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Observations on the development of plants III. Development of *Centaurium umbellatum*

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Some interesting facts in the development of *Centaurium umbellatum* have been observed in earlier experiments (1960, Roczn. Nauk Roln. 81 A, 2), and these findings allowed to establish the following: *Centaurium umbellatum* has a long stage of very slow growth of the rosette. Stem elongation and the development of generative organs in general do not require treatment with lower temperatures. The plants undergo their full developmental cycle after a sufficient long day induction. On the other hand, submitted to a short day regime the plants continue to grow slowly and remain at the rosette stage.

The influence of vernalization with low temperature is quite definite and consists in speeding up the growth and the generative development and prompting the flowering which is in this case far more abundant.

These preliminary experiments carried out on relatively scanty material, had to be repeated and extended. Therefore in the years 1958—1960 the following experiments were carried out.

METHODS

Scheme of experiments: sowing — 18.IV, germination — 29.IV, transplantion of seedlings — 23.VIII.

After transplantion the plants (with 4 leaves) were divided into three groups:

A. Control: the plants were kept in the winter season in the open and later continued to grow in natural conditions.

B. The plants were grown in a greenhouse in normal daylight conditions. During the whole winter, successive series of plants were placed out of doors for a 15-day period to make them undergo natural vernalization.

Periods of natural vernalization:

I — 15.X. — 30.X. III — 15.XII. — 31.XII. V — 15.II — 1.III.
II — 15.XI. — 30.XI. IV — 15.I. — 1.II.

The following temperatures were noted during the succesive periods:

	t° max.	t° min	average	total for perioá
I. 15.X. —30.X.	+6.5 — 12.7	—1.0 — 8.0	2.6 — 9.2	106,4
II. 15.XI —30.XI.	—0.3 — 8.8	—2.4 — 5.1	—0.8 — 7.7	30.9°
III. 15.XII. — 31.XII	1.6 — 12.8	—1.1 — 6.4	0.4 — 8.2	51.1°
IV. 15.I. —1.II.	—5.1 — 6.5	0.1 — 15.1	4.6 — 9.5	—20.7°
V. 15.II —1.III.	—0.5 — —8.5	6.1 — 11.7	6.4 — 2.4	17.2°

Plants of all series, except the fourth, sustained the open air treatment well. In the fourth series the majority of plants froze, therefore it has not been included in the statistics.

C. The plants were kept in the open in natural winter conditions. In the course of winter successive series were transferred to the greenhouse: part of the plants was submitted to continuous illumination and part was grown in short day conditions i.e. 8 hours daylight.

Dates of transfer of the successive series of plants to the greenhouse:

I — 15.X. III — 15.XII. V — 15.II.
II — 30.X. IV — 15.I.

RESULTS

A. The plants grew steadily and passed into the generative stage with fewer leaves than those grown in the greenhouse. Bud formation and flowering proceeded at a uniform rhythm. By the end of July the flowers began to wither, the leaves turned yellow and the plants gradually died, by the end of August the majority had withered.

B. The speed and intensity of the vegetative growth (measured by the rate of increase of leaves in the rosette) is shown in the table 1.

The rate of increase in the control series as well as in series I and II is approximately the same. In series III and V it is definitely more intensive. The differences as shown in the diagram are significant. Thus these data confirm our previous observations that lower temperatures have a positive influence on the process of differentiation of the leaves. Considering the results of the present and of the experiments B and C it can be assumed that lower temperatures and the length of the vernalization period are more significant for the development of the plant than its age.

Analyzing the growth (e.g. in series I and II as compared with the control group) it may be surmised that, immadiately after the low tem-

perature period, development of new leaves is stimulated — but this effect decreases gradually. The figures in Table 1 represent, of course, mean values. The observation of particular plants implies yet another fact — namely that, the later individual plants pass on to the generative stage, the more intensive is their vegetative development. Such plants develop small rosettes from axillary buds. This kind of plant vegetatively highly developed occurred more often in the vernalized series, and very seldom in the control. Finally it may be added that the vernalized series had larger leaves.

