582.998.4:581.451.035

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 67-16 (1967)

SOME OBSERVATIONS ABOUT THE EFFECT OF LIGHT ON THE LEAF SHAPE IN *TARAXACUM OFFICINALE* L.

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259th Communication

(Received 24-X-1967)

1. INTRODUCTION

Taraxacum officinale shows a variable leaf shape, the two extreme types are: a smooth, rounded one and another with deep incisions. Outdoor experiments indicated that the manifestation of these shapes could be light controlled. The rounded shape was found to be connected with low light intensity conditions(1).

It has been found in several other species that light can influence heteroblastic development, and in general the simpler shapes are observed in low light intensity conditions and the more dissected or lobed ones are promoted by higher light intensities (2, 3). Also the length/breadth ratio (L/B) has been used as a shape criterium, and reduced light intensities led to a higher L/B ratio (4).

Frequently, the effect of light intensity was explained through changes in the level of photosynthates. However this opinion is not unanimous, and the hypothesis that light acts upon the synthesis of a more specific factor has been proposed (5, 6,).

In this paper some preliminary attempts aimed at obtaining more information on this matter are reported.

2. MATERIALS AND METHODS

The plant material used was strain no. 1 of the laboratory collection. The general pattern of leaf shape in this strain is about the same as those described in (1). In the first experiment (the results presented in section 3a) plants grown outdoors were used. These were replanted on the 15th March in 15 cm ⌀ pots with a soil mixture. The experiment began the 12th April. Plate 1a shows one of these plants, photographed on April 2nd, 1965.

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The experiment described in sections 3b and 3c were carried out with young plants having about ten leaves. The seeds were planted in soil at 20 °C, after germination, the plants were grown at 20 °C with 16 hours fluorescent light/day at about 60.000 ergs. $cm^{-2}sec^{-1}$. A week before starting the experiments, plants selected for uniformity were replanted in pots of 8 cm ⌀. The watering was always done by hand, trying, as far as possible, to provide the same water supply to all treatments. The air temperature in all experiments was 20 °C and the humidity 70%. The white light was obtained from Philips TLM 125 W/33 fluorescent tubes. Different light intensities were produced either with copper gauze screens or by changing the number of tubes. The colour set-up was the same as described by DE LINT (7), now installed in one of the climatized rooms of the phytotron. The intensity in the 'low intensity' cabinets was about 1.000 ergs. $cm^{-2}sec^{-1}$ and in the 'high intensity' cabinets about 9.000 ergs. $cm^{-2}sec^{-1}$. Light measurements were made with a photocell, calibrated against a thermopile for each light source. The 'leaf dissection index' was used as a measure of the degree of dissection. This index is the ratio SA/SB, where SA is the actual leaf area and SB the empty area between lobes. Thus, the more dissected the leaf, the lower the index, cf. fig. 1.

FIG. 1. Defining the dissection index SA/SB of a *Taraxacum officinale*-leaf. Leaf example chosen from plate 1a. See text.

The areas were determined with a planimeter using photographs taken just after harvest. The L/B ratio was calculated from daily measurements of individual leaves. Dry weight determinations were made on material kept in a ventilated oven at 70 °C for 48 hours, followed with one hour at 105 °C.

3. EXPERIMENTAL RESULTS

a. Leaf dissection index and dry matter production as a function of the energy dose.

Plants grown outdoors were replanted in pots and kept at 15 °C under natural daylight until the beginning of the experiment, i.e. when they had formed about ten new leaves.

At this stage, some flower buds were already visible and were removed. The treatments comprised a range of total light energy (Q) between 10 and 120 cal. $day^{-1}cm^{-2}$ (400–700 nm). The first leaf, less than 20 mm long at the start of the treatments, was taken as number one and the changes in shape were compar-

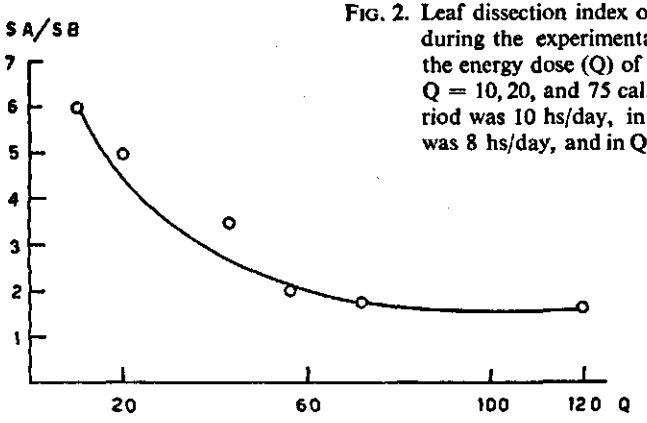

FIG. 2. Leaf dissection index of the 10th leaf expanded during the experimental period, as a function of the energy dose (Q) of white fluorescent light. In Q = 10, 20, and 75 cal. $cm^{-2}day^{-1}$ the photoperiod was 10 hs/day, in Q = 56 $cal.cm^{-2}day^{-1}$ it was 8 hs/day, and in Q = 120 16 hs/day.

ed on leaf number basis. Every two weeks a sample of four plants was taken for dry matter, leaf area, and leaf shape determinations.

At the beginning of the experiment, the plants had only dissected leaves (Plate 1b). This shape was maintained only in those receiving Q = 56 cal. $day^{-1}cm^{-2}$ or more; with 42 cal. $day^{-1}cm^{-2}$ or less, a gradual change to the rounded form was observed. Fig. 2 shows the reaction in leaf number 10, see also plate 2. The leaf dissection index decreased (more dissected leaves) as the energy dose increased. Figure 3 shows that the rate of change depends on Q, the lower the dose, the faster the change. In fig. 4 log dry weight increase is plotted as a function of time for three different energy levels. Log dry matter production was roughly linear with time. None of the light doses yielded values below the

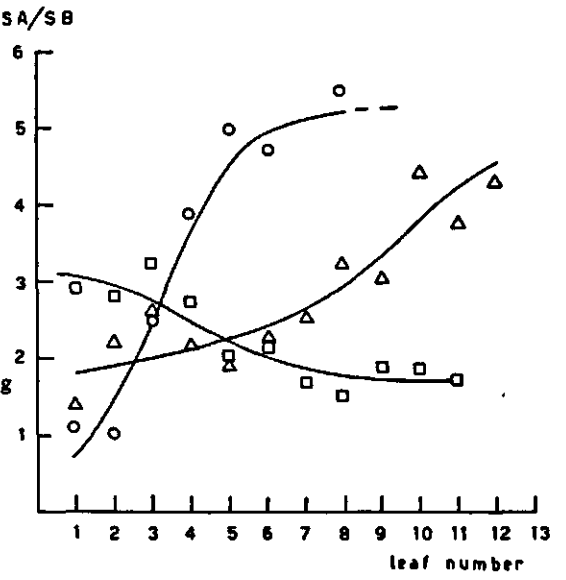

FIG. 3. Leaf dissection index in the different leaves expanded during the experimental period under three different Q-values, viz., 75 $cal.cm^{-2}day^{-1}$ (□), 20 $cal.cm^{-2}day^{-1}$ (△), and 10 $cal.sec^{-2}day^{-1}$ (○) of white fluorescent light in photoperiods of 10 hs/day.

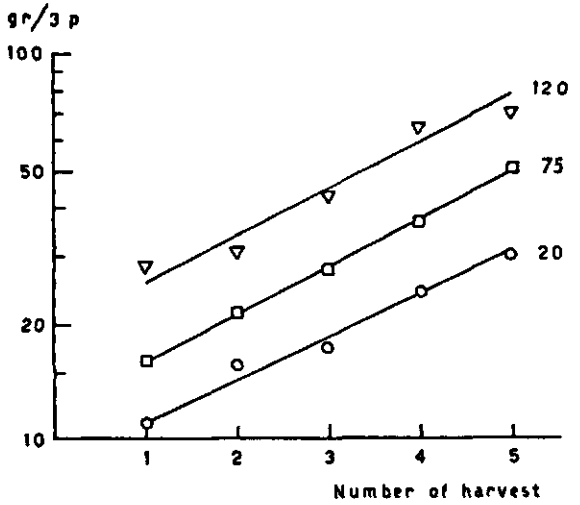

FIG. 4. Log dry weight increase as a function of time for three different Q-values, viz., 120, 75, and 20 cal.cm^{-2}day^{-1}. The period between two harvests is 2 weeks.

compensation point. If the inverse of the leaf dessection index and log dry weight are plotted together against Q, both show the same trend in the range of energies used (Fig. 5).

b. Influence of the duration of the daily light period.

