	1	2	3	4	5	1	2	3	4	5
1	100	100	100	100	100	100	100	100	100	100
6	66	50	77	35	53	102	88	140	77	112
11–15	77	72	59	41	51	105	109	130	98	125
	rel. root weight					rel. shoot weight				

Exp. no. m. eq NO₃	1	2	3	4	5	1	2	3	4	5
1	100	100	100	100	100	15	13	25	26	20
6	84	96	127	106	102	12	9	13	12	9
11–15	104	101	116	87	112	11	9	11	11	8
	rel. total plant weight					root/shoot × 100				

DISCUSSION

The results of our experiments show that etiolation phenomena, at low light intensities normally manifest by undifferentiated vegetative stem elongation, stimulation of midrib elongation, reduced leaf blade development and poor root growth, all are suppressed at low nitrate supply. Low nitrate supply, moreover, enhances flower initiation, apparently irrespective of light intensity. The same holds for the relative increase of root development at low nitrate supply.

It is not well possible to define a normal nitrate content of the nutrient solution without further specification. HEWITT (3) has listed a number of nutrient solutions used in water culture by different workers. The nitrate concentration generally varies between 5 and 15 m.eq, but there are examples of good growth also at much lower concentrations. CHAPMAN and LIEBIG (2), e.g., obtained normal growth of Citrus in sand culture with a nitrate concentration of 0.5 m.eq, but only if the solution was frequently refreshed, in order to keep concentration constant. The possibility to avoid depletion of the nutrient salts by frequent renewal of the solution in water culture allows the use of lower concentrations than in soil culture. Low concentrations of nutrients are known to facilitate uptake by the plant. These points give some uncertainty in experiments of the type described, since a plant at low nitrate concentration but with enlarged root system may well absorb the same total amount of nitrate as a plant at high concentration with a poorly developed root system. The best way to

study this will be by analysis of the nutrient solution after some period of growth which, so far, has not been done in our case.

In most studies the influence of macro-nutrients is determined by dry matter production. HOAGLAND (4) defines an optimum nutrient solution as the minimum concentration which gives maximum yield. In our experiments, however, the formative effects of nitrogen clearly are of more importance than the increase in dry matter.

The early flowering of the plants grown at a low nitrate concentration strongly points to the idea of KRAUS and KRAYBILL (5) about the C/N ratio in the plant as a causal factor in sexual reproduction.

The importance of the C/N ratio has been less emphasized since the discovery of the photoperiodic control of flowering, and also because of a large amount of contradictory evidence. MURNEEK (9), e.g., emphasizes that in many cases sexual reproduction precedes the accumulation of carbohydrates and the increased C/N ratio. If a relation exists between the C/N ratio and the stage of development, this probably holds only for certain parts of the plants while large parts in this respect may be different. Therefore, chemical analysis of plant tissue appears unsatisfactory as long as it is uncertain what special part of the plant is critical.

A better approach seems to be the application of conditions which are likely to emphasize either the supply of carbon- or of nitrogen compounds. We thus found that, in lettuce, low nitrate supply favours the onset of flower initiation, independent of the light intensity received by the plants at a constant daylength. We have not yet investigated in how far also the photoperiodic response is quantitatively influenced by the nitrate supply. Since our aim was to study primarily the vegetative development, only daily light periods of 12 hours have been given. If we assume that, owing to low nitrate supply, the susceptibility for flower induction is raised, also the critical daylength may be shifted to shorter days. As soon as flower bud initiation has taken place, however, bud development may well be favoured by transfer to higher nitrate concentrations. This may be one of the reasons for the contradictionary results regarding the relation between C/N ratio and flowering.

LOOMIS (7) proposed the concept of the growth/differentiation balance to replace the C/N ratio as a developmental criterion. LOOMIS (8, p. 6) states that when "growth is checked by some method which does not correspondingly reduce the supply of photosynthates, carbohydrates previously used in growth accumulate and become stimulus and the raw material for increased differentiation". The idea of a competition between vegetative growth and differentiation has been expressed in different ways by a number of investigators, and is quite generally accepted.