Table 1

The speed and intensity of the vegetative growth
(measured by the rate of increase of leaves in the rosette)
(mean number of leaves)

Date	Vernalization time	Series				
		I	II	III	V	K*
October 15	Series I	14.9	—	—	—	14.9
October 30		14.9	—	—	—	15.3
November 15	Series II	16.3	16.6	—	—	16.6
November 30		17.0	16.6	—	—	16.9
December 15	Series III	19.7	19.3	19.8	—	19.8
December 30		21.9	21.1	19.8	—	21.5
February 15	Series V	28.5	27.1	28.3	26.2	26.2
March 2		30.3	28.5	31.3	26.2	28.0
March 16		33.0	30.7	34.5	31.5	30.0
March 31		36.6	33.5	38.7	36.7	32.7
April 27		38.3	36.3	48.3	44.0	36.1
May 11		40.8	38.8	54.7	50.1	38.8
June 8		45.6	45.8	61.5	60.3	46.4
July 6		50.3	50.0	75.5	67.8	52.0
Total increment		35.4	35.1	60.6	52.8	37.1
Increment from March 2		20.0	21.5	44.2	41.4	24.0

* Control

Observations of the generative development of particular plants at 4 periods are summarized below (Table 2).

1. As regards the rate of transition to the generative stage there are no significant differences between the particular series, perhaps only a slight delay in the controls. In the latter the number of plants which remained in the rosette stage (until the end of observation) was slightly higher, nevertheless one may affirm that vernalization is not necessary for the transition to the generative stage. Neither the course of tempe-

rature during the fortnight period when the plants were kept in the open, nor the age of the plant had any influence in this respect.

2. On the other hand vernalization affects the intensity of flowering — the inflorescence is bigger and more developed. The vernalized plants very often formed new rosettes which later developed stems and started flowering. The number of plants with several stems is distinctly higher in the vernalized series.

Table 2

Generative development of particular plants at 4 periods (number of plants)

Series	May 7		June 12			July 21			August 25		
	r	*l*	*r*	*l*	*p*	*r*	*l*	*p*	*r*	*p*	*u*
I	16	4	7	4	9	2	2	16	1	6	13
II	17	3	5	8	7	3	2	15	2	4	14
III	15	5	6	4	10	4	0	16	2	7	12
V	16	4	8	5	7	3	5	12	2	8	10
K	18	2	8	7	5	5	6	10	4	6	10

Explanations: *r* — rosette, *l* — stem elongation, *p* — flowering period, *u* — gradual dying.

3. When there is no vernalization or when the plants are submitted to low temperatures but for o short period — the uniformity of the developmental rhytm, so characteristic for plants passing the winter in the open, is disturbed, while on the other hand — a larger scale of individual variability is noticeable in the intensity of growth, the rate of transition into the generative stage and the life cycle. As a rule, plants blooming earlier, have a shorter flowering period and they also die sooner. With plants which took longer to blossom it often occurred that the rosette continued to expand, developing lateral rosettes.

C. While in series „B" the influence of short vernalization periods in conditions of gradually prolonged normal daylight was tested on plants of various age, in series „C" the plants of the successive series remained outdoors for increasingly long periods and then in the greenhouse were subjected to continuous or reduced illumination. Depending on the daylength the development of plants varied considerably. Therefore only observations on the rate of development of new leaves are given in table 3. Under conditions of continuous dyalight (Table 3) leaves were found to grow at first equally or more intensively than under short day. The difference in the development of new leaves decreased rapidly, however, and vanished altogether after the development of flowers. Thus

the total number of leaves in each particular series is distinctly lower than in series growing under short day conditions; the actual quantity of active leaves is still smaller, as proper life of leaves under continuous illumination is shorter and the lower ones gradually die.

The longer the vernalization period, the shorter the period of growth and differentiation of the leaves; the plants start flowering after developing a smaller number of leaves and at an earlier period. On the other hand the rate of differentiation of leaves over similar periods of time is higher in series submitted to a longer vernalization treatment.

Over the period from the end of vernalization (15.II.) until the blooming (11.V.) the average number of leaves in series V amounted to 16.7, for the same period in series I — to 9.4, in series II to 14.3, in series III to 12.7, in series IV to 10.9.