In this experiment young plants raised as described in 2. were submitted to 8, 12 or 16 hours of white fluorescent light per day; the light intensity was 63.600, 42.500 and 31.200 ergs.cm^{-2}sec^{-1} respectively, in order to supply the same total amount of energy per day. Another group received a 16 hours photoperiod at 15.000 ergs.cm^{-2}sec^{-1}, the dose then was half that of the above. All plants had only rounded leaves when the experiment started.

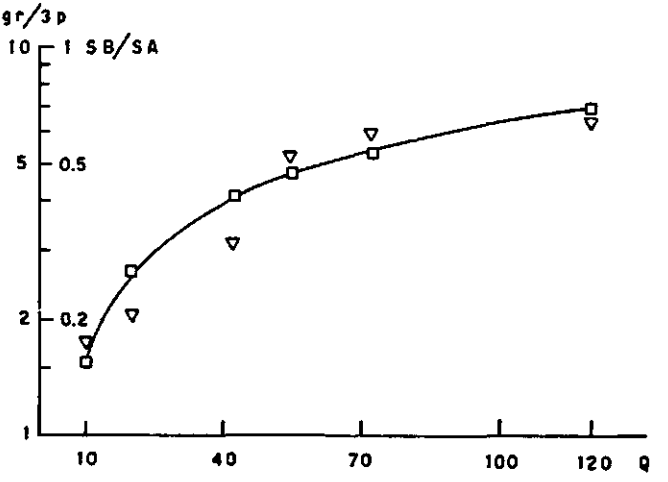

FIG. 5. Dry weight after the 5th harvest (□) and the inverse of the leaf dissection index at the 10th leaf (▽), on log. scale, as a function of Q.

The leaf shape after the 7th leaf which expanded during the experimental period is shown in table 1 and plate 3.

The first dissected leaf produced was between leaf numbers 6 and 8, independent of the duration of the photoperiod, in the three groups with higher energy dose. In the group which received 16 hours/day but at Q/2 only rounded leaves were formed. Thus, the induction of the dissected shape was independent of photoperiod in equivalent energy supply conditions.

These data suggest that the induction of the dissected shape does not depend on a specific length of the photoperiod or on the light intensity, but on an energy dose threshold.

TABLE 1. Leaf shape after the 7th leaf, expanded during the experimental period. White fluorescent light of intensities and duration stated in the table. At the beginning of the experiment all leaves present were rounded.

Conditions of illumination	Leaf shape
15000 ergs.cm^{-2}sec^{-1}, 16h/day	Rounded
31200 ergs.cm^{-2}sec^{-1}, 16h/day	Dissected
42500 ergs.cm^{-2}sec^{-1}, 12h/day	Dissected
63600 ergs.cm^{-2}sec^{-1}, 8h/day	Dissected

c. Effect of red, blue and far red light after a period of white light.

i. Effect on the dissected shape. Young plants received a basic period of 6 hours per day of white fluorescent light of either high intensity (hw) 50.000 ergs.cm^{-2}sec^{-1} or low intensity (lw) 20.000 ergs.cm^{-2}sec^{-1}. Immediately there-

TABLE 2. Leaf shape after the 7th leaf expanded during the experimental period. Hw = 50.000 ergs.cm^{-2}sec^{-1}, lw = 20.000 ergs.cm^{-2}sec^{-1}, white fluorescent light 6 hours per day. Fr = far red, r = red, b = blue light, all at ca. 9.000 ergs.cm^{-2}sec^{-1} 8 hours per day, d = dark. For the spectral characteristics of the sources and filters see (7).

Conditions of illumination	Leaf shape
hw + d	Rounded
hw + fr	Rounded
hw + r	Dissected
hw + b	Dissected
lw + d	Rounded
lw + fr	Rounded
lw + r	Rounded
lw + b	Rounded

after, 8 hours of blue (hw+b, lw+b), red (hw+r, lw+r), or far red (hw+fr, lw+fr) were given at a relatively high intensity: 9.000 ergs.cm^{-2}sec^{-1}. The con-

trols received only the white light period (hw+d, lw+d). At the beginning of the experiment only rounded leaves were present.

As can be seen in table 2, the dissected shape was obtained only in hw+r and hw+b. When the basic white period was of low intensity or when it was followed by darkness or far red light, only rounded leaves were produced.

In another experiment a basic white light period of high intensity was followed by 8 hours of red, blue, or far red, but of lower intensity, viz. 1.000 ergs. $cm^{-2}sec^{-1}$, with the same general result; the dissected leaves were formed only when red or blue light was given after the basic period. See plates 4 and 5.

The photosynthetically active energy provided by the additional period of red or blue, relative to the high intensity white light period, was of the order of 18 to 20% when the colours were given at high intensity and of about 2% when this intensity was low. However, the leaf area in these treatments was much greater, and consequently, the dry matter production was also much greater. Therefore, it is difficult to say whether the red or blue light effect was a direct one, or whether it was indirect through the increase in leaf area and the production of photosynthates.

In the plants which received only the basic period of 6 hours (hw+d, lw+d) or this period plus far red (hw+fr, lw+fr) the growth was rather poor. It was, therefore, possible that there might be an fr effect which was being masked through limited leaf growth. For this reason, a similar experiment was carried out starting with larger plants, which resulted in satisfactory leaf growth rates.

For this experiment the following daily irradiations were used:

1. 6 hours white light (60.000 ergs.$cm^{-2}sec^{-1}$) only.
2. 6 hours white light (60.000 ergs.$cm^{-2}sec^{-1}$)
   plus 8 hours red (ca 900 ergs.$cm^{-2}sec^{-1}$).
3. 6 hours white light (60.000 ergs.$cm^{-2}sec^{-1}$)
   plus 8 hours blue (ca 900 ergs.$cm^{-2}sec^{-1}$).
4. 6 hours white light (60.000 ergs.$cm^{-2}sec^{-1}$).
   plus 8 hours far red (ca 1.300 ergs.$cm^{-2}sec^{-1}$).
5. 12 hours of white light (60.000 ergs.$cm^{-2}sec^{-1}$) only.
6. 12 hours of white light (60.000 ergs.$cm^{-2}sec^{-1}$)
   plus 8 hours of red (ca 900 ergs.$cm^{-2}sec^{-1}$).
7. 12 hours of white light (60.000 ergs.$cm^{-2}sec^{-1}$)
   plus 8 hours of blue (ca 900 ergs.$cm^{-2}sec^{-1}$).
8. 12 hours of white light (60.000 ergs.$cm^{-2}sec^{-1}$)
   plus 8 hours far red (ca 1.300 ergs.$cm^{-2}sec^{-1}$).

It can be seen in table 3 and plates 6 and 7 that far red retarded the formation of dissected leaves when applied after a 6 hours white light period. Red and blue light promoted the dissection as in the first experiment. When the white light period was 12 hours, the leaf dissection index decreased (so dissection increased) and no far red effect was observed.

ii. Effects on the L/B ratio. The criterium for leaf shape showed a somewhat different reaction to the supplementary colour treatment.

