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Observations on the development of plants

XVII. Effect of varying photoperiodic conditions on the development of several species of *Chenopodium*

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Abstract:

The influence of light intensity and daylength on four short-day species of *Chenopodium* was analysed. The following species were tested: *Ch. ficifolium, Ch. glaucum, Ch. rubrum* and *Ch. hybridum.*

Under short day, generative initiation was accelerated, the abundance of flowering, and growth and leaf differentiation processes were reduced. Under light of low intensity, the rhythm of development of the plants growing under long day is similar to that under short day.

The development of axillary buds indicates a decrease in the intensity of vegetative differentiation and elongation growth, with an enhancement of the generative tonus; the buds in the axils of the highest growing leaves form directly inflorescences without preceding leaf differentiation. Inversion of the shape of leaves on lateral shoots was noted.

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Various species of the genus *Chenopodium* have been repeatedly investigated from the point of view of their photoperiodic reactions. According to Mathon (personal communication) most of the species studied are characterized by a short-day reaction. This type of reaction has been described in the following species:

Ch. ambrozioides (Moscovec 1943). *Ch. foetidum* (Chouard 1950). *Ch. glaucum* (Chouard 1950, Cummings 1959), *Ch. opulifolium* (Chouard 1950), *Ch. polispermum* (Chouard 1950, Jacques 1957), *Ch. rubrum* (Cummings 1959), *Ch. vulvaria* (Mathon 1960). *Ch. album* was described by Cummings (1959), Chouard (1950) and Mathon (1961) as a short-day plant, and by Petru, Horawka and Krekule (1961) as a plant with a weak reaction to long day. Mathon considers *Ch. murale* as

a photoperiodically neutral plant According to Chouard (1950) and Jacques (1957), *Ch. bonus Henricus, Ch. capitatum* and *Ch. botrys* exhibit a long-day reaction.

From among the species enumerated *Ch. album, Ch. glaucum, Ch. polyspermum, Ch. rubrum, Ch. bonus Henricus, Ch. opulifolium, Ch. vulvaria* and *Ch. murale* belong in this country to the ruderal flora, and with the exception of the last three species they are common plants. The remaining three *Ch. ambrozioides, Ch. foetidum* and *Ch. botrys* are considered as ruderal plants (Szafer 1924). *Ch. hybridum, Ch. urbicum, Ch. ficifolium* and the rare *Ch. foliosum* found in Poland have not been studied as regards their photoperiodic reaction.

The genus *Chenopodium* has been the object of an interesting wide-scope ecophysiological analysis by Cummings-Bruce (1961). This author collected 35 *Chenopodium* species growing in America and found in them mostly a short-day type of reaction of varying intensity in dependence on their provenience. A number of these species are cosmopolites with a very wide area. The biotypes of *Ch. rubrum* investigated by this author were collected from an area reaching from Alaska to California. The development of the plants was observed at various daylengths and light intensities.

The optimal thermal and photoperiodic conditions for flowering varied with the geographical situation: at higher, temperatures (20°) flowering initiation occurs in the north within the daylength range of 6—24 hrs., in the south, on the other hand, within 6—12 hrs. In northern regions the plants reach the stage of florescence even under continuous daylight (which in these regions has a specific intensity and spectral composition). The critical limit of daylength in the south does not exceed 12 hrs.

The wide area of the *Chenopodium* species allows the conclusion that between these species the protoperiodic reaction exhibits a wide variability. The most common type would be the short-day reaction (hence the beginning of flowering of the Polish species occurring as late as July). The degree of delay in flowering, and generative development inhibition appearing with increasing daylength would then be dependent on the light intensity, and the number of daylight hours, thus on the light, respectively, light and thermal conditions, and as shown by the studies of Cummings, it is an ecotype character.

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The present observations were made on *Ch. rubrum, Ch. glaucum, Ch. ficifolium* and *Ch. hybridum.* Seeds were collected from plants growing in the environs of Puławy, Lublin District. All the four species exhibit the short-day reaction type of varying intensity. Besides observations on the

time of flowering, detailed observations were performed on *Ch. ficifolium* and *Ch. glaucum* as regards leaf differentiation and variability in leaf and axillary bud development on the growth axis.

Chenopodium glaucum

The development of plants sown on June 1, thus in summer under conditions optimal for our climate, on Sept. 8 (autumn, seeding under waning light conditions) and on Feb. 20 (early spring — rising light conditions) was compared. The plants grow under natural varying daylength (N), natural daylight shortened to 8 hrs (N_8), daylight prolonged to 16 hrs (N_{16}) and to 24 hrs (N_{24}) by a 500W lamp. One group of plants was placed in a light chamber under illumination of 4000 Lux of constant length (8 and 19 hrs).

Observations in detail were performed on the plants sown in summer, and the results are compiled in tables 1 and 2, and shown in figs 1—3, the habitus of the plants is illustrated by photos 1 and 2.

The influence of daylength is very strong, showing a distinct interaction with light intensity; the plants differ in habitus, sometimes in the

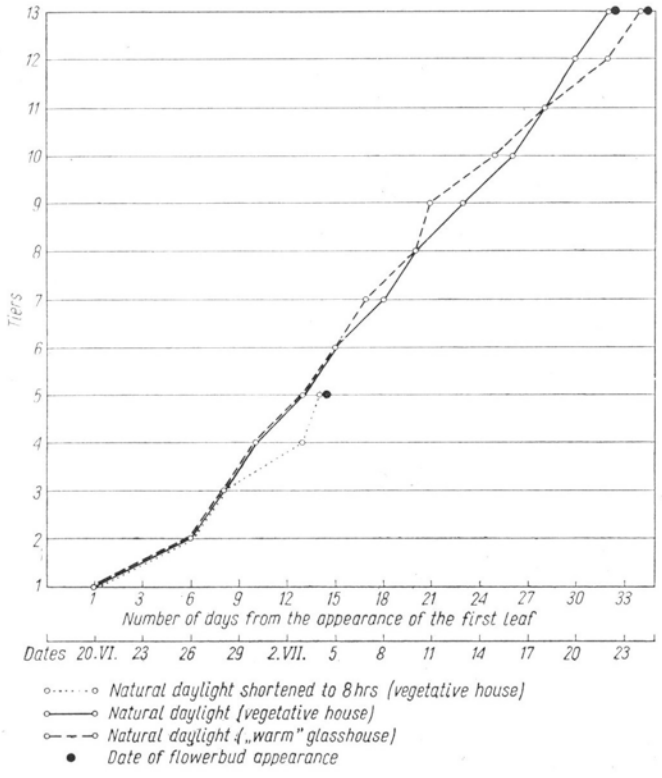


Fig. 1. *Chenopodium glaucum*, seeded June 1. Rhytm of main leaf differentiation and date of flowering

