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Hormonal Regulation of Reproductive Development in Higher Plants

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Abstract. The present paper deals with the hormonal regulation of reproductive development, *i.e.* flowering and sex manifestation. Representation of hormonal regulation of flowering is based on the concept of florigen as a two-component, complementary system of flowering hormones, which consists of gibberellins and anthesins. Data are presented on the effect of extracts of gibberellin - and anthesin-type substances from the leaves of flowering and vegetatively growing plants under non-inductive conditions of day length. Experiments with flowering of plants under the influence of graftings serve as a basis for considering the question about the common nature of one of the florigen components — anthesins, for various plant species.

The mechanism controlling tuberization in both intact and grafted plants is based on the participation of all the components of the hormonal system and constitutes one of the most vivid manifestations of integration of all the organs in the whole organism.

Hormonal Regulation of Plant Flowering

A quarter of a century ago (CHAÏLAKHYAN 1958), we suggested the hypothesis of the two-component nature of florigen as a complementary system consisting of two groups of flowering hormones: gibberellins influencing the formation of flowering stems, and anthesins influencing the formation of flowers. The production of the complex of these flowering hormones, florigen, in the process of induction in short-day and long-day species proceeds *via* different pathways. In short-day species constantly containing gibberellins, induction is related to the formation of anthesins in the leaves; in long-day species constantly containing anthesins induction is connected with the formation of gibberellins (Fig. 1).

Such a pattern of different ways of forming one and the same hormonal complex, florigen, in short-day and long-day species has resulted from the concept of the two-phase character of flowering, according to which in long-day species the critical flowering phase is the first one of flowering stem formation taking place under long days, while in short-day species the critical phase is the second one of flower formation taking place only under short days.

The available proofs of the existence of the two groups of flowering hormones composing florigen are different. As far as gibberellins are concerned, methods of isolating them from plants and their chemical nature and structure are known, their function as hormone-regulators of flowering in annual long-day, long-short-day and short-long-day, biennial, and perennial plants has been proved experimentally (LANG 1965, PHARIS and MORPH 1969, ZEEVAART 1976). As for anthesins, their chemical nature and structure are not known, but the concept itself is based on numerous data obtained in

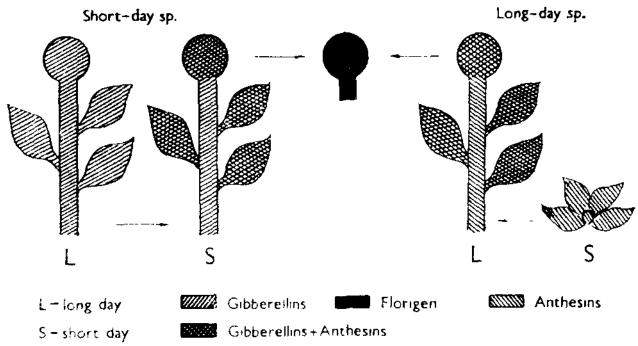

Fig. 1. Photoperiodic induction. Left — synthesis of flowering hormones in leaves and stems: gibberellins and anthesins in short-day species; right — synthesis of flowering hormones in long day species; center — formation of flowering hormones — florigen.

biological experiments with grafting, where different components of florigen are combined.

The elaborate methods for extracting gibberellin-like substances from plants have been employed by many authors to study their presence. In our laboratory, gibberellin-like substances were extracted with aceton from leaves of flowering long-day *Nicotiana sylvestris* and vegetative short-day *N. tabacum* cv. Mammoth grown under long days. The effect was tested using the drop method of treating *Rudbeckia* rosettes which had been continuously maintained under conditions of non-inductive short days. In both cases the rosettes treated with the extracts formed stems and started to flower, while the control untreated specimens remained in a rosette state. The noteworthy fact was the ability of vegetatively growing *Rudbeckia* rosettes to form stem sideshoots and to start flowering upon treatment with substances from leaves of vegetatively growing Mammoth tobacco plants. This led to the conclusion that the above phenomenon occurred due to the combination of gibberellin-like substances contained in the extracts from the leaves of tobacco Mammoth and anthesins available in *Rudbeckia* leaves under short days (Figs. 2, 3, upper row).

