THIRD POSITIVE (C-TYPE)[1] PHOTOTROPISM IN THE AVENA COLEOPTILE

O. H. BLAAUW and G. BLAAUW-JANSEN

Botanisch Laboratorium, Utrecht

SUMMARY

The third (C-type)[1] response results from a tonic and a tropistic effect of the irradiation. The Bunsen-Roscoe reciprocity law applies to the tonic as well as to the tropistic component. A simple dependence on the duration of the stimulus does not exist, but is simulated by the time interval required for effectuation of the tonic component. It is concluded that the C-type curvature is identical with the first positive curvature, but is evoked by larger doses of unilateral light because of a desensibilisation of the coleoptiles by the tonic effect of the long unilateral irradiation itself. This desensibilisation process takes a minimum period of 4 resp. 15 minutes to be effective with red-preirradiated or dark-cultivated coleoptiles, respectively.

1. INTRODUCTION

The C-type response in the oat coleoptile is believed to be determined by the duration of induction rather than by the total energy of the light dose (THIMANN & CURRY 1960; ZIMMERMAN & BRIGGS 1963; PICKARD & THIMANN 1964; EVERETT & THIMANN 1968; PICKARD 1969: BLAAUW & BLAAUW-JANSEN 1970).

When studying the effect of red light on the geotropic and phototropic responses of the oat coleoptile one is confronted with the role of the time interval between red irradiation and the induction of geotropic or phototropic curvatures (BLAAUW 1961; BLAAUW & BLAAUW-JANSEN 1964; WILKINS 1965). This we combined with the statement of early authors (PRINGSHEIM 1909; ARISZ 1915; FILZER 1928, 1931) that the effect of blue light in phototropism would be the result of an interaction between a phototonic and a phototropic effect. BURKHOLDER (1941) moreover found that the amount of phototropic curvature is not altered appreciably by variations between 30° and 165° in the angle of incidence of strong unilateral light falling continuously on the plants during a period of eighty minutes.

Thus we supposed the induction period of the C-type curvature to be composed of three parts:

a In the first part irradiation has a tonic effect independent of the direction of the light stimulus.

[1] The curvature that – in accordance with Du Buy and Nuernbergk – is called third positive curvature is identical with the curvature that is termed second positive curvature or system III curvature in recent American papers. As this curvature is represented in ridge C of fig. 3 in our preceding paper it will be called C-type curvature in this paper.

b In the second part the tonic effect of the light stimulus is developed, in light as well as in darkness.
c In the third part irradiation has a tropic effect. The light is to be applied unilaterally and induces a phototropic curvature.

This hypothesis reduces the dependence of the extent of the curvature on the duration of the light stimulus to a dependence on the duration of the time interval between the tonic and the tropic stimulus. If so, the possibility arises that the Bunsen-Roscoe reciprocity law holds for the tonic as well as for the tropic effect of the light.

2. MATERIAL AND METHODS

Material and methods were described in our previous paper (BLAAUW & BLAAUW-JANSEN 1970). Light intensity was controlled by the use of neutral filters (NG, Schott u. Gen., Mainz).

3. RESULTS

3.1. Analysis of the C-type curvature in three components

A continuous unilateral irradiation of 10 minutes with blue light ($\lambda = 458$ nm $\log I = 1.17$) resulted in a C-type curvature of ca. 10°. *Table 1* shows the results of a progressive substitution of the horizontal light by light from above. This substitution does not diminish the curvature. Yet by a horizontal irradiation during 2 or 5 minutes, not preceded by a vertical one, negative curvatures were obtained. In the next experiments part of the period of the vertical irradiation was substituted by a dark period. The resulting curvatures are represented in *table 2.* Insertion of a dark interval and shortening of the duration of the vertical irradiation do not diminish the effect of the vertical irradiation.

Next the effect of extension of the dark interval between a fixed vertical and a fixed horizontal irradiation was investigated. *Table 3* shows that the effect of the vertical irradiation is developed within a dark period of 5 minutes and diminishes after 20 minutes.