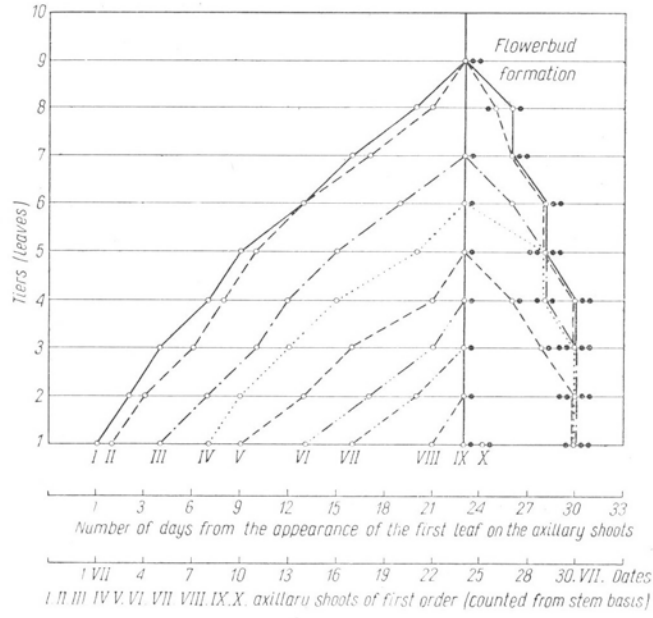


Fig. 2. *Chenopodium glaucum*, seeded June 1. Development of axillary shoots in plants growing under natural long day

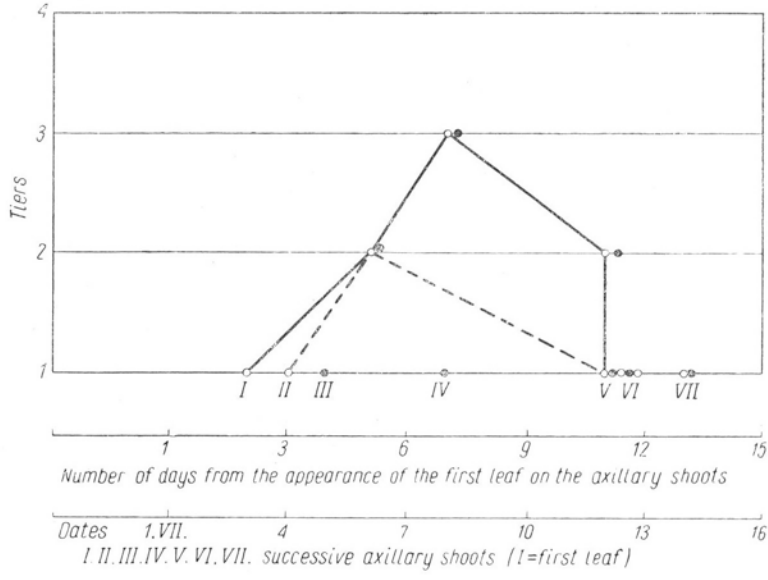


Fig. 3. *Chenopodium glaucum*, seeded June 1. Development of axillary shoots in plants growing under short day

profusion of flowering, the intensity of growth processes and leaf differentiation, and also by the character and course of development of axillary buds.

From the point of view of generative development, *Chenopodium glaucum,* as has been established earlier, is a typical plant with a pronounced quantitative short-day reaction. Under 8hr daylinght, in dependence on the seeding date, 14—15 days after appearance of the cotyledons, the apical primordium of the inflorescence appeared in the form of a well visible bud. A maximal speeding up of generative initiation, with simultaneous reduction of development of the vegetative parts of the plant and of the period of growth, were observed in plants growing under short day at low light intensity in the light chamber (Photo 3). The plants flowered apically after differentiation of two pairs of leaves. The axillary buds in the axils of the cotyledons and the first two leaves did not develop. In the axils of the second leaf pair they at once appeared in the form of short inflorescences with several flowers.

Under 8-hr natural daylight (N_8) with seeding dates Feb. 20 and Sept. 8, initiation took place also after differentiation of two pairs of leaves. In this case, however, growth was somewhat more intensive, thus the shoots longer, the leaves larger, and small two-leaved axillary shoots developed from the axillary buds of the cotyledons and of the first pair of leaves. Under summer daylight shortened to 8 hrs much stronger plants developed (Photo 3), and the inflorescence buds appeared after previous differentiation of ten leaves (Fig. 1). Plants from the summer seeding growing under natural long daylight, after differentiation of the fifth pair of leaves, were transferred under short day of 8 hrs for 2, 4, 6, 8, 10 and 12 days (9 plants in each group). Then they were placed again

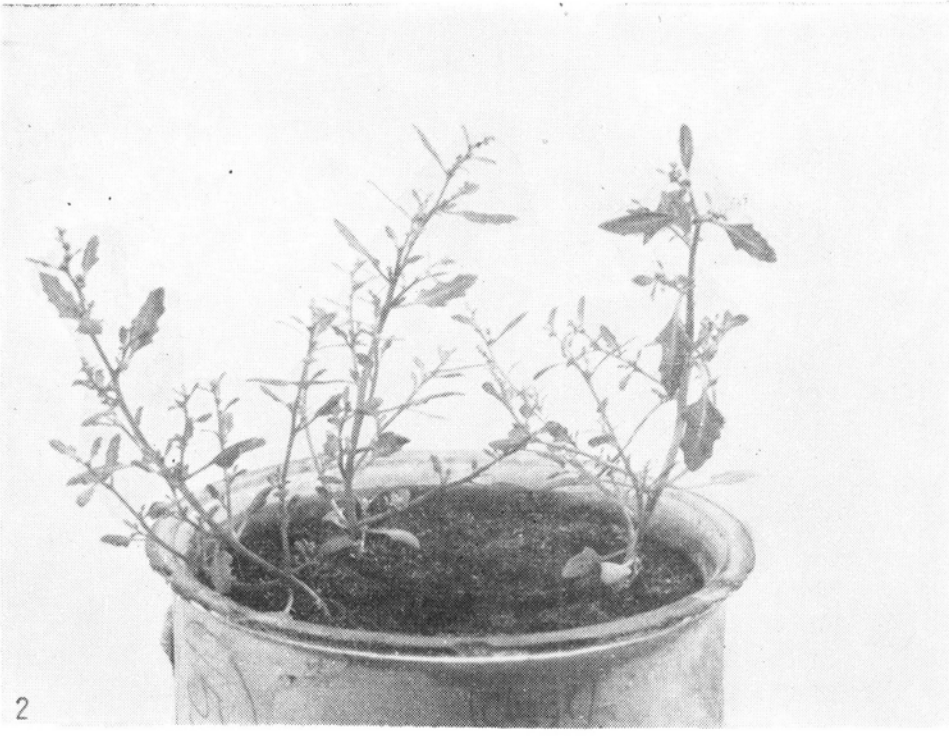
Table 1

Chenopodium glaucum. Summer seeding
Effect of increasing number of short days on budding (n = 9)

