ACTA SOCIETATIS
BOTANICORUM POLONIAE
vol. XXXVI — nr 3
1967

Observations on plant development. XIV.

Interactions between seeding time, age of plant, vernalization length and florescence of *Potentilla supina*

A. LISTOWSKI and I. JACKOWSKA

Potentilla supina develops generative shoots from axillary buds of the main rosette. These buds may be set at various daylengths and various light intensities so that *Potentilla supina* may be considered from this point of view as a photoperiodically neutral plant.

The further growth of flower buds exhibits, however, a number of photoperiodic and thermic relations.

Under long (and continuous) daylight, with spring seeding, thus in conditions of higher light intensity, the buds of this plant rapidly develop into generative shoots. Efflorescence also occurs under continuous daylight of lower intensity (3500—4000 lux), vernalization acting in this case as an intensifying and accelerating factor.

Under short day, irrespective of the light intensity, generative development was inhibited. The axillary buds differentiated slowly only leaves, generative shoots do not develop and the plant did not flower unless subjected to vernalization. The main apex generally remained vegetative in the plants of this group.

The present experiments were carried out in the period 1964—1965 in order to gain a closer knowledge of this plant which seems interesting from the point of view of its efflorescence, and the conditions and character of its bloom.

(Table 1.)

Plants of the same age or at the same time were subjected to vernalization. This treatment was performed in a cold vegetation house under constant normal day of eight hours (then the plants were wheeled with the barrows into a dark chamber, hence the somewhat higher night temperatures). The mean day and night temperatures of vernalization for five-day periods varied from 2.6—7.7 and 1.8—8.5°C, respectively. After vernalization the plants grew in a glasshouse at 15—20°C.

The results of the observations on the reactions of the plants are complied in Tables 2 and 3.

The continuous line in Table 2 denotes the period from the observation of perceptible elongation growth of the axillary buds in the first plants, thus from shooting, to the day of flowering of the maximum number of plants (number of days denoted by figures above line). In combinations D, H and F two maxima occur because only part of the plants came into flower earlier than the analogous plants in the control combination (max. a), probably owing to the effect of lower temperature. The remaining plants bloomed at the same time as the controls (max. b). The second flowering in combinations B and J is marked by the zigzag line.

Table 1

Scheme of experiment

Seeding date	Control combination (nonvernalized)	Age of plants at beginning of vernalization	Combination	Vernalization, 30 days	Combination	Vernalization, 60 days
I August 8	K I	100 days	A	Nov . 16—Dec. 16	B	Nov. 16—Jan. 15
II August 29	K II	79 ,,	C	Nov. 16—Dec. 16	D	Nov. 16—Jan. 15
		100 ,,	G	Dec. 7—Jan. 7	H	Dec. 7—Feb. 5
III September 19	K III	58 ,,	E	Nov. 16—Dec. 16	F	Nov 16—Jan. 15
		100 ,,	I	Dec. 28—Jan. 28	J	Dec. 28—Feb. 28

Table 3 gives the accelerated or delayed passage to the generative phase occurring in the particular combinations.

The following conclusions may be drawn from the data listed in Tables 2 and 3:

1. Nonvernalized plants of seeding I and II flowered at the same time, in July, the plants from seeding III – somewhat earlier. The uniformity of flowering was relatively high, the greatest in plants from seeding III (100% within 10 days).

In the first part of July plants of the control combinations and those vernalized for 30 days flowered, so did those of the combination subjected to longer vernalization, in which flowering was accelerated by this treatment. The time of flowering in all these cases would seem to be regulated by the cyclic growth processes, the phase of intensive differentiation, and leaf growth and senescence.

In the control plants and those vernalized for a short time the leaves started turning red in June, first the lower ones and then successively the others until they dried up completely. At the same time the differentiation and growth of new leaves slowed down to an almost complete growth stagnation.

At the beginning of August the weight of dry leaves amounted to about 50–60 percent of the dry matter of the plants already in full bloom. Inasmuch as the process of slowed down differentiation of new leaves in the main rosette could be obseved in June in all the plants, the rate of wilting of leaves in the particular plants was not equal, particularly in the combinations subjected to short vernalization, more plants dried up slower and this was associated with their later efflorescence. The inhibition in leaf development observed would explain the shift in the period of flowering to July, thus to the beginning of waning light conditions, as the result of the diminution or abolition of the inhibitory effect exerted by leaves in the first place on shoot growth and on the formation of flower organs.