Table 1. Effect of a vertical illumination, followed by a horizontal one in phototropism. $\log I = 1.17$. $\lambda = 458$ nm.

Minutes vertical	Minutes horizontal	Curvature in degrees		
		expt. I	expt. II	expt. III
–	10	9.8	–	11.0
2	8	–	–	12.6
5	5	14.0	10.6	15.7
8	2	12.0	11.9	–
9	1	13.9	14.3	–
–	2	–	–2.0	–
–	5	–	–0.1	–

Table 2. Partial substitution of the vertical irradiation by a dark period. Log I = 1.17. λ = 458 nm.

Minutes vertical	Minutes dark	Minutes horizontal	Curvature in degrees		Minutes horizontal	Curvature in degrees	
–	–	10	8.4	9.3	10	10.9	8.9
–	–	1	0.5	0.5	2	3.0	-3.0
9	0	1	14.4	16.3	2	–	–
4	5	1	15.7	18.5	2	17.8	14.8
2	7	1	18.3	18.4	2	12.6	13.8
1	8	1	13.6	13.3	2	9.2	8.2
½	8½	1	8.9	9.1	2	3.3	–
¼	8¾	1	3.8	3.8	2	–	–

Table 3. Effect of extension of the dark interval between fixed irradiations. Log I = 1.17. λ = 458 nm.

Minutes vertical	Minutes dark	Minutes horizontal	Curvature in degrees	
			expt. I	expt. II
1	0	1	4.9	4.5
1	2	1	10.5	10.1
1	5	1	19.0	15.3
1	10	1	19.6	15.5
1	20	1	17.3	15.9
1	40	1	13.2	14.9

Finally we extended the unilateral stimulation of 1 minute from *table 3* to a series of unilateral light doses, fixing the vertical irradiation at a dose of 3×10^3 erg/cm^2 and the interval on 20 minutes. A control series was not irradiated from above. A duplicate of the dose-response curve of the first positive curvature emerged (*fig. 1*), a shift to higher doses of unilateral blue light being the

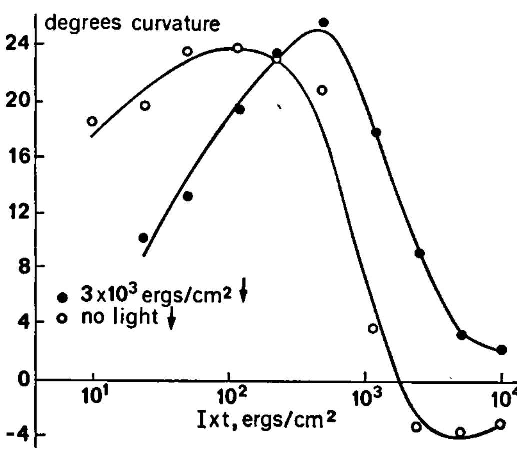


Fig. 1. Shift of the dose-response curve for first positive curvature to higher energies by a pre-irradiation with blue light, administered from above.

only difference (see also MEYER 1969). The height of the maximum remained the same (see discussion). Apparently the vertical pre-irradiation desensibilizes the first phototropic system of the coleoptiles. Thus the curvature resulting from a vertical irradiation, a dark interval, and a unilateral illumination is on the one hand identical with the C-type curvature, on the other hand with a desensibilized first positive curvature.

3.2. The validity of the Bunsen-Roscoe reciprocity law for the C-type curvature

In the above experiments we analyzed the unilateral light stimulus yielding a C-type curvature into a tonic and a tropic stimulus. Next the validity of the reciprocity law for each of these components was investigated. The dose-response curves at two light intensities ($\lambda = 458$ nm) differing by a factor 12 were determined for both components.