n = 9	Date of bud appearance								
	July	11	13	15	17	19	21	23	25
No. of short days	2		—					4	5
	4					1	7		1
	6			2		1	1	5	
	8			1	3	3	2		
	10			2	1	3	2	1	
	12			3	1	1	2	2	

——— short day — — — — natural long day

No. of plants in each combinat. = 9



Photos 1 and 2. *Chenopodium glaucum*, seeded June 8.

1 — Plants growing under natural long day; 2 — Plant growing under natural daylight shortened to 8 hrs
(photo taken at begining of August)

under natural long day. Their course of budding is shown in table 1. The result of this experiment is a good illustration of the strong reaction of the plants following exposure to short day.

The development of axillary buds is shown in fig. 3, the axillary bud of the first pair of leaves develops six leaves before coming into flower, the buds of the third and fourth pair at once develop a small inflorescence, the axillary buds of the first and second pair of the first order develop at once into inflorescence buds. Under long summer day the plants come into flower after developing on the average 24—26 leaves. The leaves are much larger, the shoots longer and thicker, axillary bud development is intensive, and flowering profuse (Fig. 2 and Photo 1). In table 2 some

Table 2

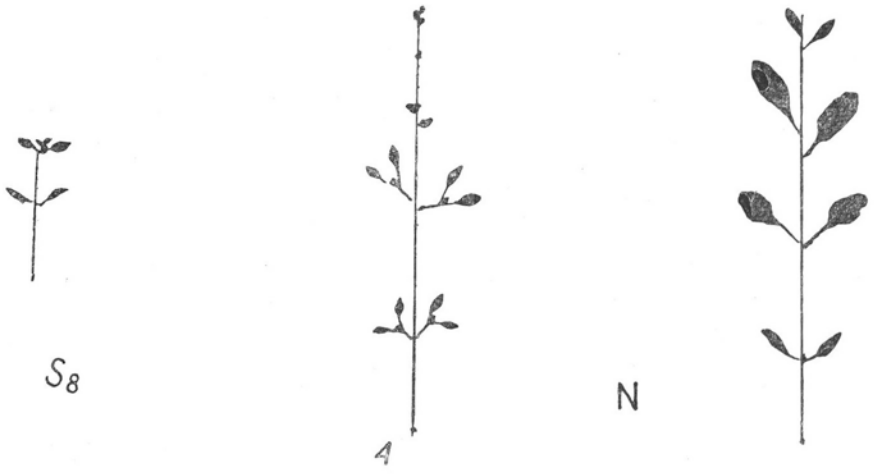
Chenopodium glaucum. Plants from summer seeding growing under natural daylight (measured on July 26)

Combination	Mean length cm	Weight g	No. of leaves at flowering	Leaf		Length of 3th lowest internodes			Mean length of axillary shoots of first order		
				Length	Width	1	2	3	1	2	3
N_8	11.8	1.3	10—12	1.9	0.8	0.9	1.0	1.6	9.0	6.5	3.5
N	21.6	7.2	24—26	4.3	1.6	0.5	1.4	2.3	12.6	7.2	3.6

characters of the plants growing under natural long day and natural shortened daylight in June and July are listed for comparison (measurements made on July 26). The greater length of the first internode in plants growing under short day is noteworthy. At first the elongation growth of these plants is distinctly faster, it lasts, however, for a shorter time, hence the decreasing length of the higher internodes. Under long day the leaves are distinctly more serrate.

The differences in the time of efflorescence and in the intensity of the vegetative growth processes between the plants growing under long and shortened day are very wide as regards the plants from the summer seeding, and smaller in those which develop in autumn under waning light conditions. This seems to be a manifestation of the interaction between daylength, light intensity and the direction of the change in the light conditions (waning or rising).

The plants sown on Feb. 20 developed under rising light conditions, thus under short-day conditions the daylength reaching at the end of March 12 hrs. In these conditions the plants flowered after developing 4 pairs of leaves, and the axillary shoots — after developing at most one pair of leaves. In the plants of the combination subjected to illumination artificially prolonged to 16 hrs, but of low intensity (the prolongation period being shorter and shorter) the axillary bud formed after the development



Photos 3 and 4. *Chenopodium glaucum*

3 — Flowering plant from light chamber grown under constant 8-hr daylength; 4 — Plants growing under natural varying daylight (photo taken on Oct.) seeded Sept. 8

of 6 leaves. The shoots growing from the axil of the first pair of leaves had 2—4 leaves, whereas the higher ones at once developed inflorescence buds. In mid April the plants of combination N begin to die. In those under 16-hr day the apical inflorescence has blown over, the main leaves have died but the growth of shoots of the first and second order continues.

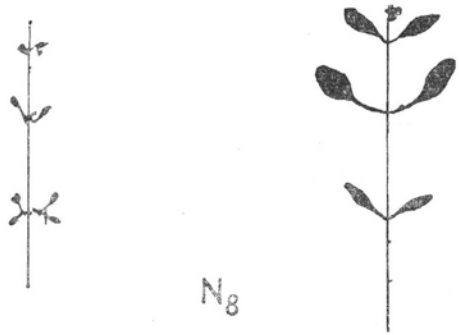
Plants seeded on Sept. 8 grow under waning daylight, as seen from photos 3—7, the differences in habitus between the plants of various combinations decrease. Setting of the apical bud occurs after differentiation of the same number of leaves in all combinations. The rate of leaf differentiation is the same in all the combinations, and flowering under N_{16} and N_{24} is delayed only a few days as compared with that of N and N_8 plants. The growth processes are gradually but consistently slightly intensified. The axillary shoots in all combinations are most frequently two-leaved with an inflorescence bud.