For the same period from the end of vernalization of series IV the respective values were: 21.4, and 7.7. for series I, 12.5 for series II, 16.7 for series III.

In the control series growth is slowest, and the total number of leaves smallest. These facts indicate that vernalization has a stimulating effect on vegetative development.

Under a short day regime the rate of growth tends to increase, the period of growth is, however, much longer (a more detailed description is given below). While the development is generally slower the differences between particular series are insignificant, nevertheless, also in this case we observe an increasement both in the quantity of leaves and in the rate of their differentiation occurring after prolonged vernalization.

Table 4 shows the rate of development of plants in the particular series over 4 phases.

The results of observation summarized in the table show a distinct dependence between the length of vernalization (and the course of temperature in this period) and the rate of generative development.

In series IV and V — which remained the longest in natural conditions, the period of growth after vernalization was the shortest; after developing 10—13 new leaves, the plants began to form stems and flowers in an almost uniform rhythm. As a rule, produced a single, short-lived inflorescence; the yellowing of the rosette began early, and all the plants died almost simultaneously.

In series III, and still more distinctly in series II, the rate of development was slightly slower with wider differences in individual growth. Particular plants developed new branchings in the inflorescence, from axillar buds, which flowered sometimes after the majority of flowers had already bloomed. In series II — a number of plants developed new stems from axillar buds. In series I the phenomenon of segregation in the individual development was intensive as well, notwithstanding the

Table 3

Number of leaves and rate of their development

Date	I		II		III		IV		V		K*	
	L	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*	*L*	*S*
October 15	**13,0**	**11,6**									**14,9**	
	1,4	1,8										
November 15	14,4	13,4	**13,3**	**11,3**								
	1,6	2,6	2,7	2,7								
December 15	16,0	16,0	16,0	14,0	**12,7**	**12,3**						
	1,6	1,8	1,8	2,3	3,9	3,2						
January 15	17,6	17,8	17,8	16,3	16,6	16,5	**12,4**	**11,0**				
	2,4	2,2	4,1	3,3	5,6	4,7	9,5	6,2				
February 15	20,0	20,0	21,9	19,6	22,2	21,2	21,9	17,2	**12,0**	**12,0**		
	0,6	1,0	1,4	0,8	2,5	0,8	1,3	1,5	3,5	3,7		
March 2	20,6	21,0	23,3	20,4	24,7	22,4	23,2	18,7	15,5	15,7	**22,5**	**20,8**
	1,6	2,0	2,5	1,7	3,1	2,8	6,5	2,0	2,1	2,6	1,7	1,6
March 16	22,2	23,0	25,8	22,1	27,8	25,2	29,7	20,7	17,6	18,3	24,2	22,4
	3,1	3,3	4,9	5,0	5,5	5,5	4,1	5,5	10,0	5,1	4,5	3,6
April 13	25,3	26,3	30,7	27,1	33,3	30,7	33,8	26,2	27,6	23,4	28,7	26,0
	4,1	7,4	5,5	6,0	1,6	8,0		7,9	1,1	9,4	3,1	4,3
May 11	29,4	33,7	36,2	33,1	34,9	38,7	—	34,1	28,7	32,8	31,8	30,3
	4,9	7,7	4,1	10,5	2,1	9,2		6,7		7,8	0,2	5,8
June 8	34,3	41,4	40,3	43,6	37,0	47,9		40,8	—	40,6	32,0	36,1
	2,3	3,8	0	4,0	0,6	6,0		5,8		5,3	0,3	7,3
June 22	36,6	45,2	40,3	47,6	37,6	53,9		46,3	—	45,9	32,3	39,8
	4,3	5,8		8,2		3,5		6,4		6,5	0,2	4,0
July 12	40,9	51,0	—	55,8	—	57,4		52,7	—	52,4	32,5	43,8
Total nomber of leaves	40,9	51,0	40,3	55,8	37,6	57,4	33,8	52,7	28,7	52,4	32,5	43,8
Increment from March 2	20,3	30,0	27,0	35,0	10,6	35,0	10,6	34,0	13,2	36,7	10,0	31,4