Table 2

Time of sowing	Combination	Vernalization		Period from beginning of growth of stems to full bloom in days								Number of days from sowing to			Percentage of flowering plants		Number of stems per plants	
		Age of plants in days	Period of vernalization in days	February	March	April	May	Juny	July	August	September	Beginning of growth of stems	Max a.	Max b.	Max a.	Max b.	Max a.	Max b.
I.	K_I	—	—							27		335	362		100		9.6	—
	A	100	30							22		340	362		100		5.0	—
	B	100	60		50					22		179	229		100		3.0	—
II.	K_{II}	—	—							27		314	341		90		15.5	
	C	79	30								50	322	372		80		4.5	
	D	79	60			64			(101)	21		165	229	341	60	10	2.1	5.6
	G	100	30							27		314	341		100		9.7	
	H	100	60			42		(97)		15		187	229	341	65	100	2.4	7.5
III.	K_{III}	—	—						10			283	293		100		17.0	
	E	58	30							27		293	320		100		13.1	
	F	58	60				30	(48)	12			215	245	305	20	100	14.0	12.0
	I	100	30							27		293	320		100		12.0	
	J	100	60			28			14			187	215		100		7.0	12.0

Table 3

Compared combination	Acceleration or delay in days			Acceleration or delay in days (after subtraction of the difference of seeding date)		
	beginning	max. a	max. b	beginning	max. a	max. b
B — K I	+156	+133				
C — K II	—8	— 31				
D — K II	+149	+102				
H — K II	+127	+112				
E — K III	— 10	— 27				
F — K III	+ 68	+ 48	— 12			
J — K III	+ 96	+ 78				
K II — K I	0	0		+21	+21	
K III — K I	+ 10	+ 27		+52	+69	
K III — K II	+ 10	+ 27		+31	+48	
B — D	+ 7	+ 29	+107	—14	+ 8	+86
B — F	+ 79	+ 58	+118	+37	+16	+76
B — H	+29	+ 21		+ 8	0	
B — J	+ 50	+ 28		+ 8	—14	
H — J	+ 21	+ 7		0	—14	
D — F	+ 61	+ 37		+19	— 5	
H — D	— 22	+ 29	+ 98			
J — F	+ 28	+ 30	+ 90			

2. The short vernalization period either exerted no influence on the development rhythm or gave in effect a slight retardation. We may be dealing here with a certain tendency to devernalization which occurerd in a part of the plants (e.g. in combinations G, E or J). This is only a suggestion because the temperature changes when the plants were transferred from vernalization to the glasshouse were not drastic therefore this retardation might be considered as a consequence of growth inhibition.

3. The effect of 60-day vernalization was very distinct. A considerable acceleration of generative development occurred in combinations B and J, however, the individual variability of the time of efflorescence was greater than in the control combinations. In combinations D and H and also in F only a part of the plants were vernalized and flowered earlier, whereas in the other part this process must not have been ended so that devernalization occurred and the plants flowered only at their normal time in July.

The first morphological effect of prolonged vernalization is an acceleration of the differentiation and growth of leaves which are larger than in the controls. However, they age quicker with simultaneous shooting of the axillary buds and inhibition fo the development of further leaves of the main rosette.

The differences in the assimilative surface between the controls and the plants flowering earlier are smaller than it could be expected from the difference in the number of leaves of the main rosette. This is due to the development of leaves on the shoots. The influence of the latter as compared to that of the young active leaves of the main rosette is much weaker, since from the axillary buds of the upper leaves (smaller and smaller) flowering, often shortened, shoots with two to three flowers develop rapidly.

Thus longer vernalization would seem to result in a diminution of the inhibitory influence of the leaves (probably diminution not abolition), and on the other hand in lower light requirements in development of shoots and flowers.

4. Age of the plants. Plants of seedings I and III subjected to vernalization for 60 days at the age of 100 days came into flower with a delay equal to that in seeding time. The influence of the plant age on the effectiveness of vernalization is appreciable as seen from the comparison of combinations H and D, and J anf F, particularly in the plants of combination F — the youngest at the moment of transfer to vernalization. The reason for this might be their lower ability of perception of the stimulus, and hence a higher vernalization minimum and a greater probability of devernalization.

These observations are in agreement with the findings in some other plants (Higazy 1962; Lang 1965; Napp-Zinn 1960, 1961). Namely, the effectiveness of vernalization increases, within certain limits with advancing age of the plants.