Attempts at isolating anthesins from plants proved to be much more difficult. More extensive and substantial experiments in this direction were undertaken by LINCOLN et al. (1964).

Our laboratory jointly with the laboratory of the Institute of Organic Chemistry, the USSR Academy of Sciences (CHAÏLAKHYAN *et al.* 1977), carried out experiments to study the effect of ethanol extracts from leaves of flowering plants of short-day tobacco Mammoth on the sprouts and seedlings of *Chenopodium rubrum*. Under the influence of these extracts, this short-day plant started to flower under conditions of continuous light, though the formation of floral organs in these plants under such conditions does not normally occur.

Recently, the same results — flowering of sprouts and seedlings of *Ch. rubrum* under continuous light — were obtained under the influence of similar extracts (CHAÏLAKHYAN *et al.* 1985) from the leaves of long-day *Nicotiana sylvestris* growing vegetatively under short days.

These experiments showed that the leaves of tobaccos, both Mammoth and *N. sylvestris*, under short days contained metabolites of an anthesin type, which induced flowering of *Ch. rubrum* seedlings under continuous light. Of particular interest is the ability of anthesin-type substances, extracted from the leaves of *N. sylvestris* growing vegetatively under short days, to induce flowering of short-day species of *Ch. rubrum* under conditions of continuous light. This apparently occurs due to the combination of anthesins

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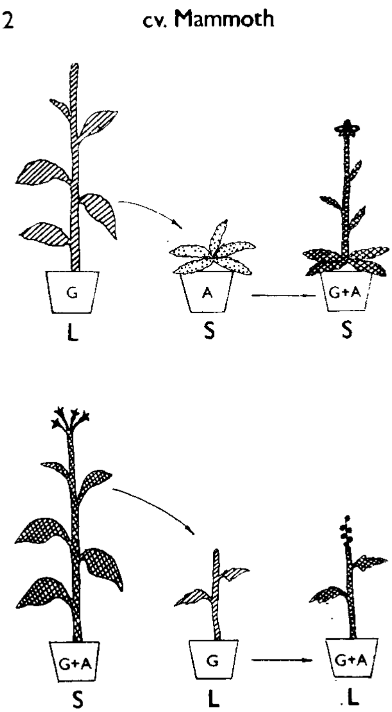

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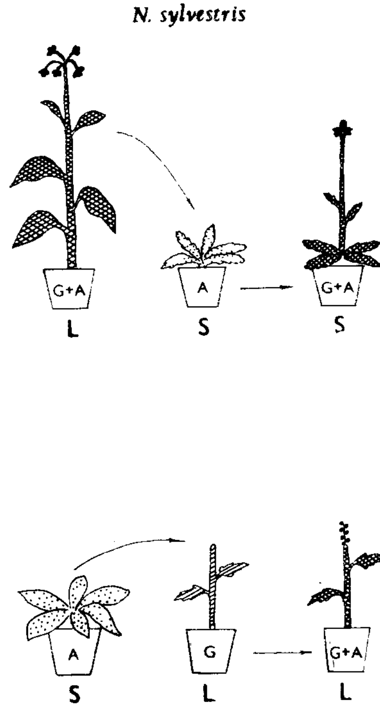

Fig. 2. Effect of extracts from leaves of short-day Mammoth tobacco on flowering of plants of *Rudbeckia bicolor* and *Chenopodium rubrum*. — Above: left — vegetative Mammoth under long days (L), center — vegetative *Rudbeckia* under short days (S), right — flowering *Rudbeckia* under short days (S). — Below: left — flowering Mammoth under short days (S), center — vegetative *Chenopodium* under long days (L), right — flowering *Chenopodium* under long days (L). G — gibberellins, A — anthesins, G+A — gibberellins + anthesins.