INTERPRETATION OF FIGS 1 AND 3 AND PHOTOS 1, 2 AND 3—7

In *Chenopodium glaucum* the leaves on young plants and those growing under low-intensity light seem to be in pairs. The same is observed in plants growing in summer under natural daylight (photos 1 and 2). This would indicate an almost simultaneous differentiation of the successive leaf pairs and a nonuniform growth of the particular shoot segments. Elongation growth of the shoot segment between

Photos 5, 6 and 7. *Chenopodium glaucum*

5 — Plants growing under natural daylight shortened to 8 hrs; 6 — Plants growing under natural daylight prolonged to 16 hrs; 7 — Plants growing under natural daylight prolonged to 24 hrs (Seeded Sept. 8, photos taken on Oct. 17)



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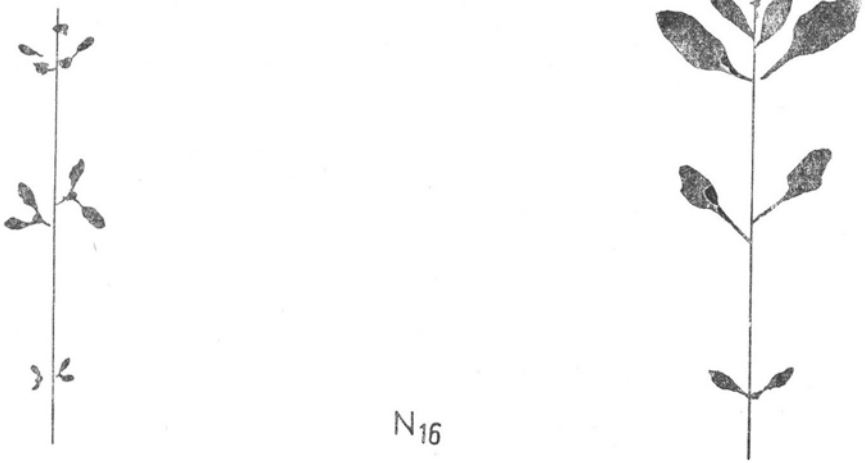

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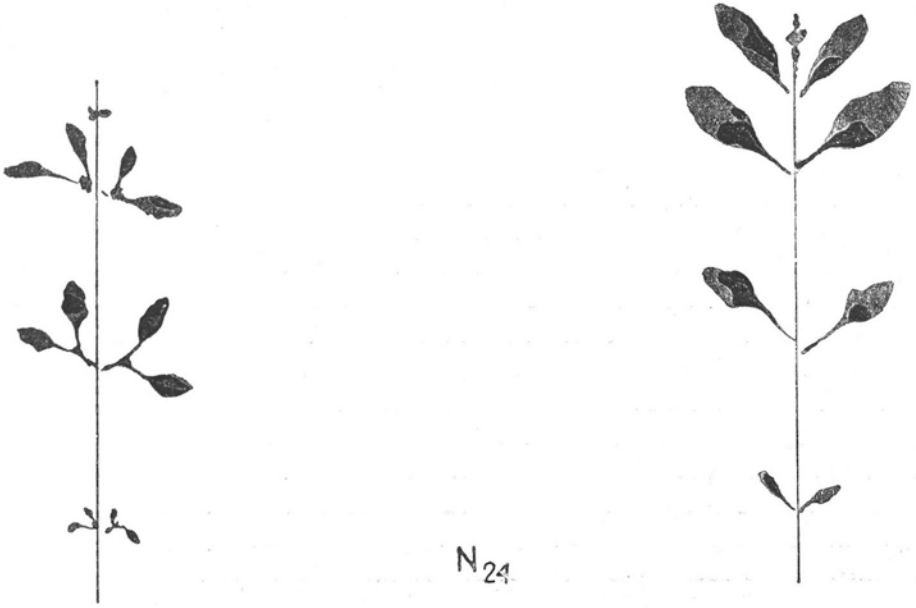

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Photos 5, 6 and 7

the leaf pairs occurs faster than between the successive leaves within the pair. The latter growth becomes more intensive only under strong illumination. On the other hand, the growth of the leaves and internodes is deleayed in relation to their differentiation processes, hence the apical bud set is visibly much earlier, at the time when part of the leaves is still in the stage of hardly noticeable primordia. In figs. 1—3 the term tier is used denoting two successive leaves which are visible in pairs or almost paired.

Chenopodium ficifolium

The observations were made on plants sown on July 5 and Sept. 8, grown under natural varying daylight, natural shortened day of 8 hrs or daylight prolonged to 16 hrs, and on plants kept in light chambers under continual 8- and 19-hr illumination of 4000 lux.

The widest difference between the plants growing under short and long daylight were noted in the plants sown in summer. These plants were kept in a vegetation house or a glasshouse, thus they grew under various night temperatures. The dates of flowering of the plants, their number of leaves and length at the moment of flowering are given for the summer seeding in table 3.

Table 3

Chenopodium ficifolium. Development of plants from summer seeding

Combination	Bud formation (bud visible)		Mean No. of leaves		Length of plants, cm	
	days after sprouting	days after change in light conditions	at moment of budding	final	at moment of bud formation	final
N_{10} (veget. house)	21	14	14.5	20.3	3.8	6.4
N (veget. house)	28	21	24.2	30.6	10.6	14.7
N (glasshouse)	28	21	27.2	31.8	18.0	25.2

If the number of short days does not exceed 6—8 given in the phase between cotyledon and first pair of leaves development, the period of budding is protracted. Part of the plants buds simultaneously with the plants growing continuously under short day (45—70%); but there are wide differences in the number of leaves in the budding plants (16—27). The stem length does not differ much from that of plants growing continuously under long day. As seen in photos 8 and 9, plants growing under a long and a short photoperiod differ markedly from each other by the size and shape of leaves and the development of axillary buds. The leaves under short day are not only smaller, but simpler in shape. The variability in size and shape along the main axis is more pronounced in plants kept under long day similarly as is the variability of development of axillary shoots. Axillary buds of the first pair of leaves are