By lowering the nitrate supply to the plant we apparently introduce a condition other than the supply of photosynthates which curtails growth (elongation), and stimulates differentiation (flowering). If so, it is, however, not at once clear why this effect of nitrogen should be, as evidence suggests, independent of light intensity and, thus, independent of the supply of carbohydrates. The same objection can be made when the increased root weight at the low nitrate concentration is explained as originating from a relative surplus of growth substrates not used by the shoot. Root weight percentage always was found to increase with reduction in nitrate concentration. Also from the figures of CHAPMAN and LIEBIG (2), who applied nitrate concentrations from 30 down to 0.01 m.eq to sand culture of *Citrus*, it appears that root growth shows a

proportional increase from 30 to 130% although there are signs of N-starvation of the plant at 0.01 and 0.05 m.eq No_3.

Formative effects of nitrogen are most striking at low light intensities, at which etiolation phenomena are suppressed by limited nitrate supply. One might think that extension growth, as stimulated by low light intensity then is curtailed by lack of nitrogen for synthesis of *e.g.* protoplasm. However, the early shooting of low nitrate plants observable also at very low light intensities, shows that they have sufficient energy at their disposal to effectuate stem elongation. We may assume that, in first instance, "reproductive" stem elongation is started by a hormonal impulse (flower induction), but that its realization requires the same amount of substrates as vegetative stem elongation or even more. The growth of the reproductive stem itself is also formatively affected by the light intensity.

It seems likely, therefore, that the differences in the formative aspects of the plants, and in their readiness to shooting, caused by differences in nitrogen supply, are not primarily due to limited availability of either nitrogen or carbon compounds, used as growth substrates, but to formative impulses mediated by their mutual proportion.

It is of interest to note that the formative effect of decreased nitrogen supply with respect to leaf shape is similar to that reported earlier as obtained by increased light intensity or decreased (night)-temperature. Low nitrate plants at low light intensity, therefore, resemble nitrate normal plants, grown at higher light intensities.

It is thus possible to sum up a series of environmental and nutritive conditions which are mutually interchangeable in intensifying or decreasing the ultimate formative effect. The establishment of the causal relation between different environmental conditions as has been done here for the factors light intensity and nitrate supply, seems a prerequisite for a better insight in the kinetics of the underlying morphogenetic processes.

In this connection a further analysis of the figures 2a and b seems of interest. If the slope of the curves in these figures, in the region between 1 to 6 m.eq nitrate, is plotted against light intensity, it seems that fairly linear relationships result, both for $\triangle L/\triangle N_{1-6}$ and for $\triangle W/\triangle N_{1-6}$ (see fig. 3a).

A full explanation of these curves is not easy. First of all, the reproducibility of these relations still has to be checked more elaborately, but the very smooth fitting of the various points seems to leave no doubt that the general trend is valid. The curve of $\triangle L/\triangle N_{1-6}$ suggests that at each light intensity the increase of L (in absolute measure) is proportional to light intensity (and has, incidentally, the value zero at 7.5×10^3 ergs/cm²sec). Thus, at 7.5×10^3 ergs/cm²sec, the increase in nitrate supply from 1 to 6 m.eq does not result in an increase in leaf length. At each of the higher intensities the increase is proportional to light intensity. This indicates that some factor directly connected with light intensity limits this further growth, now made possible by the considerable increase in nitrogen supply. It may well be assumed that the length of the leaves is increasingly curtailed with increasing light intensity at the lower nitrogen level. The increase indicated by the $\triangle L/\triangle N_{1-6}$ curve thus indicates the filling of a "gap", the size of which increases with light intensity. This reaction may, therefore, be conceived to represent a purely energetical relationship.

It should be observed, however, that the actual length of the leaves is increasingly reduced with increasing light intensity, above 15.10^3 ergs/cm² sec.,

at the lower (and still somewhat at the higher) nitrogen level. This so far un-explained morphogenetic reaction has to be taken apart from the above con-siderations concerning the effect of increase in nitrogen at each light intensity level.