L — long day conditions. *S* — short day conditions. * *K* — control

Table 4

Generative development of plants submitted to continuous light

Date	I				II				III				IV				V				*K*			
	r	*l*	p	*u*	*r*	*l*	*p*	*u*	*r*	*l*	*p*	*u*	*r*	*l*	*p*	*u*	*r*	*l*	*p*	*u*	*r*	*l*	*p*	*u*
February 26	9				8	1			6	3			5	4			9				7	2		
March 21	9				7	2			3	6	1			5	4		1	8			7	1	1	
March 31	9				7	1	1		3	1	6			2	7		1	6	2		6	1	2	
April 17	8	1			2	5	2		1	1	7				9			1	8		5	1	3	
May 7	7	2			2		7		1		6	2			5	4			5	4	5		4	
June 12	6	2	2		1		8		1		1	7				9			2	7	4	1	2	2
July 6	3	1	5		1		6	2		1	3	5				9				9	3	1	2	3
July 21	2	2	5		1		4	4			2	7				9				9	3		1	5
August 26	2	2	2	3	1		2	6			1	8				9				9	2	1	1	5

Explanations: *r* — rosette phase, *l* — stem development, *p* — plants with distinctly formed buds and flowering ones are recorded jointly, *u* — plants in which the process of decline has begun the leaves yellow, flowering ceases and the plant gradually dries up completely, *K* — control.

fact that the development was very slow — and that 2 plants to the end of observation did not outgrow the rosette stage (in series III — only 1 plant).

Here the vegetative tendencies were even more distinct — the development of small rosettes and stems from axillar buds, was observed.

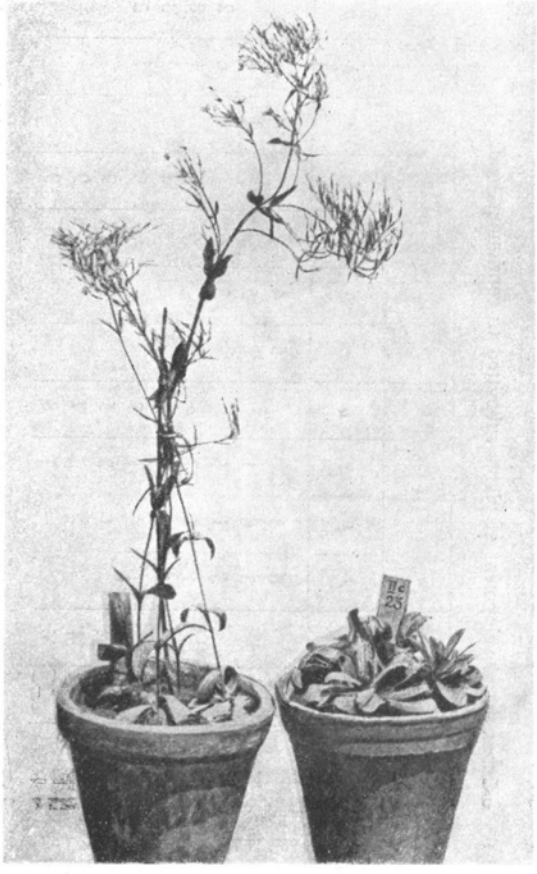

Photo 1. Plants in continuous light (left) and by short day (right)

Particular inflorescences blossomed for a considerable length of time, due to the development of new branchings which produced new flowers and again new branches.

The plants of the control series have shown a much weaker vegetative development, while segregation of the individual development of plants was distinct. The „habitus" of early blossoming plants was similar to that of plants with a high rate of development, the remaining plants showed a tendency to develop rosettes from axillar buds.

Observation was interrupted at the beginning of September when the majority of plants grown under continuous light had died. On the other hand plants which were submitted to the short day treatment continued to grow.