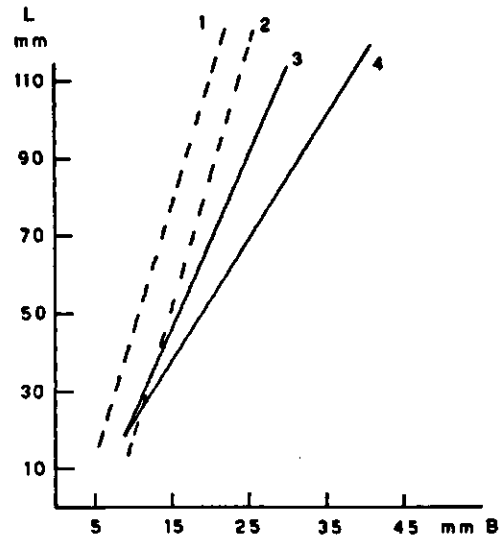

FIG. 6. Length and width of the first three leaves expanded during the experimental period. Treatments as in table 2. Curve 1 = lw + fr, 2 = hw + fr, 3 = lw + r, b, or d, 4 = hw + r, b, or d.
(Points on the lines not shown, since they formed a continuous cluster for each line, resulting from daily measurements of 3 consecutive leaves of 4 plants per treatment, during the entire growth period of each leaf).

TABLE 3. Leaf dissection index (average of four plants), at leaf numbers 7 and 10 of plants grown under 6 or 12 hours white light, followed by darkness, 8 hours red, 8 hours blue, or 8 hours far red light at intensities as indicated above, in text.

Treatment	Leaf dissection index	
	Leaf no. 7	Leaf no. 10
6w + d	13.5	3
6w + r	5.8	5.0
6w + b	6.5	3.5
6w + fr	17.5	14.5
12w + d	3.0	1.8
12w + r	2.4	2.0
12w + b	3.0	2.5
12w + fr	3.3	2.0

Independent of the intensity of the basic period, a clear effect of far red was observed. Fig 6 shows the length plotted against the breadth, for the first three leaves expanded during the treatments, which were the same as described in 3*c*, i. Each leaf was measured daily during the whole of its elongation period. The data of the three are plotted together because all followed the same trend.

The addition of far red at the end of the white light period caused proportionally more elongation in the direction of the main axis of the leaf, the midrib and the petiole elongation was enhanced and the lamina expansion depressed.

This was affected by the intensity and the duration of the white period as well as by far red. A white period of low intensity or short duration also resulted in a promotion of the length over the breadth.

The addition of far red causes a more pronounced effect in the L/B ratio than does halving the intensity. The line of hw+fr is more to the left than lw+r, lw+b or lw+d, in spite of the fact that in these treatments the intensity of the white period is much lower and the total energy supply also is much lower.

When the white light period was extended to 12 hours, the effect of far red was smaller than when the white light period was only 6 hours.

4. Discussion

a. The dissected shape.

The dissected shape is determined at an early stage of the development of the young leaf. In *Taraxacum* it is not possible to change from a rounded shape to a dissected one after the leaf is about 15 mm long. Ashby (3) in *Ipomoea* found that the degree of lobing is already fixed in leaves of 15 mm. It thus appears reasonable to assume that something produced in the more developed leaves is translocated to the primordia or to the very young expanding leaves and influences their future shape. About the possible identity of this substance or substances, Allsop (3), in a recent review, concluded that most of the existent data can be explained assuming that the decisive factor is the carbohydrate level. Increasing light intensity or increasing photoperiod at the same intensity, i.e. increasing Q, would result in a higher production of photosynthates, a higher sugar concentration in the apex and finally a more dissected or lobed leaf. Considerable support is lent to this idea by the experiments with aseptically grown *Marsilea*, in which the external supply of sugar can greatly influence the shape (3). Our results of figures 2 and 5 could be interpreted in this way. But the same relationship between shape and Q would be true if a photomorphogenic system requiring high energies were active.

The experiments of sections 3b and 3c have been undertaken assuming that some periodical or spectral dependence might be revealed if present.

Apparently there is no influence of the photoperiod; dissected leaves were formed at about the same leaf number in 8, 12 or 16 hours of white light per day if Q was kept relatively high. If Q is reduced, even in 16 hours/day only rounded leaves are produced.

The extension of a white period with different coloured lights showed effects of far red, red and blue.

The extension of a 6 hours white light period with far red inhibited the formation of dissected leaves. The young plants continued producing rounded leaves for a longer time, and the first dissected leaf in the far red treated plants was produced at a higher leaf number, with respect to the controls. Since the photosynthetically active energy supply was the same for both groups, and the dry matter production was larger in the 6 hours white + 8 hours far red than in the 6 hours white + dark, the differences in shape cannot be explained in terms of different carbohydrate synthesis. This indicates the presence of a mechanism different from the synthesis of sugars through wihch light can control leaf shape. There was no such effect of far red when the white light period was

12 hours. As we have seen before, the duration of the light period seems to have little importance. This would indicate that the influence of far red is affected by Q, the amount of white light energy.

The extension of the white light period with red or blue of either high or low intensity resulted in an enhancement of the dissection, and since the contribution to photosynthesis by the addition of these colours was relatively small, $\sim$ 2–5%, it might be supposed that after a period of high intensity white light, red or blue can activate the synthesis of some specific substance capable of inducing the dissected shape. But these colour treatments also promoted the leaf area and the leaf number in such a way that the dry matter production was much greater, so it cannot be said whether the red and blue light acted directly on leaf shape or indirectly by improving leaf area and cabohydrate synthesis.

However, it should be noted that even if the action of the red and blue is a direct one, a previous period of high intensity white light is necessary (there is no effect when the white light period is of low intensity); this high energy requirement is also seen in the experiments with different daylengths and light intensities. The required overall energy level is well above the compensation point, and seems to be in the range in which photosynthesis is light intensity dependent, and higher than those usually reported to be sufficient for flowering response or other morphogenic reactions (7, 9). Therefore it seems possible that at least part of the control exercised by light on the formation of the dissected leaves is due to the determination of the carbohydrate level or that of some product representing the activity of the photosynthetic apparatus.

To summarize, our results could be explained by the following tentative scheme: light exerts a dual control of the induction of the dissected shape, either promoting or inhibiting it. The promotion depends on a relatively high energy treshold and is enhanced by red and blue. The inhibition is caused by far red, the energy requirement being much smaller. There is no inhibitory effect if the promoting dose of white light is sufficiently high.

It could be reasonably assumed that the high energy treshold is necessary for the formation of a certain amount of a product or products which must be present if blue or red are to promote or far red to inhibit dissection.

These results do not provide evidence on the basis of which it might be concluded that these product can be identified as sugars, or some other more specific substance produced by a photomorphogenic system. Similary, they provide no evidence as to through which photomorphogenetic system far red acts.

b. The L/B ratio

The general reponse to the light factor of this criterium for shape is the same as that of the degree of dissection or lobing. At higher intensities, the ratio is smaller and the same basic explanations could be tentatively used.

In fact, BENSINK (4) with lettuce and WASSINK (10) with *Gladiolous* pointed out that there is a close relationship between the energy dose and the L/B ratio. Moreover, CO_2 supply changes the ratio in the same direction as increase in light intensity does (11). Again, the postulation of the sugar level as a key factor ap-

pears to be a suitable one. This could account for the higher L/B ratio in the low intensity basic period series in relation to the high intensity basic period series, but it is hardly possible to reconcile it with the effect of far red. Comparing curves 2 and 3 in fig. 6, we see that in spite of the fact that the plants in 2 have a high intensity basic period, thus a higher energy dose than those in 3, curve 2 is more to the left, due to the far red treatment, that is in the direction of the 'low intensity effect'. Thus the L/B ratio is under photomorphogenic control by a system different from the production of carbohydrates. Of course, the evidence of such a system does not exclude the possibility that the carbohydrate level could also play a role: circumstancial evidence for this is available in the literature (4).

5. Summary

Some effects of light on the leaf shape of strain no. 1 of *Taraxacum officinale* L. have been studied. Leaves with rounded leafblades develop at low light energy values, leaves with dissected blades at high light energy values. A dissection index is defined (see fig. 1), decreasing with increased degree of dissection. Equal daily energies appear to have the same effects, irrespective of their composition with regard to light intensity and duration of photoperiod. Degree of dissection was closely correlated with increase in dry weight in relation to energy dose. Coloured supplementary light of different intensities was applied after high or low intensity white (fluorescent) light periods of different energies, on young plants, with only rounded leaves at the start. Dissected leaves only formed when a short (6 hours) high intensity white light period was followed by supplementary blue or red. When followed by dark or far red, or if basic light of low intensity (6 hours) was applied, rounded leaves persisted, but far red was found to inhibit dissection more than darkness did (cf. e.g. Table 3.). With a basic light period of 12 hours of high intensity, dissected leaves were produced in all cases, also with supplementary dark or far red.