To a large extent, the same relations hold for the curve $\triangle W/\triangle N_{1-6}$. It would appear, however, that a special difficulty is presented by the negative part of the curve. From a purely energetical limitation, it seems doubtful that a mere increase in a not then limiting component (nitrogen) would result in a decrease in size. Here an additional, formative effect of the one-sided increase in nitrogen clearly comes in. Admitting this, the disturbing thing then is the nice fitting of the negative lower point in the curve through the other, positive ones, for which the above suggested, primarily "energetical" explanation might fit. This dis-cussion inevitably leads to the conclusion that we still understand far too little from the cooperation of energetical and formative reaction chains and especially from their mutual relation to rate-limiting factors, to arrive at a full explanation at this moment. Further observations, especially at still lower light intensities, and still lower nitrogen concentrations, will probably lead to a further under-standing. Also spectral relationships may be elucidative in this respect.

The most tempting general suggestion, in order to reconcile the several aspects, brought forward above, would appear to be that from low to high light intensities the energetic implications of an increased nitrate supply become increasingly important with respect to the formative ones, while this segregation is smooth enough to explain the fitting of mainly formatively determined points and mainly energetically determined points into the same curve. This clearly indicates – as could be expected – that the interaction between formative and energetic reaction chains is not of the simple "Blackman" type.

The $\triangle L/\triangle N$ and $\triangle W/\triangle N$ curves for an N-increase of 6 to 11 m.eq (see fig. 4b) appear to contain some further support for the suggestion formulated in the last paragraph.

A last, remarkable feature is the suggested parallelity of the $\triangle L/\triangle N$ and $\triangle W/\triangle N$ curves. The absolute increase in length and width thus are about the same for each light intensity. This might also suggest an important energetical component in the reaction pattern. Whatever this may be, it explains the change in shape of the leaf (as indicated in fig. 3a, b). Length is much larger than width; if both continually increase with equal ammounts, the L/W relation obviously decreases as is found with increasing light intensity at each nitrogen level.

SUMMARY

During the vegetative stage of development, lettuce plants normally form closed rosettes of broad leaves along a short stem. These leaves are characterized by strong mesophyll development relative to midrib elongation. The stem inter-nodes start to elongate, to form a reproductive stem, only after flower initiation has taken place. This process is known as shooting.

Grown at low light intensities, lettuce plants show vegetative stem elongation which, at very low intensities, resembles dark etiolation. Relative leaf length (length/width, L/W) increases, owing to midrib elongation, mainly at the base, and reduction of leaf blade development. However, when plants are grown at relatively low nitrate concentrations, e.g., at 1 m.eq NO_3 instead of at 15 m. eq,
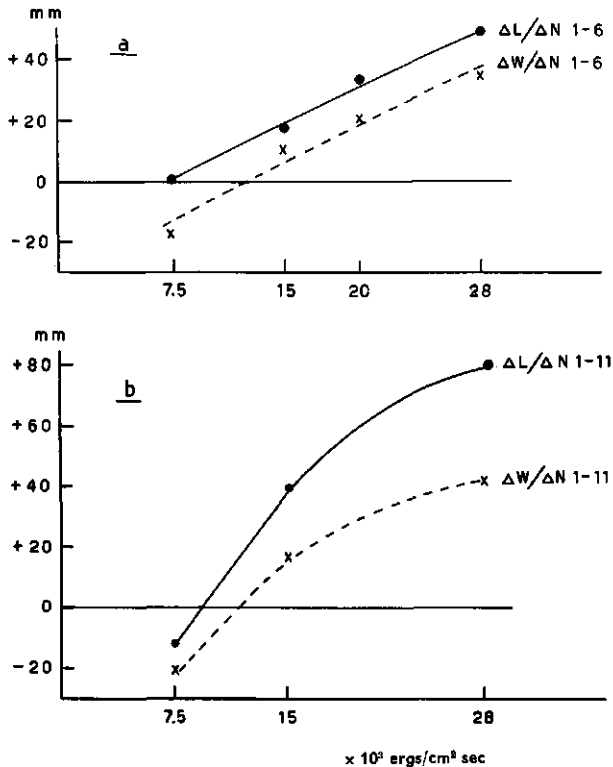
FIG. 4. The effect of an increase in nitrate supply from 1 to 6 m. eq NO_3 (a) and from 1 to 11 m. eq NO_3 (b) on leaf length ($\triangle L/\triangle N$) and leaf width ($\triangle W/\triangle N$) plotted against light intensity. Data derived from the slopes of the curves in fig. 2 a, b.