First the effect of vertical light doses between 150 and 9×10^3 ergs/cm^2 at two intensities was tested, followed after a dark interval by a horizontal light dose (I = 70 ergs/cm^2 sec during 30 sec). This unilateral exposure on itself evoked slightly negative curvatures. The total duration of the treatment was 20 minutes. *Fig. 2* illustrates that the response to the tonic stimulus given from above indeed depends on the light dose irrespective of duration or intensity of the irradiation.

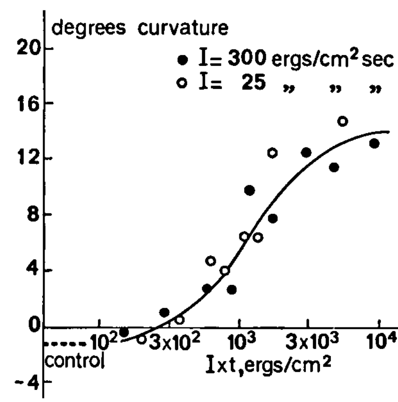


Fig. 2. Dose-response curve for the effect of light, administered from above at two light intensities, followed by a fixed unilateral irradiation.

In the experiments of *fig. 3* a vertical pre-irradiation of 2×10^4 ergs/cm^2 was given followed by a horizontal stimulus ranging between 30 and 4×10^4 ergs/cm^2 at intensities of 10^4 and $1/12 \times 10^4$ ergs/cm^2 sec, Between the vertical and the unilateral irradiation a dark interval was interposed of such a duration that the total treatment length was 20 minutes. The curves for the two intensities coincide, so the effect of the horizontal component, too, depends on the stimulus dose.

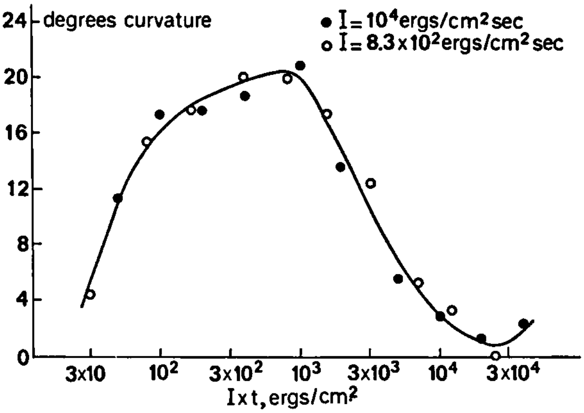
3.3. Interaction of vertical and horizontal stimulus

In *table 4* the effects of various doses of vertical irradiation if combined with various doses of horizontal light are summarized. The total duration of treat-

Table 4. Curvatures resulting from the combination of various doses of horizontal and vertical light.

Horizontal irradiation in ergs/cm²	Vertical irradiation in ergs/cm²											Total duration of treatment in minutes
	–	500	800	1100	1800	2000	3500	5000	9000	20.000	40.000	
900 (t = 1′)	7.0	12.3	13.7	–	15.5	–	–	15.4	–	–	–	20
1800 (t = 2′)	0.3	5.0	4.5	–	7.2	–	–	15.0	–	–	–	20
2100 (t = 30″)	1.2	–	–	–	–	12.8	–	13.4	16.5	15–4	–	20
	0.9	**1.6**	**7.8**	**12.5**	–	**17.0**	–	**16.3**	**15.6**	–	–	**11**
8400 (t = 2′)	–4.3	–	–	–	–	2.4	–	5.4	7.0	9.2	–	20
	–4.3	–	–	–	–	**1.9**	**8.0**	**9.5**	**12.1**	**13.4**	**12.0**	**11**
18000 (t = 20′)	17.0											
46200 (t = 11′)	**12.1**											
84000 (t = 20′)	14.7											

Fig. 3. Dose-response curve for the effect of unilateral light, administered at two light intensities, and preceded by a fixed dose of light from above.



ment was 10 or 20 minutes. The amount of vertical light required for saturating the tonic effect depends on the horizontal light dose. Curvature is larger as the dose of the vertical irradiation increases, the unilateral dose decreases, and the interval is shorter.