Development of plants under short day conditions. As is evident from Table 3 the plants of the short day series, as early as July 1959 distinguished themselves by a much larger number of leaves from plants growing in conditions of continuous daylight. Moreover, the life cycle of the leaves was also much longer: while the

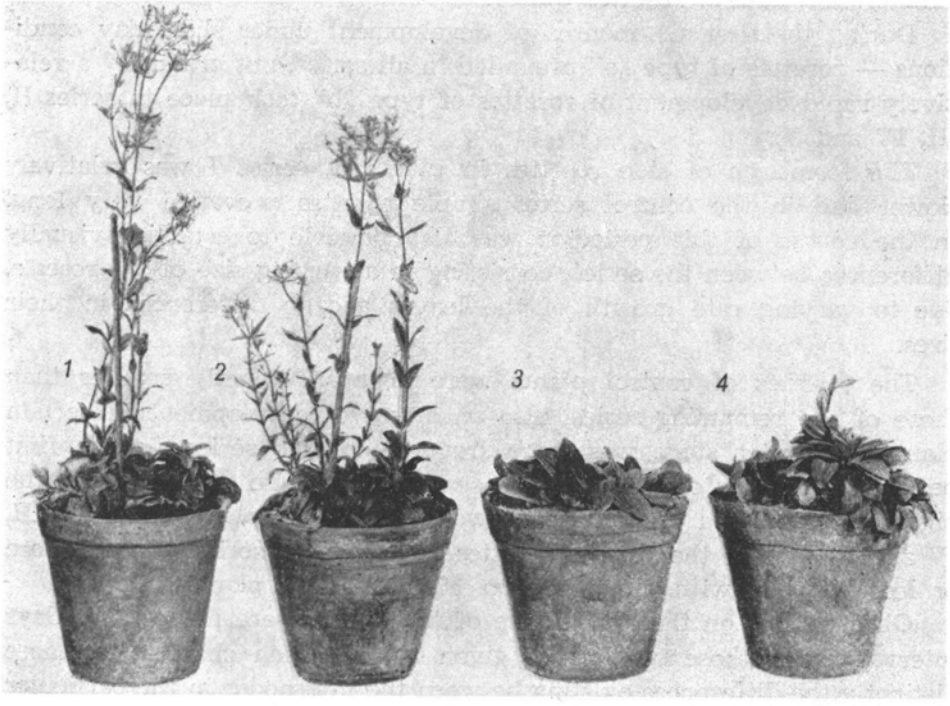

Photo 2. Various forms of plants development under short day conditions: *1* — *rrk*-plants; *2* — „pine"-form; *3* — „flat"-rosette (*r*); *4* — „bushy"-rosette (*rr*)

leaves of plants growing in conditions of continuous illumination had died — those of plants growing under a short day regime were still quite green.

In the following months the plants continued to grow and their vegetative development took various forms (Photo 2):

a) new leaves continued to grow on the main axis — very close to each other, owing to very short internodes;

b) in particular series the axillar buds developed lateral rosettes at varying times and to various degrees. This resulted sometimes in the formation of enormous „bushy" rosettes.

The development of the rosette seldom occurred uniquely according to pattern a: in this case flat rosettes were formed, which, began to grow giving a „pine tree" form in which the stem later elongated. Plants with such a single shoot had the relatively shortest life cycle.

The development of plants according to pattern b: was by far more frequent, with simultaneous development of lateral rosettes and with the plant growing along its main axis. In the stem development stage either the terminal or one of the side stems grew quicker than the rest — and later successive side rosettes developed in turn into stems, producing further new lateral rosettes quite frequently.

During the first six months of development under short day conditions — rosettes of type „a" prevailed in all series, but gradually a relatively rapid development of rosettes of type „b" took place in series II, III, IV and V.

The formation of side rosettes in plants of series I was relatively slower and in the control series simple rosettes prevailed very long. In the course of this period it was also possible to establish visually differences between the series, consisting in a varying size of the rosette, due to varying rate growth of the leaves and to differences in their sizes.

The rosettes of control plants were always distinctly smaller than those of the remaining series, also an arrest of development in certain plants at a later stage was more frequent in this series. In the first period the rosettes of the plants in series I were also smaller while the biggest rosettes and biggest leaves were formed by plants of series III, IV and V. In time the sizes of rosettes, in particular series, became more or less uniform, with the exception of the control plants.