as normally used in a HOAGLAND solution, etiolation is greatly suppressed. In that case the plants resemble those grown at higher light intensities and normal nitrate supply. At all light intensities, flower initiation and subsequent shooting was enhanced by low nitrate supply. So far, our results seem not in contradiction with the C/N theory of KRAUS and KRAYBILL. Chemical analysis however, seems an unreliable criterion, as long as it is uncertain what special part of the plant at what special time should be analized. Therefore, the application of conditions which are likely to emphasize either the supply of carbon- or of nitrogen compounds seems a better approach.

Competition between vegetative growth and differentiation, e.g., flower initiation, is quite generally accepted. It is possible that the low nitrate supply may well limit the vegetative growth and, as result of this, the relative surplus of carbohydrates may favour differentiation. Another possibility, which in our case we are inclined to accept as more likely, is that the effects caused by differences in nitrogen supply are not primarily due to limited availability of either nitrogen or carbon compounds, used as growth substrates, but that the balance of nutrient salts and available photosynthates as such has important consequences with regard to formative processes.

For a better insight in the kinetics of the underlying morphogenetic processes it is important that the same formative effect can be obtained by either light intensity, (night)-temperature, defoliation or nitrate supply.

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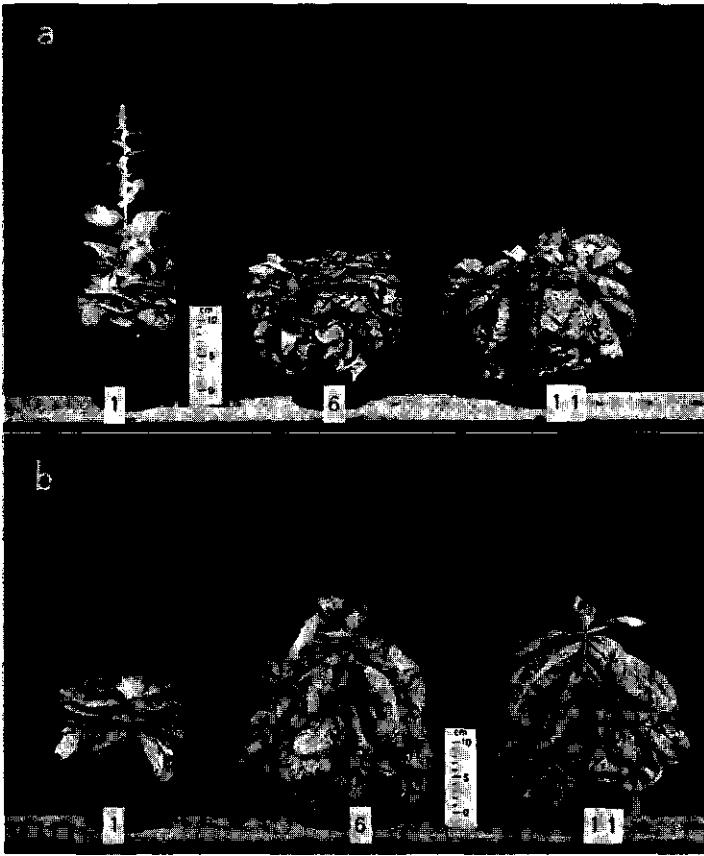
PLATE I