When the vertical light dose increases above the saturating amount, either by increasing the intensity or by increasing its duration, its effect is diminished (*table 5*).

Table 5. The effect of increasing the vertical light dose above the saturating quantity. Total duration of treatment 10 minutes.

Horizontal irradiation	Vertical irradiation in minutes						
	I = 70 ergs/cm² sec					I = 300 ergs/cm² sec	
	2′	4′	6′	8′	10′	8′	10′
I = 70 ergs/cm² sec t = 30″	14.6	13.9	15.4	15.4	7.6	7.0	2.6
I = 70 ergs/cm² sec	8.3	12.7	15.1	14.1	16.3	16.7	12.2

Controls: (unilaterally irradiated I = 70 ergs/cm² sec
30″ −3.0; −3.9
2′ −3.0; −5.5
10′ 8.3

Moreover it appeared that the optimal light dose for the tonic stimulation depends not only on the amount of horizontal light energy (*table 4*), but also on the duration of the length of the dark interval between both stimuli (*tables 5* and *6*). The optimum energy for the tonic stimulus shifts to higher quantities with longer intervals and with larger amounts of horizontal light.

These phenomena can be understood as consequences of the following hypothesis:

1. The shift of the dose-response curve to higher phototropic light doses in response to a vertical pre-irradiation is larger with larger amounts of vertical energy.

Table 6. Interaction between vertical light energy, horizontal light energy and duration of the interval between both stimuli, I vertical = 300 ergs/cm² sec λ = 458 nm

Interval in minutes	curvature in degrees: I horizontal = 70 ergs/cm² sec t = 30″				curvature in degrees: I horizontal = 260 ergs/cm² sec t = 20″				
	Duration of vertical stimulus								
	2″	4″	8″	16″	–	1′	2′	5′	10′
0	–	–	–	–	–3.3	1.3	–	–	–
1	1.8	1.3	1.8	1.5		–	–	–	–
2	3.3	5.3	3.3	2.5		–	–	–	–
5	9.1	14.8	16.3	13.8		10.8	8.9	3.0	–
10	10.7	13.7	15.9	12.9		11.1	10.5	14.0	4.0
20	3.9	5.6	9.6	11.8		4.9	7.3	8.3	12.1
40	–	–	–	–		1.8	1.8	2.7	4.1

2. Ca 10 minutes after termination of the vertical irradiation the sensitivity for positive curvatures increases again. The dose-response curve moves back to its former position on the abscissa.

In the schematic *fig. 4* the consequences of a small and a large dose of vertical light for the effect of 2 doses of unilateral phototropic light are indicated. The dose-response curve a is shifted to b and c, respectively. The response to a fixed dose of unilateral light (x) increases as the dose-response curve moves to the right (b), but when the maximum of the curve has passed this fixed point with increasing doses of vertical light, the response decreases again (c). For a higher dose of phototropic energy (y) this occurs when the dose-response curve has moved further to the right, that is to say, with a larger dose of vertical light.

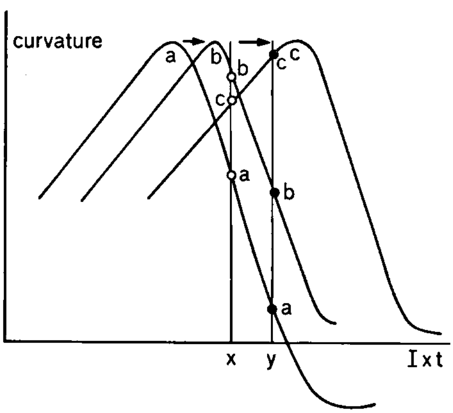


Fig. 4. Schematic figure illustrating the consequences of a shift of the dose-response curve from a to b or c for the effect of two doses x and y of unilateral light.