Leaf shape as expressed by the length : breadth ratio, showed a clear elongating effect by far red addition, independent of the intensity of the basic period (6 hours). Equally, reduction of the intensity of the basic light period (6 hours) promoted elongation of the leaves.

The possible importance of the carbohydrate level and of photomorphogenic control is discussed.

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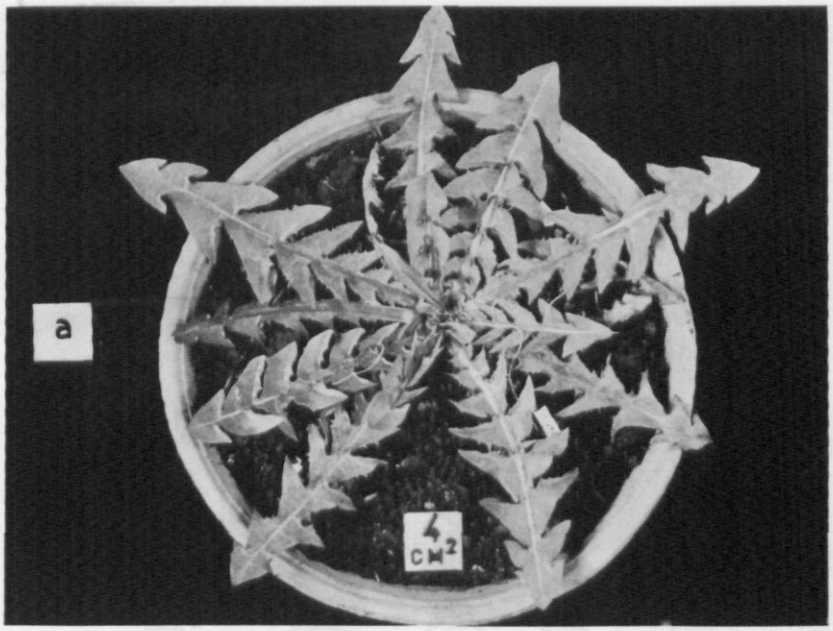
Acknowledgements

This study was carried out at the suggestion and under the direction of Prof. Dr. E. C. Wassink to whom I express my sincere thanks for his criticism and advice.

Also I am thankful to the University of Buenos Aires for the fellowship which gave me the opportunity to work in this laboratory.



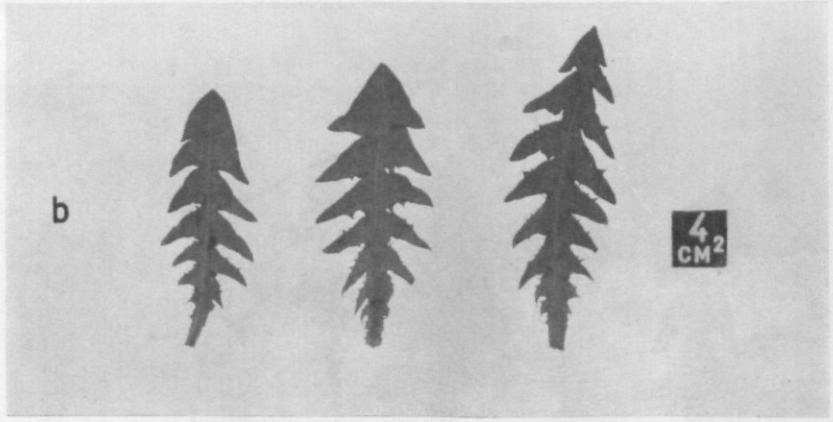


PLATE 1. a. A plant of *Taraxacum officinale* L., strain no. 1, grown outdoors, replanted in pot on 15–3–'65. Photographed 2–4–'65.

b. Shape of leaves of a plant of *Taraxacum officinale* L., strain nr. 1, as plate 1a, at start of experiment on 12–4–'65. Photographed 12–4–'65.

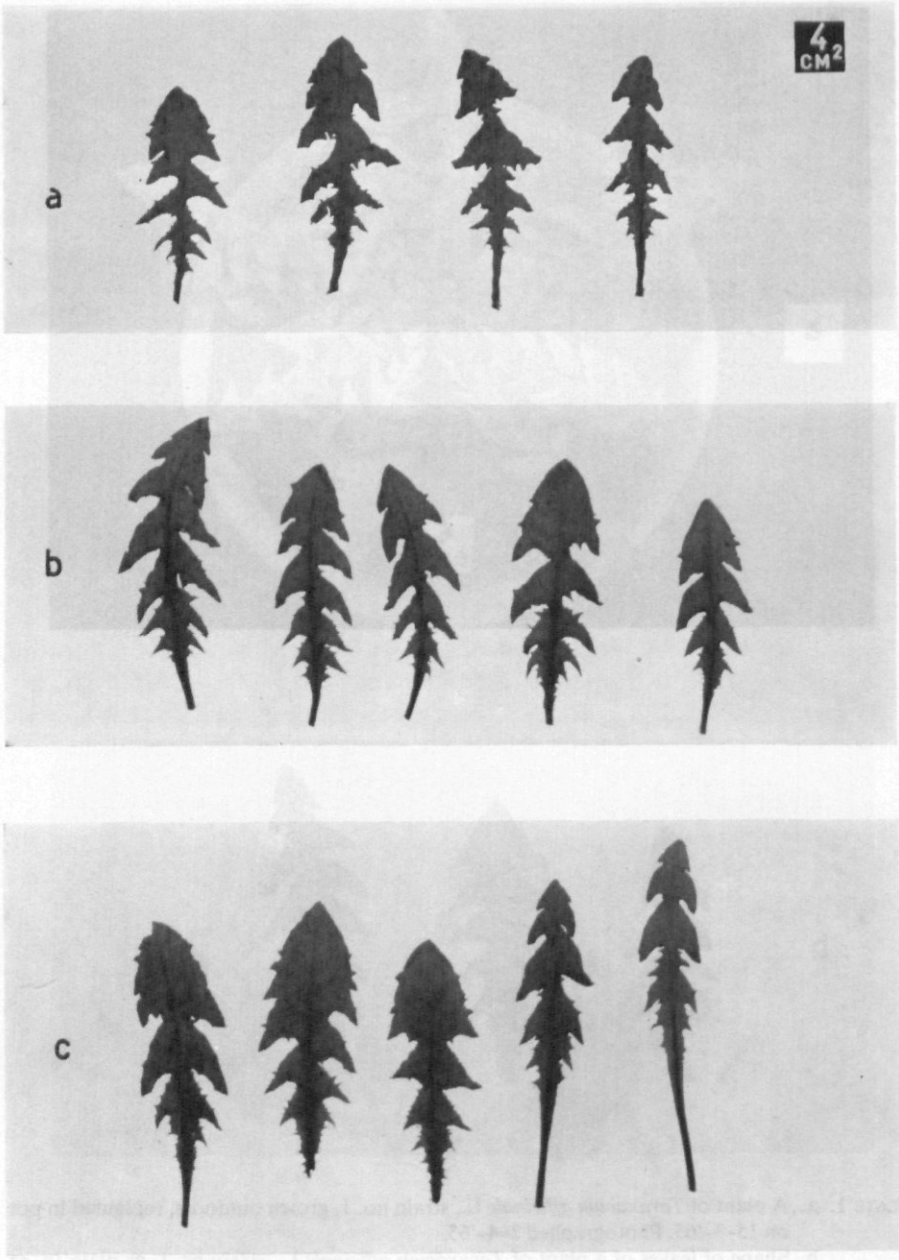
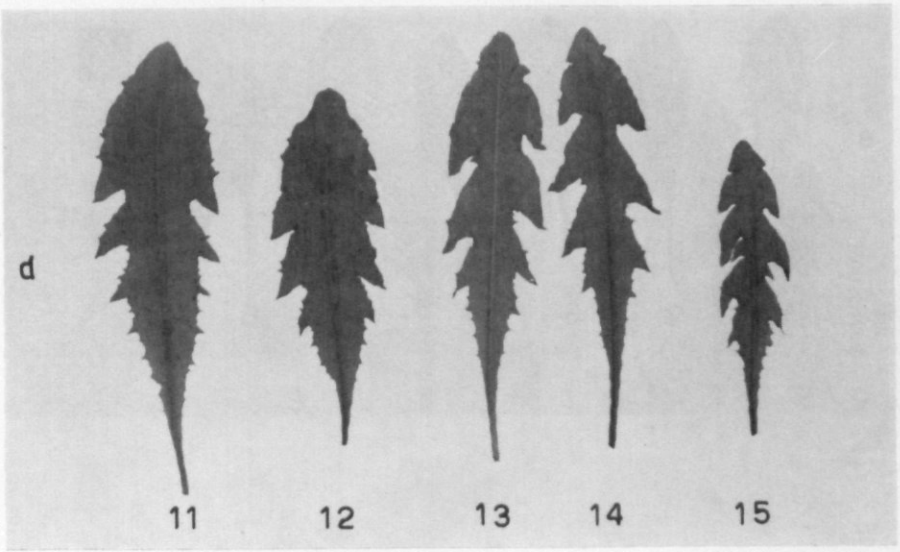