5. Seeding time and development of the plants, and the effect of vernalization. In the present experiments the differences between combination B and the remaining combinations in the date at which the plants pass into the generative phase were slight or negligible when the differences in seeding time are taken into account, the only exception being combination F. On the other hand, the rhythm of efflorescence of the plants in combinations D and H was different than in B and also differed from that in J. This observation can neither be ascribed to the age of the plants (H was vernalized at the same age as B and J) or to the vernalization temperature. The fact is that there is a greater variability in the response to the temperature stimulus. This may be due to the interaction between the influence of light on the growth of plants, and the accumulation of photosynthesis products in the period preceding vernalization.

At the first seeding date, day, particularly at the beginning of development of the plants, was still rather long and did not inhibit leaf growth, therefore accumulation of dry matter was greater. The plants of seeding III, from the beginning of their development were subjected to short day and waning light intensity, thus to conditions strongly inhibiting growth.

The plants from seeding II had relatively the least favourable conditions, corresponding to the middle part of the curve characterizing waning light conditions. Vernalization supposedly occurred in these plants in conditions of greater deviation, as compared with the plants from the two other seeding times, from the optimum ratio between the weight of the plant and the amount of carbohvdrate reserves. This fact may have influenced the course of the vernalization process.

6. The mean number of shoots per plant (Table 2) at the beginning of the flowering phase did not differ much in the plants of various combinations. The diffe-

Phot. 1. Shortened shoots bearing one flower each in plants vernalized for 60 days.

rences became more pronounced as blooming progressed, and the number of shoots was found to be the highest in the controls. Noticeably differentiated axillary buds appeared only beginning with the 9th or 10th leaf of the main rosette. Only some of these buds differentiated in the course of winter into distinctly recognizable leaf primordia, growing, however, very slowly and spreading radially around the main apex. In further development only part of these primordia transformed to flowering shoots.

7. The plants in the combinations subjected to 60-day vernalization, particularly in combination B, exhibited characteristic deviations in their development.

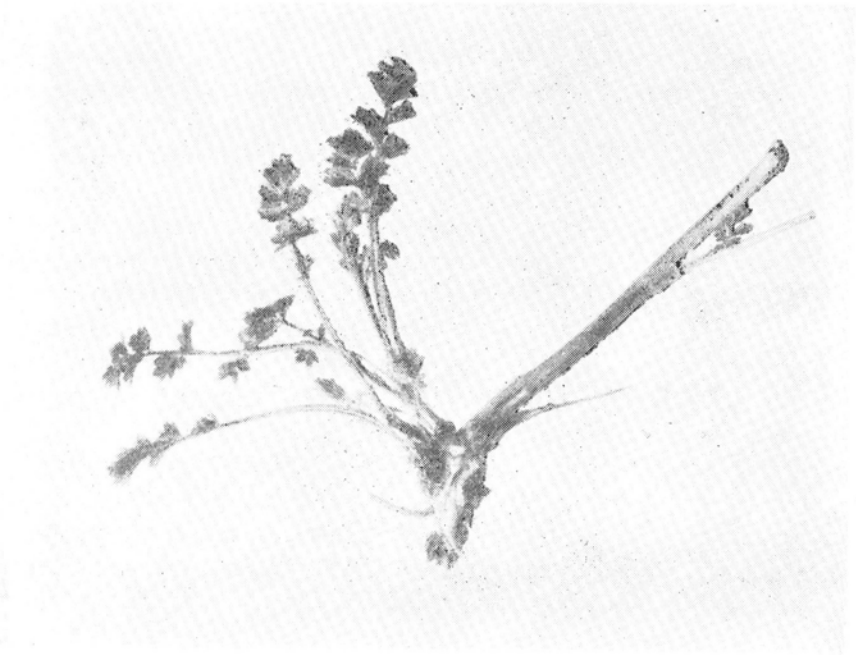
a) In seven (of 45) plants of combination B, the main apex developed into a flowering stem.

b) Both in combination B and in combinations H and J the formation of greatly reduced one-flower stems was observed. This gave an impression as if "pedicels" with single flowers were growing out of the leaf axils (photo 1).