4. DISCUSSION

From the above experiments it is concluded that the C-type curvature is identical with the first, but is evoked by larger doses of unilateral light because of a desensibilisation of the coleoptiles by the long irradiation itself. As a minimum stimulus duration of 4 minutes is required for initiating C-type curvatures (BLAAUW & BLAAUW-JANSEN 1970), this desensibilisation process would take some 4 minutes to be effectuated.

Several early and recent authors might be cited in support of these conclusions. Some of them were occupied with the study of the auxin distribution in phototropically stimulated plants or with the differences in appearance, in zones of perception and in zones of maximum sensitivity between the two positive responses, others studied the effect of an all-sided pre-illumination on a subsequent phototropic response or the phenomena of the summation of stimuli.

For a long time the first positive curvature was considered to be a tip respons, the C-type curvature to be a base response. This notion was based on the difference in localisation of these responses and on the observation that the apical region is much more sensitive to light than the other regions of the coleoptile. In our opinion the supposed difference in localisation can be ascribed to uncontrolled effects of red light. Pre-irradiation with red light indeed shifts the phototropic curvature to the tip of the coleoptile (*fig. 5*). The same applies to the effect of red light on the geotropic curvature (BLAAUW 1963, HUISINGA 1965). In the experiments of this paper, in which the red-light regimen was strictly standardized, no difference in localisation occurred (*fig. 5*).

For the first positive curvature it was proved that the tip of the coleoptile is much more sensitive for stimuli evoking this response than lower zones. The same applies to stimuli leading to a C-type curvature (EVERETT & THIMANN 1968, PICKARD 1969).

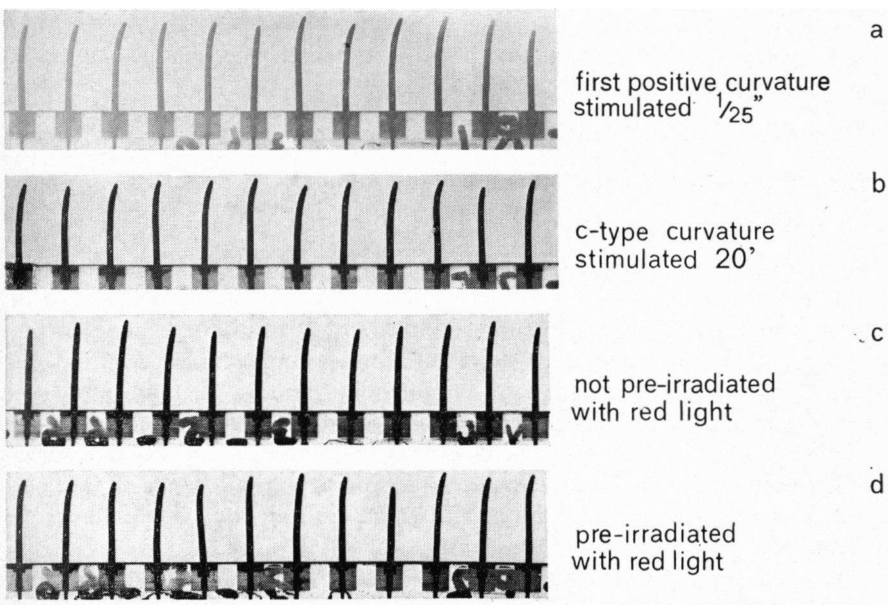


Fig. 5. Pre-irradiation with red light shifts the phototropic curvature to an apical zone. The localisation of the curvature does not differ for first and C-type curvature.

BRIGGS (1963) and PICKARD & THIMANN (1964) demonstrated that lateral transport of auxin occurs during both types of response, in the tip as well as in isolated basal sections, be it that the lower zones require much more light energy to induce the lateral transport. So from experiments of this kind no argument for the existence of a qualitative difference between the positive responses can be derived.