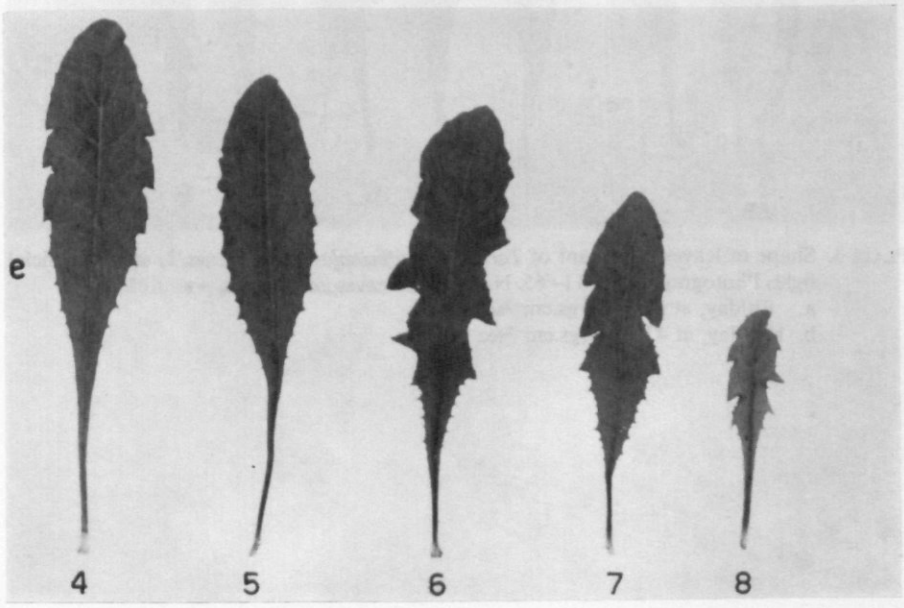
PLATE 2. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, grown under artifical light. Photographed 30–6–'65. Numbers at leaves (if given) indicate sequence at plant; higher number: younger leaf.

a. 16 h/day white fluorescent light, I = 87.000 ergs.cm^{-2}sec^{-1} (Q = 120 cal/day).

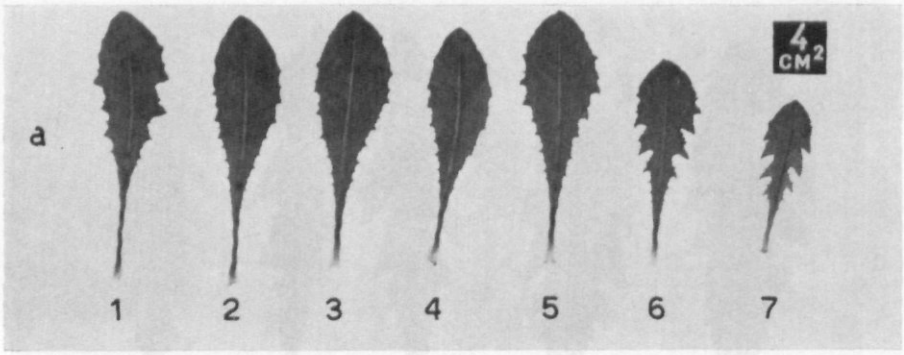
b. As a, but 10 h/day (Q = 75 cal/day).

c. As b, but I ∞50.000 ergs.cm^{-2}sec^{-1}. (Q = 42 cal/day).





d. As b, but I ∼25.000 ergs.cm^{-2}sec^{-1}. (Q = ∼20 cal/day).
e. As b, but I ∼12.000 ergs.cm^{-2}sec^{-1}. (Q = 10 cal/day).



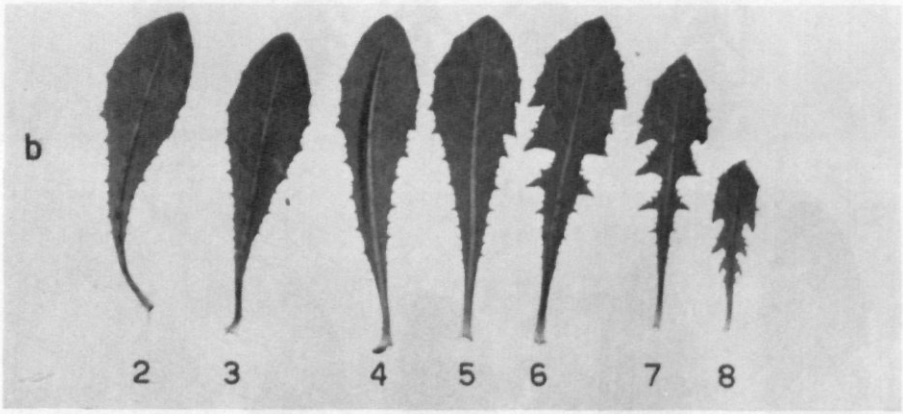
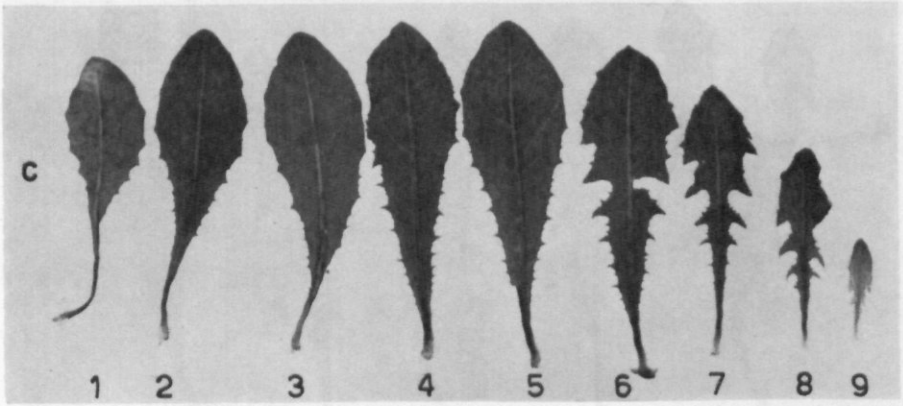
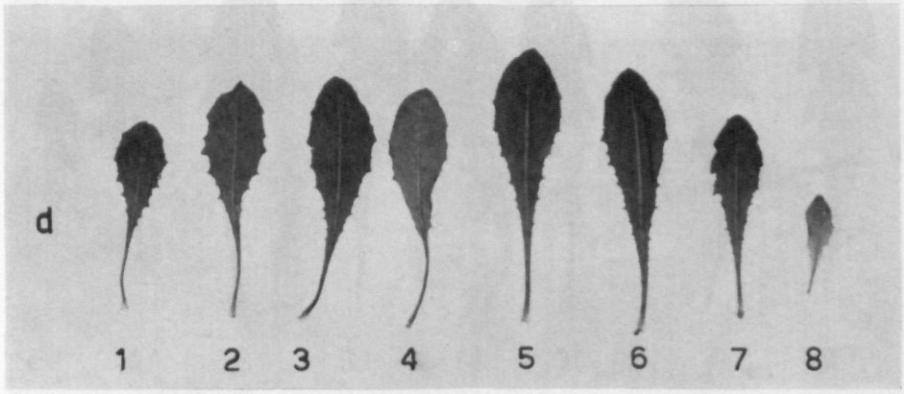


PLATE 3. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, under artificial light. Photographed 19–11–'65. Numbers at leaves, see plate 2.
a. 8 h/day, at 63.600 ergs.cm^{-2}sec^{-1}.
b. 12 h/day, at 42.500 ergs.cm^{-2}sec^{-1}.





c. 16h/day, at 31.200 ergs.cm^{-2}sec^{-1}.
d. 16h/day, at 15.000 ergs.cm^{-2}sec^{-1}.