Fig. 3. Effect of extracts from leaves of long-day *Nicotiana sylvestris* on flowering of plants of *Rudbeckia bicolor* and *Chenopodium rubrum*. — Above: left — flowering *Nicotiana sylvestris* under long days (L), center — vegetative *Rudbeckia* under short days (S), right — flowering *Rudbeckia* under short days (S). — Below: right — vegetative *Nicotiana sylvestris* under short days (S), center — vegetative *Chenopodium* under long days (L), right — flowering *Chenopodium* under long days (L). G — gibberellins, A — anthesins, G+A — gibberellins + anthesins.

available in the leaves of *N. sylvestris* under short day, and gibberellins available in the leaves of *Ch. rubrum* under long days (Figs. 2, 3, lower row).

Until now, only a few experiments are known in which flowering has been obtained using the combination of two vegetative components in graftings (LANG 1965, CHAÏLAKHYAN 1970, ZEEVAART 1976).

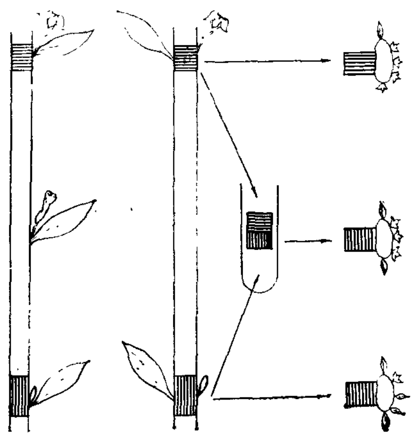

Fig. 4. Stimulation of flower bud formation on segments of the lower stem part in tobacco Trapezond under the influence of diffusates from segments of the upper stem part in culture *in vitro.*

It is hard to obtain positive results (flowering) in such experiments apparently due to the existence of inhibitors of flowering in the leaves under an unfavourable day length (LANG *et al.* 1977). The data that we present here about the stimulating effect of extracts from the leaves of vegetative plants appear to be additional evidence in favour of the hypothesis of the two-component nature of flowering hormones.

The formation of flowering hormones in photoperiodically neutral species is not related to certain photoperiodic conditions of the environment and the formation of their complex, *i.e.* florigen, takes place under any day length. The cause of flowering in photoperiodically responsive species appears to be a stimulus which arises in the leaves under favourable photoperiodic conditions, while in neutral species it is a stimulus arising in the leaves and shoots under any day length as a result of age changes. In many neutral plants such as tobacco Trapezond, flowering is controlled by the phenomenon of physiological gradient. The gradient of flowering depends upon the physiological conditions of various stem parts, and is determined specifically by the content of substances of a hormonal nature in the tissues adjacent to the buds at various levels.

The gradient of flowering may be altered by means of graftings. Lower buds transplanted to the upper levels start to flower more rapidly, while upper buds transplanted to the lower are delayed in their growth and development. Moreover, diffusates from segments of the cortex of different stem levels have varying abilities to stimulate the formation of flower buds on stem segments *in vitro*. Diffusates from upper stem levels exercise a greater ability for such stimulation than diffusates from lower stem levels (KONSTANTINOVA *et al.* 1982). The nature of the substances contained in these diffusates still remains to be studied (Fig. 4).

The common character of the hormonal complex, *i.e.* florigen, in plants of various photoperiodic groups is supported by the results of experiments with graftings: short-day tobacco Mammoth under conditions of long days and long-day tobacco *N. sylvestris* under conditions of short days, when grafted on to *N. tabacum* cv. Trapezond, flower under the influence of hormonal substances supplied by the leaves of stocks of photoperiodically neutral Trapezond (CHAÏLAKHYAN *et al.* 1976).