In germ our hypothesis on the nature of the second positive curvature can be found in the papers of PRINGSHEIM (1909). In his opinion during continuous irradiation a raising of the tonic disposition of the coleoptiles occurs from the very onset of illumination. Taking the length of presentation times as a measure of the tonus of the plants, he concluded that during the first 5 minutes of an all-sided pre-irradiation the tonus is raised dramatically but between 5 and 20 minutes hardly any further lenghtening of the presentation time could be observed. Thus a coleoptile would respond to a stimulus of long duration, in itself strong enough to cause negative curvatures, with a positive curvature because of the raising of its tonus during the irradiation.

ARISZ (1915) continued the experiments on the phototropic responses of pre-irradiated coleoptiles. Like PRINGSHEIM he considered the first and the C-type curvature as qualitatively identical. In his opinion the negative response would be superposed on the positive response. He reported that an all-sided pre-irradiation has four different effects on the response of coleoptiles to a subsequent unilateral irradiation:

A pre-irradiation shorter than 5 minutes and immediately followed up by the phototropic stimulus

1. lowers the sensitivity for the first positive response (more energy is required to induce a definite curvature).
2. enhances the occurrence of negative curvatures at stimuli of low energy.

A pre-irradiation of longer duration than 5 minutes

3. prevents negative curvatures.
4. induces the development of large positive curvatures at stimuli of the negative region.

ARISZ combined the latter phenomenon with the results of experiments in which an all-sided irradiation of short duration was immediately or after some interval followed up by a unilateral phototropic stimulus. With an interval of about 5 minutes the usual negative curvatures were replaced by a large positive response (cf. POHL 1960). He concluded that the prevention of negative curvatures in both cases was the consequence of a process which depends on the energy dose of the all-sided irradiation, but which requires some 5 minutes to be effectuated.

The experiments of MEYER (1969) show the effects 1, 3 and 4 of ARISZ. Presumably the effects 3 and 4 are caused by a displacement of the dose-response curve for first positive curvatures to higher energies. MEYER (1969), too, suggested a simple shift of the dose-response curve to be the cause of the lack of a negative response after a stimulus of the negative region with coleoptiles that were pre-irradiated from above. Indeed a shift of the curve was induced in experiments in which she pre-irradiated the coleoptiles from above, but an accompanying enhancement of the maximum of the curve made her reject her suggestion. This enhancement, however, was likely to be due to the influence of red light transmitted by her blue Schott filter, as with a strict regimen of red irradiation no enhancement was induced by our very pure blue vertical light (*fig. 1*). Meyer's own experiments indicate the capacity of her coleoptiles to react to red light. Her table 1 shows a clear-cut influence of red light on the extent of (in that case) negative curvatures (–14.2° for the dark controls, –6.7° for the red-irradiated coleoptiles).

An other objection to the hypothesis of the dose-response curve being simply shifted to larger energy doses might be the absence of negative curvatures in the shifted curve (*fig. 1* and *3*). The incapacity of pre-irradiated coleoptiles to develop negative curvatures might be compared with the missing of negative curvatures in decapitated coleoptiles. Decapitation, too, diminishes the sensitivity to phototropic stimuli (POHL 1960). It must be kept in mind that the negative response is a dose-dependend response, with the restriction that the required energy is to be administered within 3–5 minutes (ARISZ 1915, BLAAUW & BLAAUW-JANSEN 1970). If the negative region of the dose-response curve is shifted to ca 4-fold light doses the light intensities at which negative curvatures can be expected become restricted to a range between 50 and 100 ergs/cm^2 sec. At lower light intensities not enough energy is added up in the limited period of 3–5 minutes, at higher light intensities the positive curvatures of Ridge B (BLAAUW & BLAAUW-JANSEN 1970, *fig. 3*) occupy the region where the shifted negative curvatures would be expected. Here the assumption is made that the high-intensity curvatures B are not shifted by the vertical pre-irradiation.