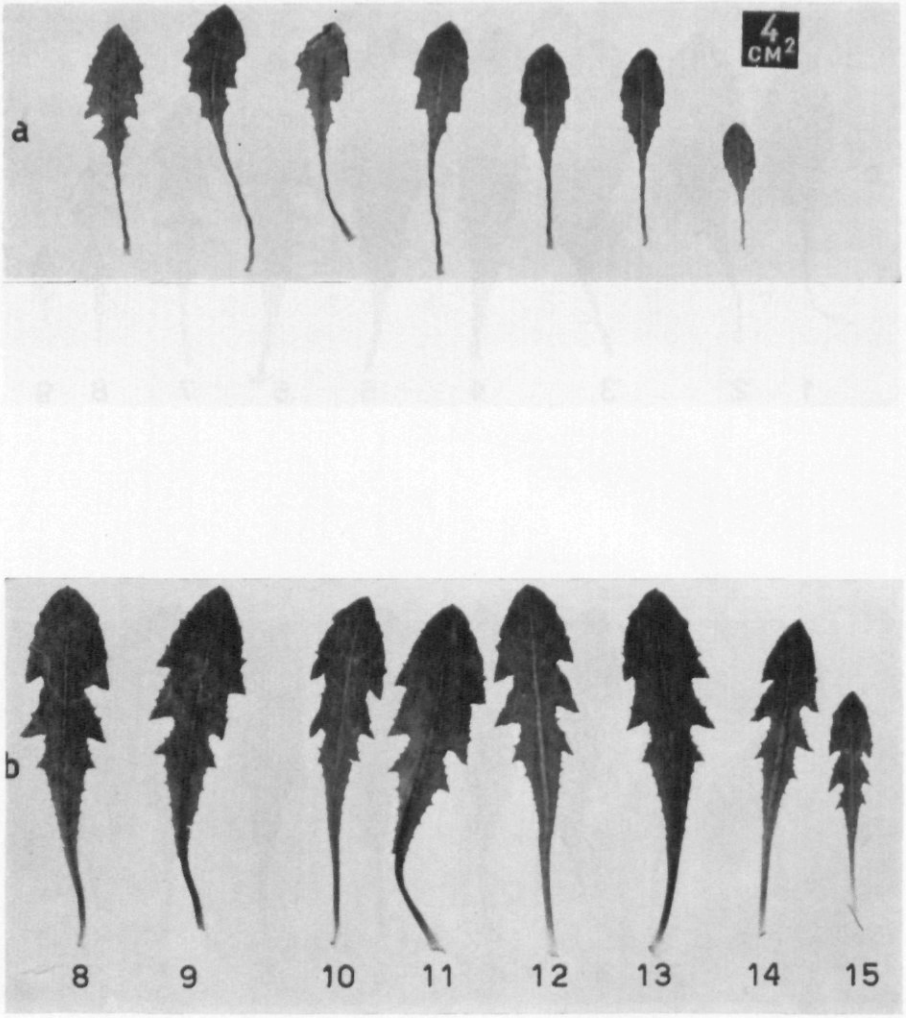
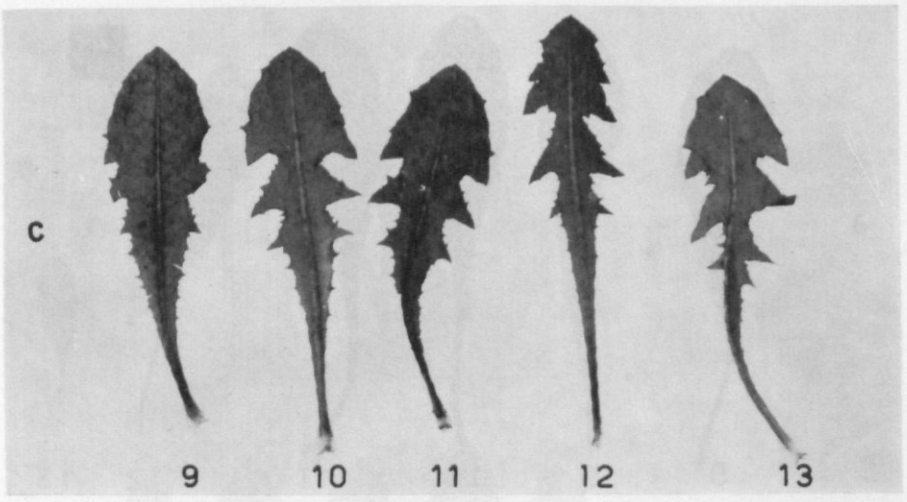
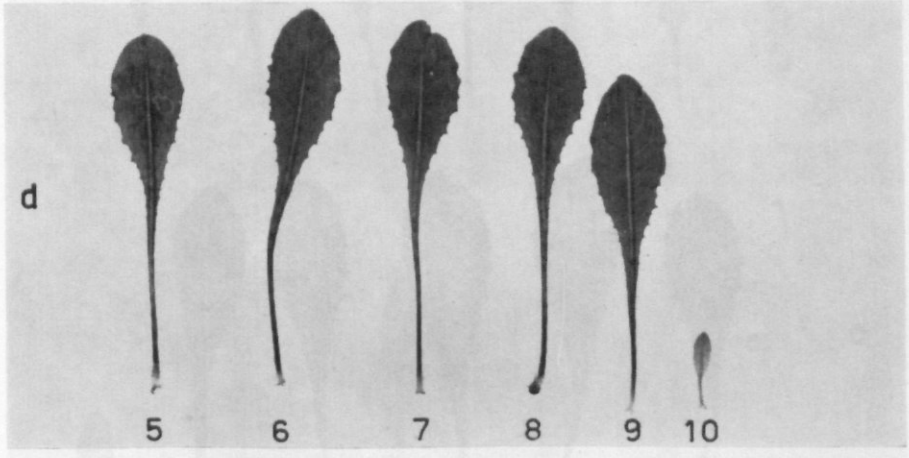


PLATE 4. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, as affected by supplementary illumination with coloured light. Photographed 17–11–'65. Numbers at leaves, see plate 2.

a. 6 h/day white fluorescent light at ∼50.000 ergs.cm^{-2}sec^{-1}.

b. As a + 8 h red light at 9.000 ergs. cm^{-2}sec^{-1}.





c. As a + 8 h blue light at 9.000 ergs.cm^{-2}sec^{-1}.
d. As a + 8 h far red light at 9.000 ergs.cm^{-2}sec^{-1}.