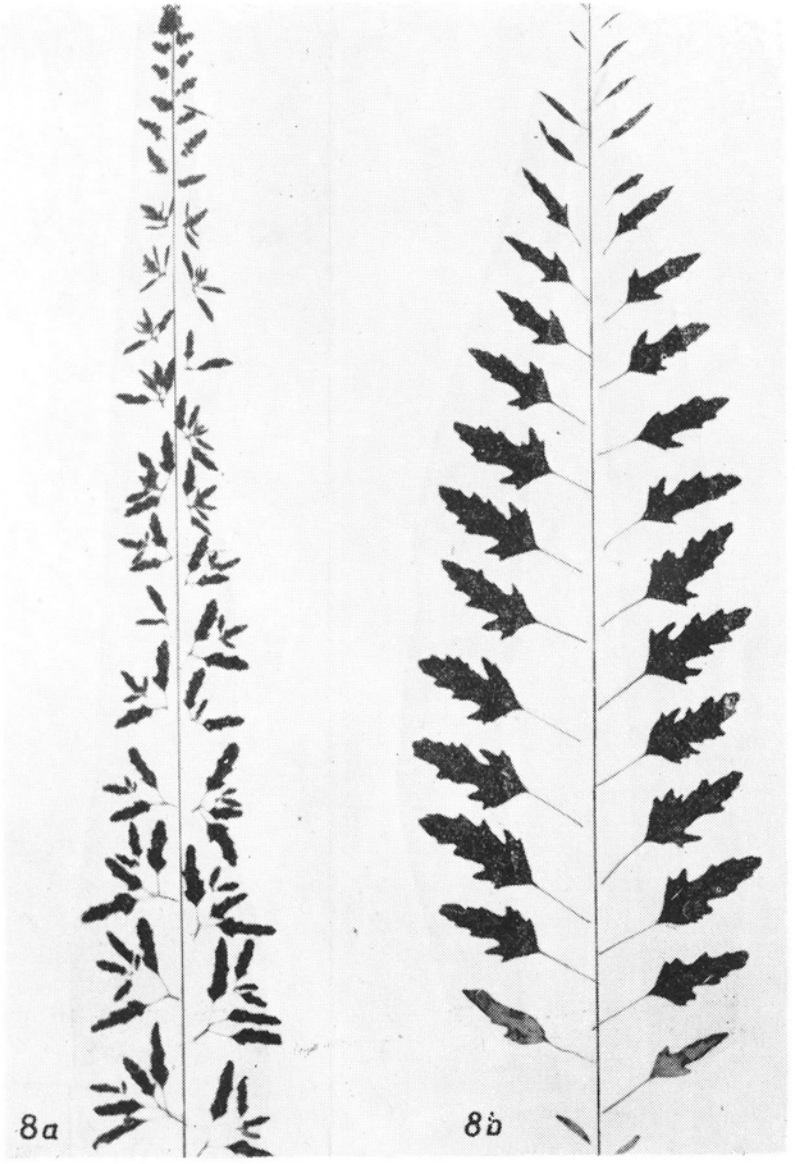


Photo 8. *Chenopodium ficifolium.* Plant growing under natural long daylight in full bloom

a — development of the axillary buds; *b* — leaves of the main stem

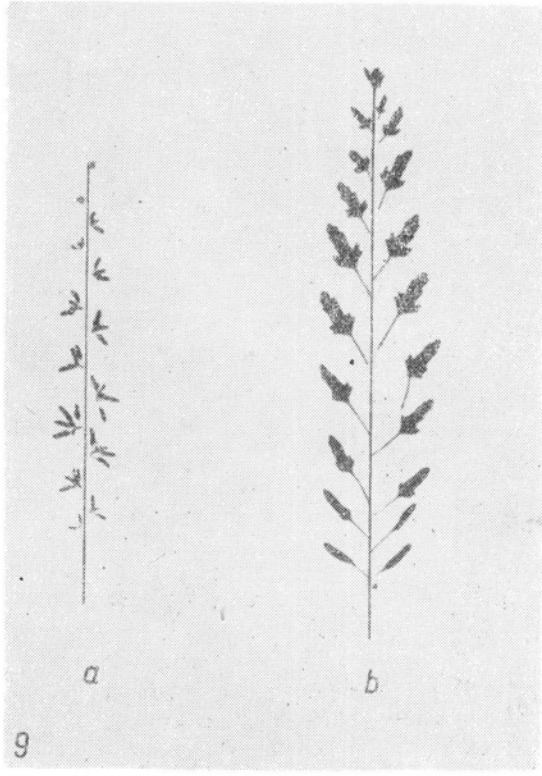
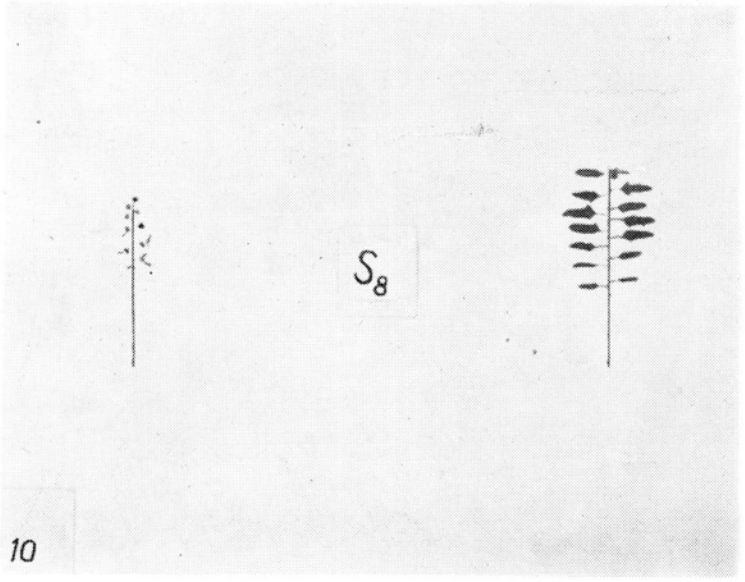
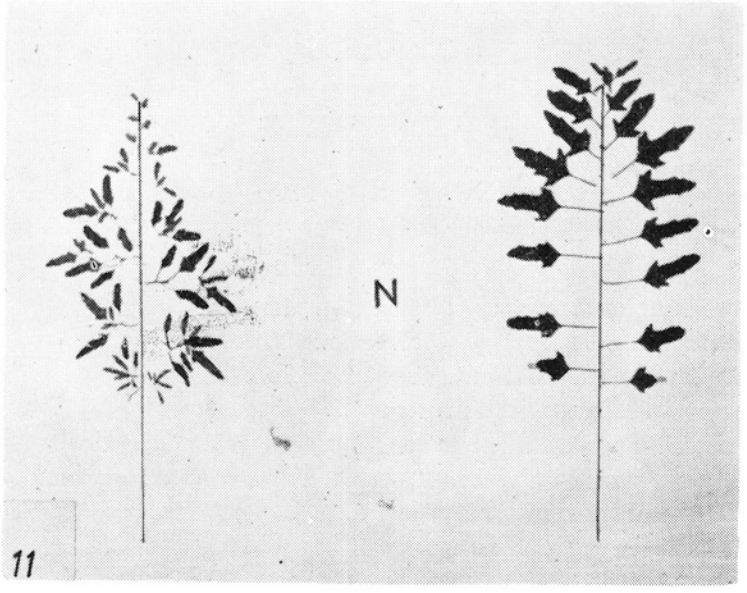