In Arisz' experiments the influence of a short all-sided pre-irradiation had subsided between 30 and 60 minutes. This "Abklingen" set in already within 2 minutes after the pre-irradiation ended. If the pre-irradiation was continued till the phototropic stimulus was given, the subsiding did not occur. BRIGGS (1960) mentioned a comparable delay of 20 minutes between exposures as necessary for a complete recovery from the first exposure for *Zea* coleoptiles. From our *table 6*, too, emerges the disappearance of the effect of the vertical irradiation after 20 minutes. The statement of MEYER (1969) that the regeneration of the positive reaction (after a vertical pre-irradiation) is completed before the regeneration of the negative reaction (20 minutes for the first, 60 minutes for the last) affirms the report of ARISZ (1915). He found that the capacity for positive curvature had returned after 30 minutes, the capacity for negative curvature, however, had not yet fully returned after an hour.

Also from experiments in the field of the summation of stimuli emerges a crucial time interval of 4 minutes. BOTTELIER (1934) studied the effect of two successive irradiations on the velocity of the protoplasmic flow. It appeared that two light doses given within an interval of 3 minutes worked as one double dose. If the interval between the irradiations was prolonged beyond 4 minutes, a separate reaction to each stimulus followed. The first irradiation did no longer influence the effect of the second one with a minimum interval of 10 minutes. Thus the effect of an irradiation on the protoplasmic flow has died away after 10–15 minutes, but the effect on the phototropic curvature persists for a considerably longer time.

From the experiments of ARISZ (1915) can be concluded that the light dose required for inducing negative curvatures is to be given within a period of 3–5 minutes. BOTTELIER (1934) derived from these and from his own experiments the conclusion that only stimuli given within 3–5 minutes are completely added up. Similar results were obtained in unpublished experiments by A. van Dongen and J. Lion in this laboratory. They stimulated coleoptiles unilaterally with two light doses of the first positive region. When the first stimulus was followed immediately by the second, negative curvatures were developed. When, however, the stimuli were more than 4 minutes apart positive curvatures were produced with red-cultivated coleoptiles. For dark-cultivated coleoptiles the period during which the two light doses were added up to one double dose appeared to be 15 minutes.

In our conception these phenomena have to be considered not as the consequence of a limitation of the period during which the coleoptiles can summarize a series of stimuli but as the consequence of a process which is induced at the onset of the irradiation, influences the tonic disposition of the coleoptiles, and is effectuated within 3–5 minutes for red-cultivated coleoptiles, within 15 minutes for dark-cultivated coleoptiles.

This observation is in accordance with our observation (BLAAUW & BLAAUW-JANSEN 1970) that for the development of the C-type curvature dark-cultivated plants require a minimum stimulus duration of 15 minutes, red-pre-irradiated plants of 4 minutes.

According to RAYLE *et al.* (1970) the lag in the response of corn and oat coleoptile segments, when moved from low to high IAA concentrations, is shortened from 10–15 minutes to 2 minutes when the step-up in the auxin level is diminished. This shortening of the lag-time might be connected with the difference in lag between dark and red-preirradiated coleoptiles in the C-type phototropic response.

Lastly there must be mentioned the report of PICKARD (1969) who observed the occurrence of a lag-time with the development of the C-type curvature. She estimated a lag of 3.3 minutes to occur between the onset of illumination and the beginning of curvature. In our previous paper (BLAAUW & BLAAUW-JANSEN 1970) we demonstrated that from Pickard's graphs giving the extent of C-type curvature versus stimulus duration a minimum stimulus duration of 210 seconds emerges. Apparently curvature begins to develop as soon as the minimum stimulus duration is reached.

There remain to be discussed the relatively large curvatures resulting from a combined vertical and horizontal irradiation (*tables 1* and *2*). Apparently the *C-type* curvature results from

1. a light dose P influencing the tonic condition.
2. a time interval T in which P is taking effect.
3. a light dose Q effectuating the actual curvature.

With a continuous unilateral irradiation P and Q are identical. This means that the situation is not optimal for curvature because

a. for development of a maximum curvature P has to be larger than Q (*table 4*).
b. Q is applied during the period in which P has to be effectuated.