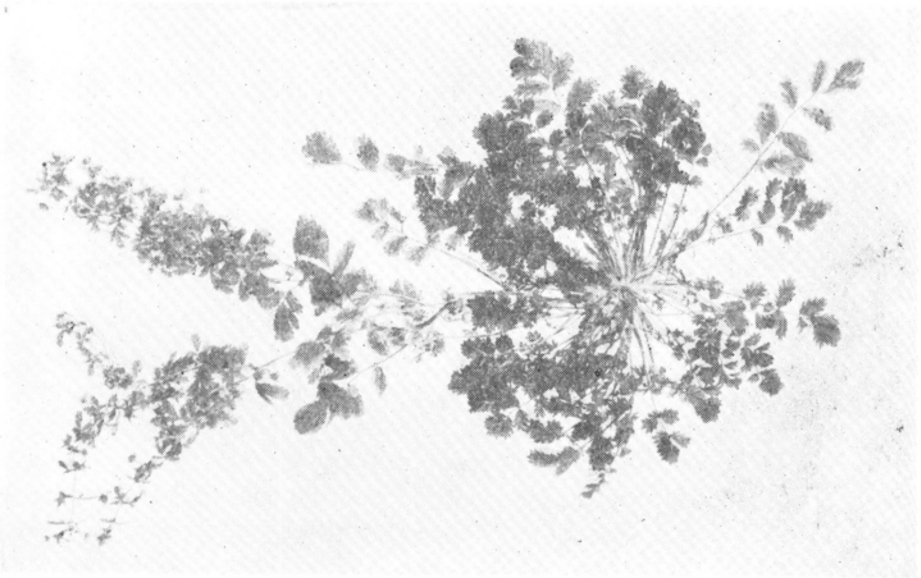
c) In combination J as well as in combinations B and H, intensified development was also manifested by a stronger differentiation and growth of leaf primordia. In combination J the number of differentiated primordia increased in the period of elongation growth and efflorescence from 2.4 to 7.0 per plant.

8. The development rhythm of plants in which under the influence of vernalization flowering was accelerated may be described as follows:

February: Elongation of primordia into shoots and efflorescence. Very intensive flowering. Numerous secondary stems, mostly shortened, developing on shoots from leaf axils.



Phot. 2. Shoot primordium developing from (dead) leaf axil on lateral shoot



Phot. 3. Plant of combination B in full phase of secondary flowering (on flowering shoot leaf, three removed). Primordia and several developed leaves before entering the ,,stagnation" period are well visibile

March. Wilting of main rosette leaves and progressive ascending drying up of leaves on lateral shoots.

May – June. Lateral shoots almost completely dried. Only apex green and still growing. Drying up of main rosette leaves.

June – July. Development of new leaf primordia in axils of lower dead leaves and youngest leaves of main rosette (the latter rather numerous in combination J). Rapid development of some of the primordia into stems flowering at once (repeated flowering – zigzag line in Table 2). Simultaneous intensified activity of main apex in new leaf differentiation. In plants in which the main apex has developed into a stem its role is taken over by one the previously set primordia (photos 2 and 3).

The transformation of the main apex as the result of prolonged vernalization is reported solely by Chouard for *Geum* (1960, p. 209). these polycarpic plants then becoming monocarpic and dying.

Transformation of the main apex in *Potentilla supina* has been observed by the author in earlier experiments (1965), in plants sown in April or May, i.e. under optimum conditions for rapid generative development. Part of these plants died after blowing over, and in the remaining ones, similarly as in the present experiment, the buds in the lower part of the stem started shooting. The death of some of the plants in the former experiment was caused by exhaustion, and not by the fact of development of the main apex into a shoot.

In the plants of combination B, in which cases of transformation of the apex into a stem had been observed, development advanced without change in the rate of mass increment and in the number of leaves and primordia as compared with the plants in which the apex continued to differentiate vegetatively. Both in the former and in the latter a rest phase occurred characterized by drying up of leaves and shoots, and separating the phase of generative activity induced by the prolonged vernalization from the phase of development of new shoots which set in in July, that is more or less in the same period as it did in the control plants (this course was characteristic for the plants of combinations B and J and some of combinations D and H).

9. As effect of what is referred to here as prolonged action of lower temperature may be listed: in the first place stimulation of generative development in the sense of accelerated efflorescence, and intensification of this process, i.e. an increased number of flowers with reduced blooming time; in some cases a change in the direction of growth of the apex and probably also the occurrence of shortened shoots. Vernalization speeded also up the rhythm of ontogenesis, thus the senescence of the plant organs, not only leaves but also shoots.

The phase of summer "stagnation" associated with drying of leaves, was also observed in the control plants. This phase, in plants vernalized for 60 days was deeper and involved both dying of leaves and shoots, followed by their secondary differentiation. Thus the rhythm of ontogenesis was the same as in the controls. As the result of vernalization, however there occurred a shift in time of the phases of activity, a reduction of the period of inhibitory influence of the leaves and a deepening of the stagnation phase.