Photo 9. *Chenopodium ficifolium*. Plant growing under natural daylight shortened to 8 hrs

a — development of the axillary buds; *b* — leaves of the main stem
(Seeded on July 5, photos taken on Aug. 10)

inactive, the further ones develop into shoots with an acropetal gradient involving the number and size of leaves of the first order, and the increasing generative tendency. As regards leaves, the fifth pair attains a shape specific for adult leaves, with the largest leaves in the middle of the shoot. After seeding on Sept. 8, that is under waning light conditions, the plants were in the cotyledon phase at the end of September, in the period of the autumn equinox. The flowering and the rhythm of leaf differentiation are shown in fig. 4, and the development of axillary buds in fig. 5. The character of the latter shows a variability analogous to that in *Ch. glaucum* and in the plants sown at other dates. The same graphs show the course of differentiation of plants kept in the light chamber. The graphs were plotted on Nov. 9, i.e. 44 days after cotyledon development. At this time in the short-day plants, the cotyledons were still alive, whereas in those under long day, not only the cotyledons but the lowest leaves were already shed. The maximal number of leaves in the plants exposed to continual short day was 12 and in the plants under 19-hr long day it was 30 after 30 and 42 days, respectively. The development of axillary buds





Photos 10 and 11. *Chenopodium ficifolium*

10 — Plant growing in light chamber under 8-hr day; 11 — Plant growing under natural waning daylight

(Seeded on Sept. 8, photo taken on Oct. 9)

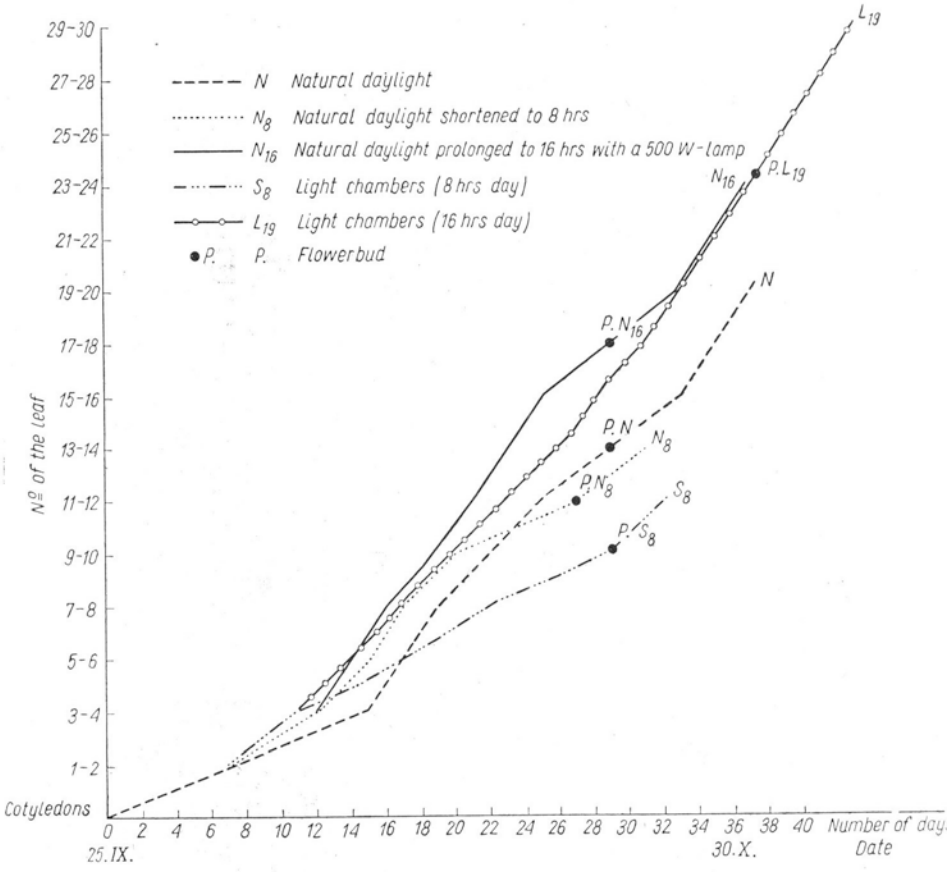


Fig. 4. *Chenopodium ficifolium*, seeded July 5. Effect of daylength on bud development and main leaf differentiation rhythm

as illustrated in fig. 5 shows a distinct gradient of the intensity of generative development in acropetal direction.

Observations made on plants seeded on Feb. 20 are not described since they lead to analogous conclusions.

Ch. ficifolium exhibits in its development the short-day type of reaction, however, somewhat less pronounced than in *Ch. glaucum*. The ontogenetic variability along the main axis is well expressed, inversion of the leaf shape is also visible.

INTERPRETATION OF FIG. 4

Similarly as in *Chenopodium glaucum* bud formation is noticeable earlier, from the moment when the highest leaves have reached a noticeable size. On the graph the black circles denote the day when the bud became visible. The highest leaves are of course then differentiated as primordia, but their morphological noticeability is connected with a certain growth phase both of the leaf and of the internode.