PLATE I.   Plants grown (a) at a high (35,000 erg/cm²sec.) and (b) at a low (20,000 ergs/cm²sec.)
light intensity, at three nitrate concentrations, 1, 6, and 11 m. eq NO_3.
At high light intensity an early flower initiation causes reproductive stem for-
mation at the lowest nitrate supply.
The vegetative stem elongation at the low light intensity is fully suppressed at
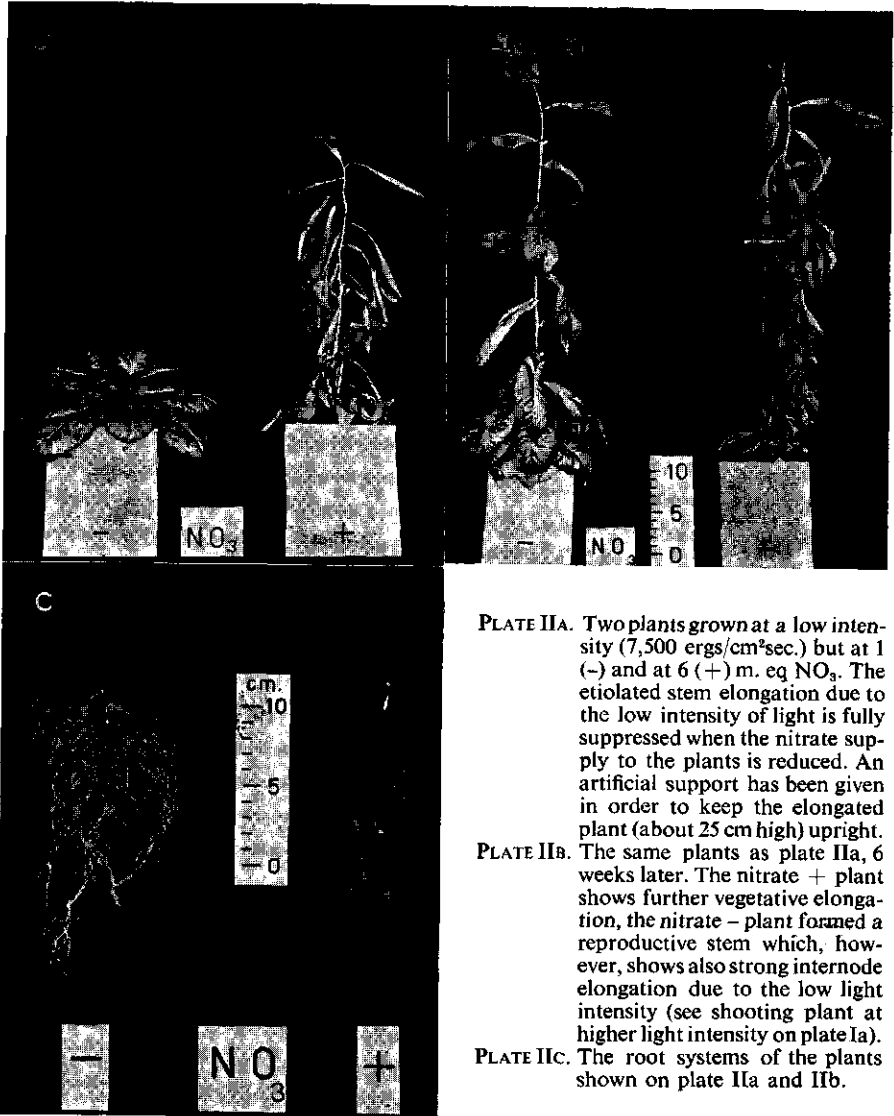the lowest nitrate supply.

PLATE II

PLATE IIA. Two plants grown at a low inten-
sity (7,500 ergs/cm²sec.) but at 1
(−) and at 6 (+) m. eq NO₃. The
etiolated stem elongation due to
the low intensity of light is fully
suppressed when the nitrate sup-
ply to the plants is reduced. An
artificial support has been given
in order to keep the elongated
plant (about 25 cm high) upright.

PLATE IIB. The same plants as plate IIa, 6
weeks later. The nitrate + plant
shows further vegetative elonga-
tion, the nitrate − plant formed a
reproductive stem which, how-
ever, shows also strong internode
elongation due to the low light
intensity (see shooting plant at
higher light intensity on plate Ia).

PLATE IIC. The root systems of the plants
shown on plate IIa and IIb.