Observations on the appearance of the plants were made at 10 days intervals; only those results are given below which characterize more distinctly the differences existing between the internodes in the particular series (Table 5).

It results from observations that rosettes of type „b" develop most quickly in series III — V. Ten months after placing the last series in the hothouse, an increasing number of plants developed either main or lateral stems. After a year's growth under shart day conditions the majority of plants in series III — V had either reached the stage of stems or produced buds or even flowers. A certain delay was visible in the series II and I — and, particularly, in the control series.

It results from observation of short day plants that longer vernalization has a stimulating effect not only on the vegetative but also on the generative development — and that, despite the inhibiting influence of reduced daylight, after a sufficiently long period the majority of plants reached the stage of stem elongation and later budded and blossomed.

Table 5

Development of plants under short day conditions

Date	I	II	III	IV	V	K*
May 16	8*r* 1*rr*	6*r* 3*rr*	7*r* 2*rr*	5*r* 4*rr*	6*r* 3*rr*	9*r*
July 21	7*r* 2*rr*	3*r* 6*rr*	2*r* 6*rr* 1*rrl*	2*r* 7*rr*	4*r* 4*rr* 1*rl*	8*r*
August 26	4*r* 5*rr*	2*r* 7*rr*	2*r* 6*rr* 1*rrk*	2*r* 7*rr*	4*r* 4*rr* 1*rll*	8*r* 1*rr*
September 22	4*r* 5*rr*	9*rr*	2*r* 6*rr* 1*rrk*	2*r* 7*rr*	2*r* 6*rr* 1*rk*	6*r* 3*rr*
November 10	3*r* 5*rr* 1*rl*	9*rr*	1*r* 7*rr* 1*rrk* (3 plants died)	2*r* 5*rr* 2*rrll*	2*r* 6*rr* 1*rk* (1 died)	
January 8,60	2*r* 4*rr* 2*rrll* 1*rp*	8*rr* 1*rrll*	2r 4*rr* 2*rrll* 1*rrk*	1*r* 4*rr* 2*rrll* 1*rl* 1*rp*	2*r* 3*rr* 1*rrl* 2*rrk*	6*r* 3*rr* 2*r* 6*rr* 1*rll*
February 15	2*r* 3*rr* 2*rrll* 2*rrp k* (2 begin to wither)	7*rr* 1*rrl* 1*rrp*	1*r* 2*rr* 1*rp* 4*rrp* — *k*	1*r* 4*rr* 1*rll* 3*rrk*	1*r* 4*rr* 1*rll* 1*rrll* 2*rrk*	2*r* 5*rr* 1*rll* (4 plants died)
March 5	1*r* 2*rr* 2*rrll* 2*rrp* 1*rp* (several begin to yellow)	6*rr* 2*rrll* 1*rrp* (one turns yellow)	2*rr* 1*rk* 1*rl* 4*rrp* — *k* (2 turn yellow)	3*rr* 1*rl* 2*rrll* 3*rrk* (one turns yellow)	1*r* 2*rr* 2*rrll* 1*rl* 3*rrk* (rosette withered) (*k* begins to wither)	2*r* 5*rr* 1*rp*

Explanations: *r* — only single rosettes develop adhering flatly to the soil, *rl* — initial stage of elongation of the stem *rll* — distinct development of stem (from terminal rosette) *rp* — budding *rk* — flowering *rr* — rosette develops lateral rosettes *rrl, rrll, rrp, or rrk* — analogously running stages (see above).

* *K* — control.

SUMMARY AND CONCLUSIONS

The results of the described experiments, confirm our previous observations. They also point to the rather complicated character of the influence exercised by temperature and light on the development of *Centaurium umbellatum*.

At first *Centaurium umbellatum* develops very slowly in natural conditions, short daylight has a strongly inhibiting influence on the development of the plant preventing it from flowering in the first year. Only single plants reach the blossoming stage, even if sown and set very early.