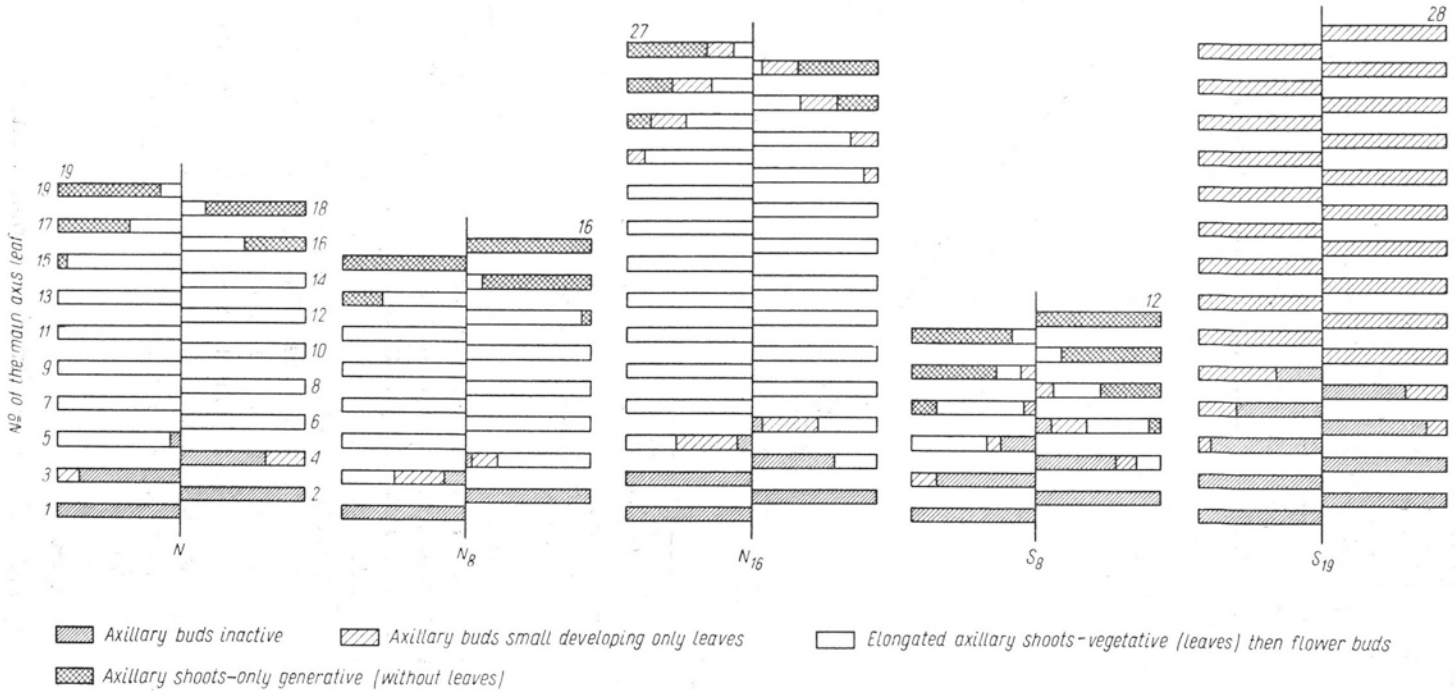


Fig. 5. *Chenopodium ficifolium*, seeded Sept. 8. Development of axillary shoots

Chenopodium hybridum

Observations were recorded only from plants seeded at one date, on Feb. 20. Leaf differentiation and the date of budding are given in fig. 6. Under short day flower initiation and growth of generative organs are distinctly accelerated, thus also the time of flowering. On the other hand, under short day a relatively faster elongation growth of the shoot is observed with prolongation of plastochrone. Elongation growth is stron-

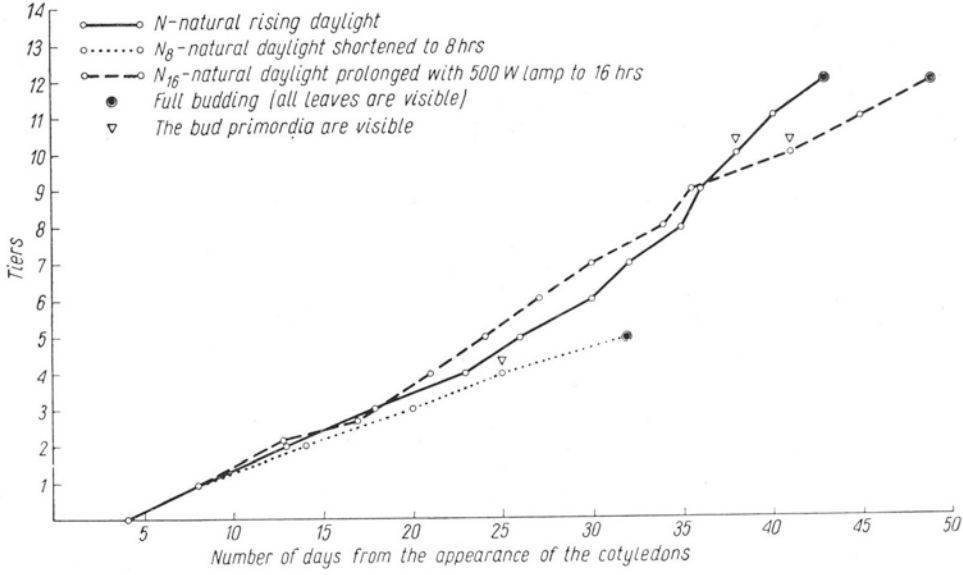


Fig. 6. *Chenopodium hybridum.* Rhythm of leaf differentiation and flowering in dependence on daylength

ger within the inflorescence under short day, this being manifested by a longer and more diffuse inflorescence. The axillary buds develop in all combinations along the entire length of the main axis, the short-day axillary buds developing immediately into an inflorescence. Under 16-hr day only the highest buds come into flower. Under normal rising daylight they are vegetative-generative with 4—6, and higher, with 2 leaves. The main leaves are largest under long day. On first-order shoots the leaves in all combinations are small with a short growth period. Both in the axillary bud development and in the leaf size a distinct gradient of ontogenetic variability may be discerned. As regards the leaf size, the first pair is small, the second larger, and further the size variability proceeds in acropetal direction.

Chenopodium rubrum

The results of observations are listed in tables 4 and 5. Under continuous illumination the leaves are distinctly larger, on longer petioles, the

Table 4

Chenopodium rubrum

N_{24} — natural daylight and illumination with 500 W in the night
N_8 — natural daylight shortened to 8 hrs

Date		No. of days from sprouting to:			
of seeding	of sprouting	beginning of bud formation		full bloom	
		N_{24}	N_8	N_{24}	N_8
Aug. 31	Sept. 12	55	38	75	65
Nov. 28	Dec. 5	106	70	115	82

Table 5

Chenopodium rubrum

Seeding date	Daylength	Mean length of plant	Mean no. of leaves to date of bud formation
Aug. 31	N_{24}	9.6	11.0
	N_8	3.6	4.0

flowering period is longer and the inflorescences contain a larger number of flowers. The short-day reaction is strong.

CONCLUSIONS

1. A quantitative short-day type of photoperiodic reaction is common to all the four species studied and is manifested at all seeding dates, both under waning and rising light conditions of high and low intensity.