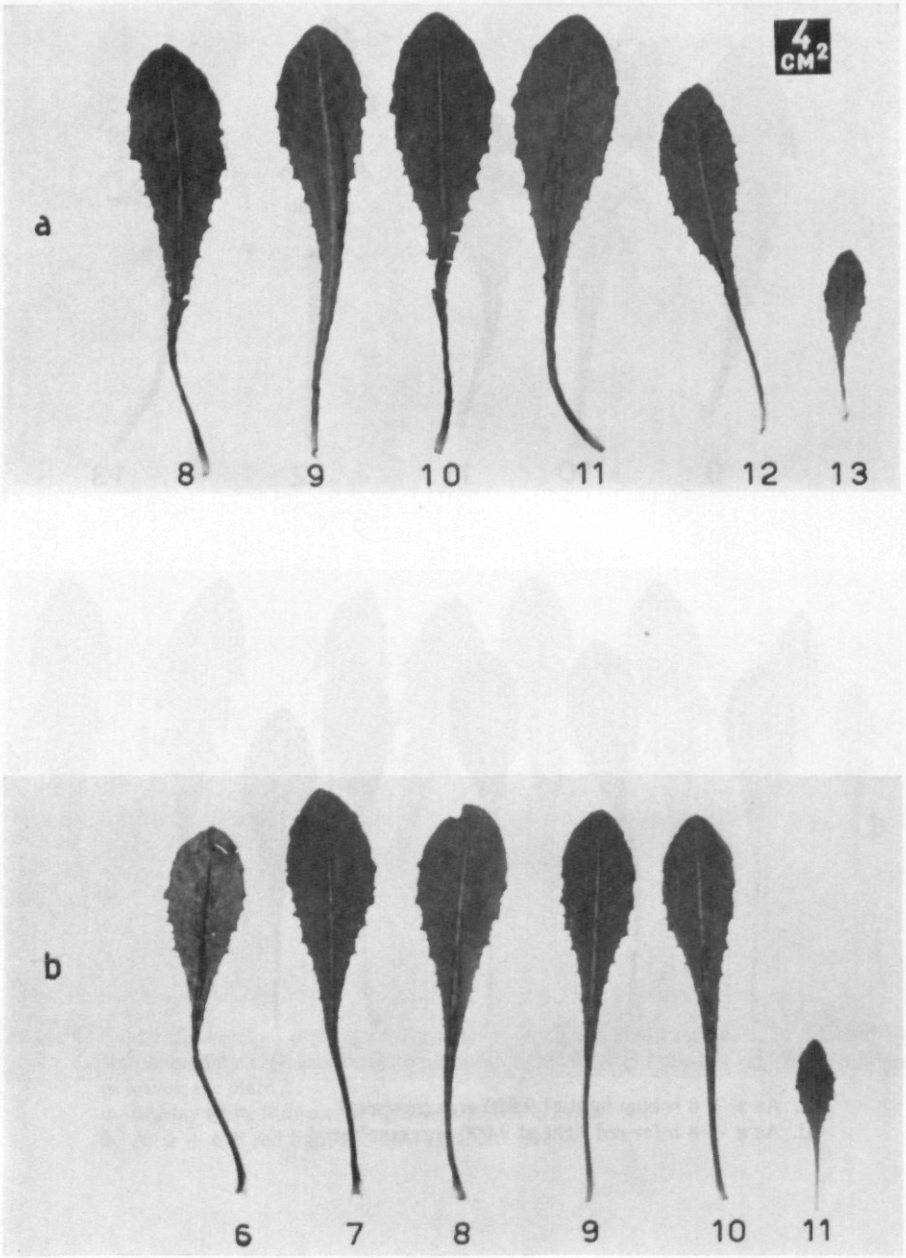
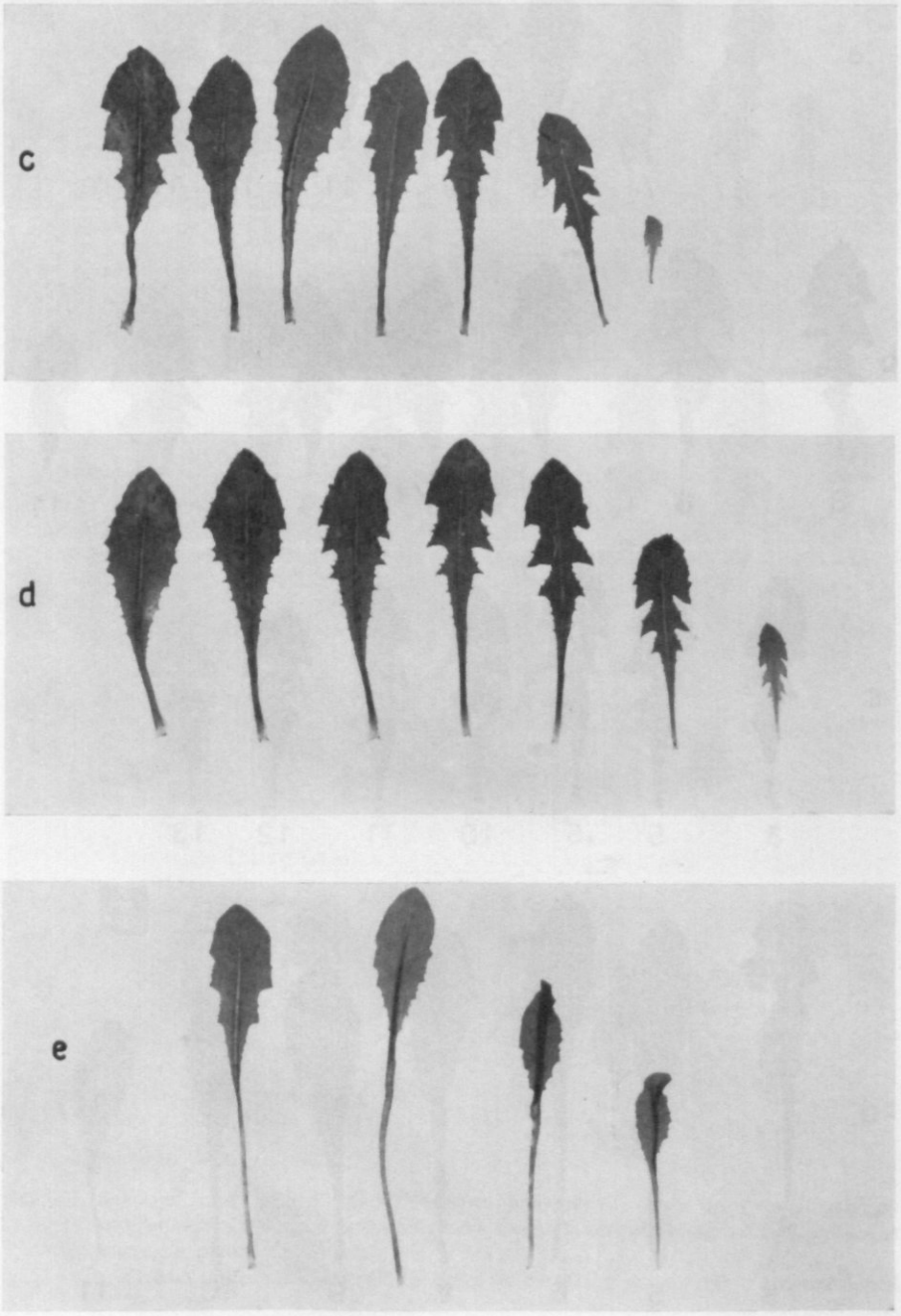


PLATE 5. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, as affected by supplementary coloured light under various conditions of illumination. Photographed 17–11–'65. Numbers at leaves, see plate 2.

a. 6 h/day white fluorescent light of ∿20.000 ergs.cm^{-2}sec^{-1} + 8 h (supplementary) red light at ∿9.000 ergs.cm^{-2}sec^{-1}.

b. As a, but with 8 h blue light, instead of red.



c. 6 h/day white fluorescent light at ∼50.000 ergs.cm^{-2}sec^{-1} + 8 h (supplementary) red light at ∼1.000 ergs.cm^{-2}sec^{-1}.
d. As c, but with 8 h blue light instead of red.
e. As c, but with 8 h far red light instead of red.