As a consequence larger curvatures than those obtained by continuous lateral irradiation are developed if P is applied from above and is followed by a smaller unilateral light dose (*table 1*). Insertion of a dark interval between P and Q is necessary when P and Q are given in short exposure times (*tables 3* and *6*). With longer exposure times the effect of P can be developed during exposure (*table 1*).

ACKNOWLEDGEMENT

We thank Miss G. S. C. Keyzer for cheerfully lent technical assistance.

REFERENCES

Arisz, W. H. (1915): Untersuchungen über den Phototropismus. *Rec. Trav. Botan. Neerl.* **12**: 44–216.

Blaauw, O. H. (1961): The influence of blue, red and far red light on geotropism and growth of the Avena seedling. *Acta Bot. Neerl.* **10**: 397–450.

— (1963): Effects of red light on geotropism of Avena. *Acta Bot. Neerl.* **12**: 424–432.

— & G. Blaauw-Jansen (1964): The influence of red light on the phototropism of Avena coleoptiles. *Acta Bot. Neerl.* **13**: 541–552.

— & — (1970): The phototropic responses of Avena coleoptiles. *Acta Bot. Neerl.* **19**: 755–763.

Bottelier, H. P. (1934): Ueber den Einflusz äusserer Faktoren auf die Protoplasma strömung in der Avena-Koleoptile. *Rec. Trav. Botan. Néerl.* **31**: 474–582.

Briggs, W. R. (1960): Light dosage and the phototropic responses of corn and oat coleoptiles. *Plant Physiol.* **35**: 951–962.

— (1963): Mediation of phototropic responses of corn coleoptiles by lateral transport of auxin. *Plant Physiol.* **38**: 237–247.

Burkholder, P. R. (1941): Some experiments with growth curvatures and growth substances. *Am. J. Bot.* **28**: 911–920.

Everett, M & K. V. Thimann (1968): Second positive phototropism in the Avena coleoptile. *Plant Physiol.* **43**: 1786–1792.

Filzer, P. (1928): Untersuchungen über Wachstumsreaktion und Krümmung bei achsenparalleler Lichtrichtung. *Jb. Wiss. Bot.* **70**: 435–492.

— (1931): Weitere phototropische Untersuchungen. *Planta (Berlin)* **12**: 362–398.

Huisinga, B. (1965): Influence of light on growth, geotropism and guttation of Avena seedlings grown in total darkness. *Acta Bot. Neerl.* **13**: 445–487.

Meyer, A. M. (1969): Versuche zur Trennung von 1. positiver und negativer Krümmung der Avenakoleoptile. *Z. Pflanzenphysiol.* **60**: 135–146.

Pickard, B. G. (1969): Second positive phototropic response patterns of the oat coleoptile. *Planta (Berlin)* **88**: 1–33.

— & K. V. Thimann (1964): Transport and distribution of auxin during tropistic response. II. The lateral migration of auxin in phototropism of coleoptiles. *Plant Physiol.* **39**: 341–350.

Pohl, R. (1960): Beiträge zum Phototropismus der Avena-Koleoptile I. *Phyton* **15**, 145–156.

Pringsheim, E. (1909): Studien zur heliotropischen Stimmung und Präsentationszeit. *Cohn's Beitr. Biol. Pflanzen* **9**: 415–478.

RAYLE, D. L., M. L. EVANS & R. HERTEL (1970): Action of auxin on cell elongation. *Proc. Nat. Ac. Sci.* **65**: 184–191.
THIMANN, K. V. & G. M. CURRY (1960): Phototropism and phototaxis. In: M. FLORKIN & H. MASON, (ed.) *Comparative biochemistry* 1: 243–309. New York. Academic Press.
WILKINS, M. B. (1965): Red light and the geotropic response of the Avena coleoptile. *Plant Physiol.* **40**: 24–34.
ZIMMERMAN, B. K. & W. R. BRIGGS (1963): Phototropic dosage-response curves for oat coleoptiles. *Plant Physiol.* **38**: 248–253.