The reaction to short day consists in an acceleration of generative development with reduction of the abundance and duration of flowering as well as of the differentiation and growth processes. The length of the plants, and the number of leaves decrease with simultaneous prolongation of the plastochrone. Under long day the leaves are larger, their number increases, and the rhythm of differentiation is accelerated.

2. The direction of the change in light conditions (waning and rising) and the interaction between daylength and light intensity distinctly affect plant development. The effect of long day, retarding flowering and intensifying growth and vegetative differentation, is reduced at low light intensity. This is particularly noticeable when natural daylength reaches the lower part of the curve of waning light conditions (at the beginning of winter). In these conditions in *Ch. glaucum* (Photos 4—7) the differences in the habitus of the plants under short day and artificially

prolonged day are relatively small. In *Ch. ficifolium* and *Ch. hybridum* this effect is weaker, the reaction to daylength being dominant.

3. The differences in axillary bud development are distinct between short- and long-day plants. The variability in the development of these buds follows the main axis (Figs 2, 3 and 5 and Photos 6 and 7). Under short day some axillary buds die, and others develop at once or almost at once into shortened inflorescences frequently with several flowers. Owing to the small number of plastochrones the variability along the main axis is reduced, sometimes even unnoticeable (e.g. in *Ch. glaucum* under short day of low intensity). In long-day conditions, when the development of axillary buds is in general stronger, the developmental variability of the axillary buds following the main axis is distinct. It is of the character of an acropetally directed decreasing vegetative tendency, this resulting in a quicker and quicker formation of inflorescences.

4. In *Ch. glaucum*, as seen in fig. 2, the axillary shoot formed in the axil of the first pair of main leaves flowers after developing 18 leaves, the shoots in the axils of the 10th, 15th and 16th leaves flower after developing two leaves, and the axillary bud of the 18th and 19th leaves at once develops into an inflorescence. The apical bud is formed on lateral shoots almost at the same time, whereas flowering of the axillary buds of second order occurs in a more acropetal direction, the differences in formation of the inflorescence bud on the highest and lowest axillary shoot not exceeding 7 days.

Ch. ficifolium exhibits an analogous very pronounced gradient of axial variability (Fig. 5 and Photos 9 and 11), thus an acropetally increasing reduction of vegetative development and an enhancement of generative tonus. Both in *Ch. glaucum* and *Ch. ficifolium* a variability of leaf size and shape is also observed along the main axis. In *Ch. ficifolium* a gradual increase of the compoundness and size of leaves is observed. After reaching a certain maximum (within the 16—12th leaf) they diminish again. The highest-growing leaves are not only the smallest, but they again exhibit highly simplified shapes. The leaves of lateral shoots as compared with the corresponding main leaf have somewhat simpler shapes, this being particularly noticeable in the first pair. Within the given axillary shoot the differences between the particular leaves are slight in shape and larger as regards size.

The variability along the main axis would seem to be the expression of ontogenetic variability, thus of variability with age. It is most pronounced in the plants which develop along one axis. This variability finds its expression, on the one hand, in changes of leaf shape and size, and on the other hand, in an enhanced degree of generativeness in acropetal direction. The simplification of leaf shape might also be considered as a symptom of inversion which indicates a certain extent of rejuvenation. This view which seems to be reasonable was formulated on the basis of

numerous observations on trees made by K r e n k e. The problem of inversion consists in that the main leaf analogous in shape to the one on the axillary shoot lies by several internodes lower on the axis.

SUMMARY

Four species of *Chenopodium* were studied as regards the dependence of development on light conditions. They all exhibited a quantitative short-day type of reaction. The reaction to short day consists in an acceleration of generative initiation with the reduction of the abundance of flowering and of the differentiating and growth processes. Under low light intensity, the development of plants exposed to long day (particularly in *Ch. glaucum*) closely resembles the rhythm observed under short day.

The graphs and tables give an analysis of the rhythm of leaf differentiation and lateral shoot development, varying in dependence on light conditions. The characteristic variability in the development of axillary shoots and main leaves along the main axis is described. It is an expression of ontogenetic variability. For the development of axillary shoots a variability gradient in acropetal direction is characteristic. It consists in a gradual decrease in the intensity of vegetative differentiation and elongation growth together with an increase of the generative tonus. Axillary shoots in the axils of the highest situated leaves usually form inflorescences at once without prior leaf differentiation. Inversion of leaf shape was noted on lateral shoots, which in the light of Krenke's hypothesis may be interpreted as the expression of partial rejuvenation.

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Obserwacje nad rozwojem roślin

XVII. Wpływ układów świetlnych na rozwój czterech gatunków *Chenopodium*

Streszczenie

Cztery gatunki *Chenopodium*, a mianowicie: *Ch. ficifolium, Ch. glaucum, Ch. rubrum* i *Ch. hybridum* przeanalizowano pod kątem wpływu na ich rozwój zmian układów świetlnych, tj. długości dnia, jak również natężenia światła.

Doświadczenia prowadzone były na dniu naturalnym przy różnych terminach siewu, jak i na świetle jarzeniowym w kamerach.

Wszystkie 4 gatunki wykazały ilościowo krótkodniowy typ reakcji. Reakcją na dzień krótki jest przyspieszenie inicjacji generatywnej z redukcją obfitości kwitnienia oraz procesów wzrostowo różnicujących. Na niskim natężeniu światła rozwój ro-

ślin rosnących na dniu długim (szczególnie u *Ch. glaucum*) zbliża się do rytmu występującego na dniu krótkim.

Na wykresach zanalizowano rytmikę różnicowania się liści, jak i rozwoju pędów bocznych bardzo różną w zależności od układów świetlnych. Opisano również charakterystyczną zmienność zarówno w rozwoju pędów kątowych, jak i liści głównych występującą wzdłuż osi głównej i będącą wyrazem zmienności ontogenetycznej.

Dla rozwoju pędów kątowych charakterystyczny jest akropetalnie skierowany gradient zmienności, polegający na stopniowym zmniejszaniu się intensywności różnicowania wegetatywnego i wzrostu elongacyjnego, a nasilanie się tonusu generatywnego. Pędy pachwinowe w kątach najwyższych liści najczęściej od razu wytwarzają już tylko same kwiatostany bez poprzedzających je różnicowań liściowych. Poza tym stwierdzono inwersję kształtu liści pędów bocznych, co w myśl hipotezy K r e n k e g o można tłumaczyć jako wyraz częściowego odmłodzenia.