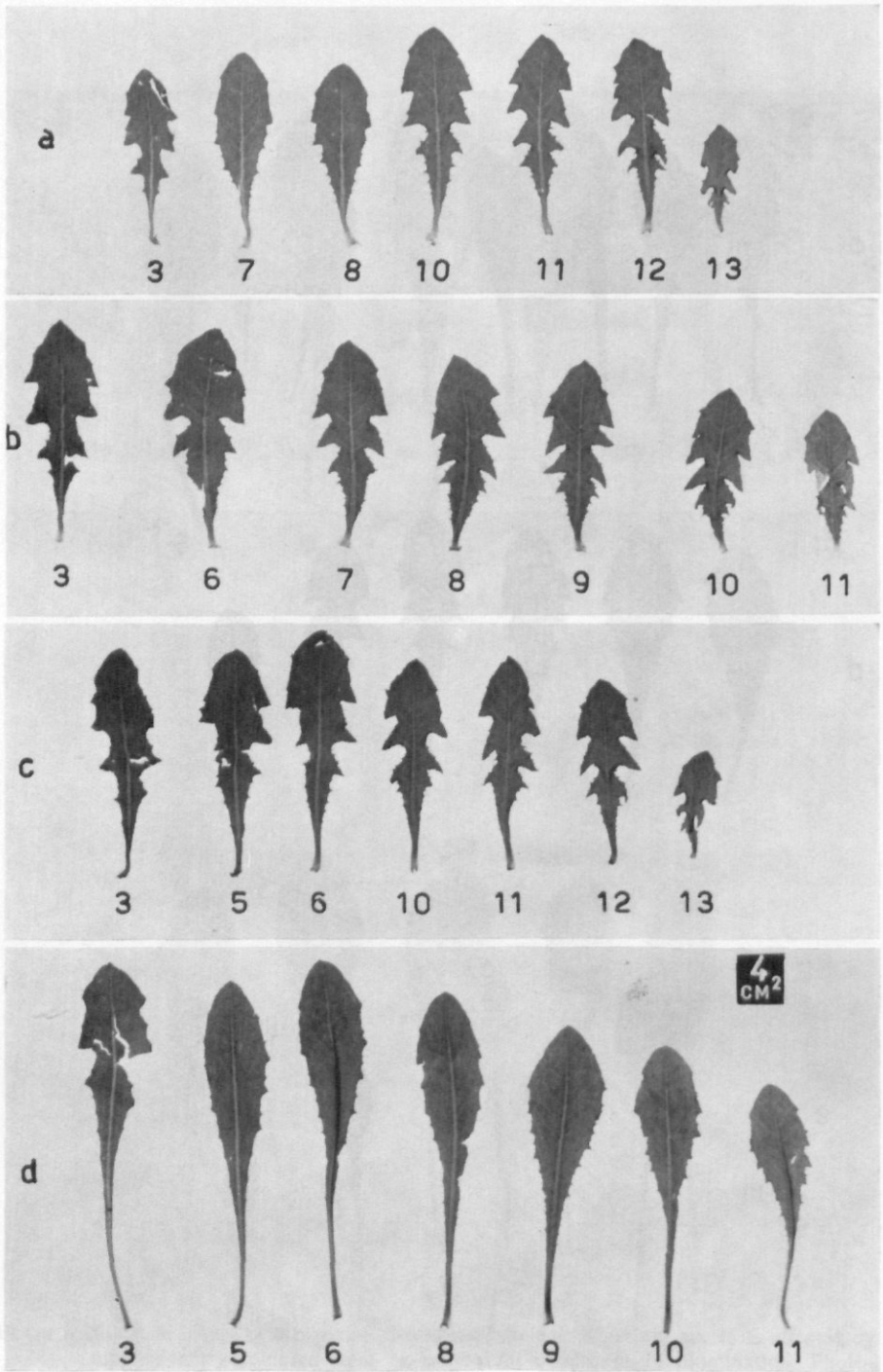


PLATE 6. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, as affected by supplementary coloured light under various conditions of illumination Numbers at leaves, see plate 2.

a. Grown under 6 h/day white light of 60.000 ergs.cm^{-2}sec^{-1}. Photographed 12–4–'66.

b. As a, but plus 8 hours of red light of ca 900 ergs.cm^{-2}sec^{-1}. Photographed 5–4–'66.

c. As a, but plus 8 hours of blue light of ca 900 ergs.cm^{-2}sec^{-1}. Photographed 12–4–'66.

d. As a, but plus 8 hours of far red light of ca 1.350 ergs.cm^{-2}sec^{-1}. Photographed 28–4–'66.

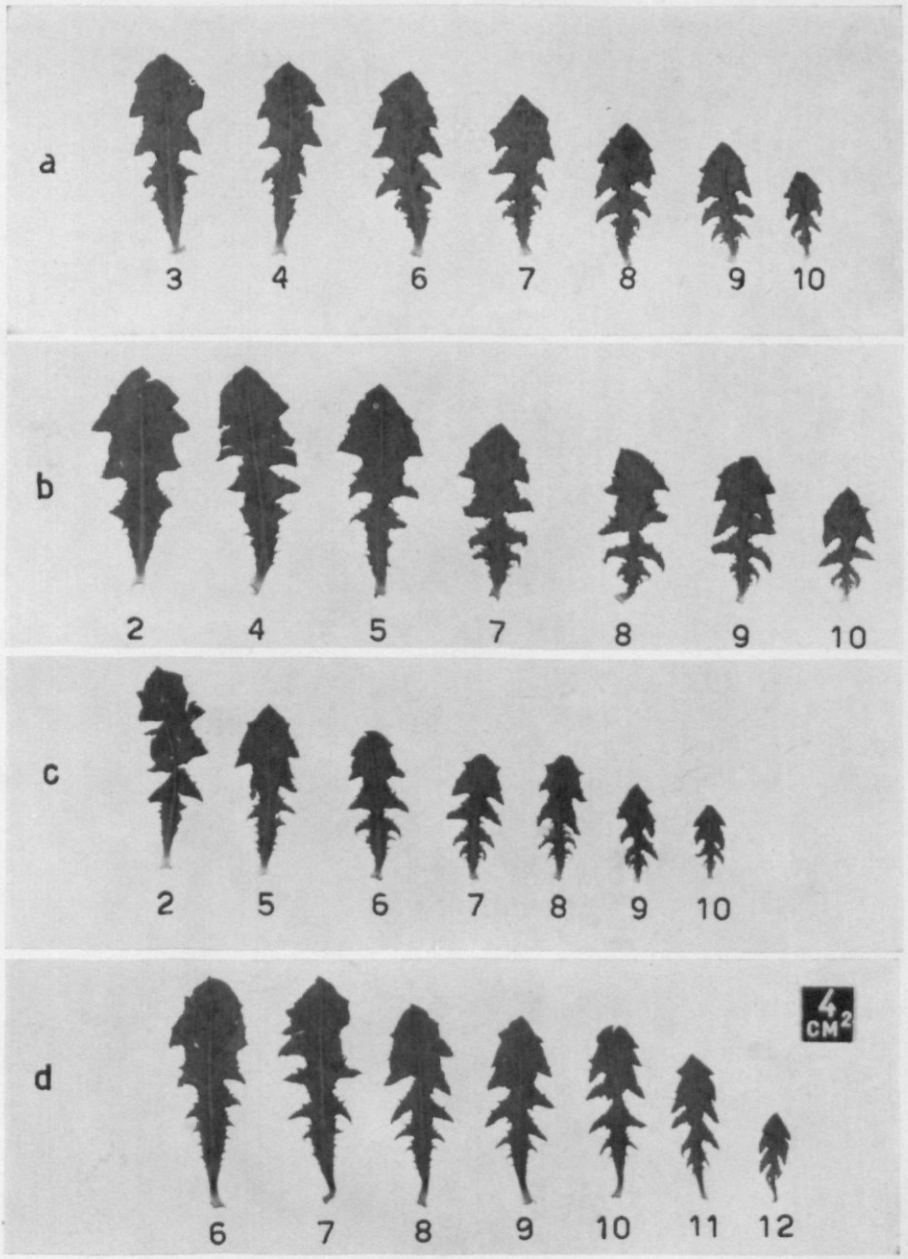


PLATE 7. Shape of leaves of a plant of *Taraxacum officinale* L., strain no. 1, as affected by supplementary coloured light under various conditions of illumination. Numbers at leaves, see plate 2.

a. Grown under 12h/day white light of 60.000 ergs.cm^{-2}sec^{-1}. Photographed 29–3–'66.

b. As a, but plus 8 hours of red light of ca 900 ergs.cm^{-2}sec^{-1}. Photographed 29–3–'66.

c. As a, but plus 8 hours of blue light of ca 900 ergs.cm^{-2}sec^{-1}. Photographed 29–3–'66.

d. As a, but plus 8 hours of far red light of ca 1.350 ergs. cm^{-2}sec^{-1}. Photographed 12–4–'66.