Nonetheless, as it appears from our observations the low temperature is not necessary for the transition to the generative phase. Submitted to continuous illumination or long day regime, the majority of the control plants show normal development, with only a slight delay and variability of individual features in particular plants. In this respect the effect of long day, without vernalization, does not constitute optimal conditions which would assure the uniform development of the analyzed population.

This function is fulfilled by the influence of low temperatures applied over a long period. As already mentioned, plants passing the winter in the open show a uniform rhythm of development — they flower and die more or less all at the same time.

In experiment „C", the longer the period during which the plants remained in „winter" conditions, the quicker was their generative development and the individual developmental differences between particular plants were smaller. It may be supposed that natural populations are composed of a considerable number of biotypes, showing different degrees of dependence between the rate of both vegetative and generative development and the length of exposition to lowered and low temperatures. A longer action of low temperature seems to bring about a kind of peculiar „conformism" in the reaction of particular plants and the population seems to be homogeneous to a considerable extent.

Low temperatures although not indispensable (in the sense of vernalization) to the development of plants, have, however, a stimulating effect on vegetative and generative development. The rate of differentiation of leaves is higher — also the leaves grow bigger — while on the other hand the length of the vegetative phase is reduced — the proper life of leaves and the entire life cycle are shortened. The plants blossom earlier in dependence on duration of low temperatures. The flowering period is at the same time shortened and its intensity is increased.

This stimulating and intensyfying effect of low temperatures is visible when one compares the development of control plants with those submitted to „vernalization" — and also when comparing plants submitted to „vernalization" during periods of various length.

On the other hand experiment „B" (15 days vernalization period) seems to indicate that the age of plants does not play any part — neither does the sum of temperatures — as far as generative development is concerned. As regards the differentiation of leaves on the other hand, it was even more intensive in series III and V (see Table 1).

A similar trend of reaction has been observed in plants growing in short day conditions. In the latter, when compared with the combinations of continuous or long day conditions, significant intensification of the vegetative development tendencies was noticeable, more marked in dependence on the length of time during which the plants were submitted to low temperature conditions. This was visibly expressed by the increase of the number of leaves, their size and development of lateral rosettes. At the same time, however, when compared with the weak vegetative development of the controls, in the vernalized plants transition from the rosette to the stages of stems elongation and bud formation was quicker and more intensive. We observe therefore not an alternative or counteracting effect of low temperatures on the vegetative and generative development of plants, but a general intensyfying influence on the development process as a whole.

And finally one more remark. When comparing the development processes of plants under various regimes — development in the sense of the course of all stages of ontogenesis — it is evident that the slowest rhythm is shown by control plants of the short day series, in which some plants perish even before completing their development cycle (such cases occur also in other short day series or in long day controls — though rather exceptionally). A little more intensive, though also very slow development is shown by short day vernalized plants. The control series under continuous light come next and the plants, submitted to longer periods of vernalization, and then kept under continuous daylight were found to grow the fastest.

It seems evident that even in a combination of most unfavourable conditions (short day without vernalization), development does occur and at least part of the plants passes the entire course of ontogenesis.

The „quantitative" character of reaction of the plants to external factors would seem to indicate this. Determined combinations of external factors accelerate (or retard respectively) in various degrees the course of process leading to flowering, they do not, however, condition the ability or inability of the plants to pass from the vegetative to the generative stage.

Development should be regarded as a uniform, one-way process. External factors may well cumulate their respective influences, or they may inhibit one another, and they may also act more or less independently, seemingly substituting each other in the phenotype effect.

The control plants of *Centaurium umbellatum* under long day conditions develop more quickly than those submitted to short day. In both cases, however, the rate of development is higher than that of the control series growing under short day regime and much lower than in the vernalized series kept under long day regime. I do not believe this to be caused by two „qualitatively" different processes, but, in both cases, to be the expression of „qualitatively" different factors acting „quantitatively" on the course of the same process.

This conclusions is suggested by observations carried out not only on *Centaurium umbellatum*, but also on other plants. It does not, however, permit to ascribe to this mechanism a general value and, conversely, both the diverse development processes as well as the dependence on the external conditions may assume in other plants a different pattern.

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(Entered: 10.VIII.1960.)