Since the present paper is only limited to a descriptive approach, the author realizes that the data reported are insufficient for concluding from the facts observed as to definite biochemical mechanisms. It is believed, however that the accelerated flowering due to prolonged vernalization might be explained by:

1) an increased initial amount of the "flower hormone(s);"

2) an earlier disappearance of the inhibitory influence of the leaves, ageing quicker under the influence of vernalization;

3) changes in the ratio of the stimulators and the inhibitors, vernalization leading quicker to such a ratio between the level of generative development activators and leaf inhibitors, which shifts the reaction towards generative differentiation.

All these alternatives may of course occur, they do not, however, give an answer to the following questions:

A. Does exposure to lower temperature give in effect accelerated senescence, and if so, what is the mechanism of its action? It should be added that earlier senescence occurs only in conditions of prolonged vernalization. When shorter periods of exposure to lower temperature were applied, frequently an opposite result was observed, namely a prolongation of the own age of leaves, a fact which seems to have attracted but little attention;

B. Is the reduction of the inhibitory influence of the leaves by vernalization the result of speeded up senescence or of the inactivation, respectively decomposition, of the specific inhibitors?

C. How is the fact to be explained from the point of view of the hormonal theory of florescence that, under the influence of prolonged vernalization, the main apex transforms into a stem and comes into flower. This question may be extended to a more general one: how does it happen that in some plants terminal, and in others systemic flowering occurs?

D. Is or is not the occurrence of shortened shoots the result of optimum conditions for the accumulation of flower hormones? How is in general the initial acceleration of growth of the primordia, then of flower development and finally of secondary shoots, leaves on them and again of flowers, to be interpreted in terms of a uniform process of activation of generative development, especially if we bear in mind that the apex continues to grow vegetatively all this time.

It would seem that Roberts (1964) is right when he says that this large number of unanswerable questions results not only from the complexity of the process studied but is also due to the fact that the answer has been sought for mostly in plants with pronounced dependence of induction of flowering on a definite length of the photoperiod or from the temperature interval. It should be stressed that an extension of analysis to various plants, and observations of the course of florescence under natural conditions are necessary.

The process of flowering is regulated by various biochemical reactions the main influence, however, seems to be exerted by the ratio between various substances, the optimum level of which varies at different stages of ontogenesis. Another factor is the interaction with external influences, and it would seem — on the basis of numerous experiments — that the processes of efflorescence and flowering may occur on various paths, and that in one and the same plant there is not necessarily only one combination which may be optimal for these processes.

REFERENCES

Chouard P., 1960, Ann. Rev. of Pl. Phys. p. 209.
Higazy M. K., 1962, Meded. van de Land. Wageningen 62: 8.
Lang A., 1965, Encyklopedia of Plant Physiology Vol. 15: 1509—1511.
Listowski A., 1965, Acta Soc. Bot. Pol. 34: 1.
Napp-Zinn K., 1960, Planta 54: 409—444.
Napp-Zinn K., 1961, Encyclop. of Plant Physiol. 14: 40.
Roberts R., 1964, Régulateurs natur. de croissance, Coll. Internationale de CNRS pp. 614.

Obserwacje nad rozwojem roślin. XIV. Interakcja między zakwitaniem a wiekiem rośliny i długością jaryzacji przy kilku terminach siewu

Streszczenie

Kontynuując doświadczenia nad rozwojem *Potentilla supina* przeprowadzono dalsze obserwacje nad interakcją między zakwitaniem a wiekiem rośliny i długością jaryzacji przy kilku terminach siewu. Wyniki zestawiono w tab. 2 i 3.

Rośliny kwitną bez jaryzacji w drugiej połowie lata, co jest regulowane cyklicznością zmian w procesach wzrostu oraz starzenia się liści.

Przyspieszenie kwitnienia w warunkach długiej jaryzacji wynika prawdopodobnie ze zniesienia lub zmniejszenia inhibicyjnego wpływu wywieranego przez liście, jak i obniżenia wymagań w stosunku do czynnika świetlnego oddziaływaniem niższych temperatur.

Efektywność jaryzacji w pewnych granicach wykazuje zależność od wieku rośliny.

Pod wpływem dłuższej jaryzacji obserwowano przechodzenie głównego wierzchołka wzrostu w pęd, tworzenie się skróconych pędów, silniej zaznaczającą się cykliczność — szybsze starzenie się roślin z letnią fazą spoczynkową, w czasie której usychają nie tylko liście — jak u roślin kontrolnych — ale i pędy kwiatowe.