The concept of a two-component complementary system of flowering hormones is in good agreement with the indispensable two-stage character of the photoperiodic response of long-short-day and short-long-day species. Thus, the flowering of *Bryophyllum daigremontianum,* as well as other long-short-day species, requires first long days for a rather long time and then short days. The influence of long days is connected with the accumulation of gibberellins and may be entirely replaced by the introduction of gibberellins into plants maintained under short days. No such replacement of short days by any chemical hormonal compound was found. However, in experiments with grafting, where stems with leaves under long days were used as stocks and shoots with leaves under short days were used as scions, the intermediate shoots began to flower with time under the influence of substances supplied from the lower leaves of the stocks (gibberellins) and from the upper leaves of the scions (obviously, anthesins) (CHAÏLAKHYAN and YANINA 1973). Thus in these species with a complicated photoperiodic response the complex of flowering hormones is also of a two-component and complementary nature.

Finally, dimorphism and hormonal regulation of sex in dioecious and monoecious plants with complete male and female flowers also depend upon the two-component system of hormones. In hemp, spinach and other plants the predominance of the male sex depends upon gibberellins supplied from the leaves; the predominance of female sex depends upon cytokinins coming from the roots. This can be clearly seen by using the integral model of sex regulation (CHAÏLAKHYAN and KHRYANIN 1982) developed in our laboratory with spinach and hemp, where the removal of roots from seedlings is compensated for by cytokinins (6-BAP), and the removal of leaves is compensated for by the introduction of gibberellins. In cultures of isolated hemp embryos *in vitro* on White's nutrient medium, the introduction of gibberellins also leads to the predominance of male plants over female ones in a ratio of about 95 : 5, and the introduction of cytokinin into the medium results in the exactly opposite relationship. Here, it should be noted that the predominance of male plants is caused only by gibberellins which cannot be replaced by other compounds, whereas the increase in the number of female plants is induced, much like cytokinins, by ethylene derivatives, and to a somewhat lesser extent by auxins and their analogues.

In all the phenomena considered, one of the florigen components — gibberellin — has been well studied, while the other still remains to be studiedf This encourages various attempts at empirical elucidation of the nature o the floral stimulus. Description of these investigations has been presented in a number of papers (EVANS 1975, BERNIER *et al.* 1981).

All the findings obtained in these investigations could give the impression that the floral stimulus is composed of numerous substances. At the same time there is ample evidence that gibberellins, being one of the components of the floral stimulus or florigen are of a common structure, notwithstanding the multiplicity of structural analogues (more than 60) in various plants. This leads to the tentative conclusion that the second component of this complex, anthesins, should also have a certain common structure. This assumption is supported not only by tests with graftings of closely related plants differing in the character of their photoperiodic response, but also with graftings of remote species such as those of long-day *Silene armeria* onto short-day *Xanthium strumarium* (WELLENSIEK 1970), long-short-day plants of *Bryophyllum* on to short-long-day plants of *Echeveria* (ZEEVAART 1982).

Thus, elucidation of the structure of one of the florigen components, *i.e.* anthesins, appears to be the object of further investigations.

Hormonal Regulation of Plant Tuberization

Hormonal regulation embraces all the aspects of vegetative reproduction and is especially vividly manifested in the formative processes — formation of roots, leaves, shoots, organs of vegetative reproduction.

Tuberization appears to be the predominant type of reproductive development in tuberiferous species which hold a prominent position among cultivated plants and the vegetation of our planet.

The concept of hormonal regulation of tuberization was developed after the discovery of photoperiodism, since short days and decreased temperature are the external factors favouring tuberization of all tuberiferous plants.

It was shown first by RAZUMOV (1931) that leaf-bearing shoots, primarily the leaves of *Ullucus tuberosus*, were the receptor organs responding to short days, resulting in the development of underground shoots (stolons) on which tubers are then formed. Further evidence for this phenomenon was provided by other authors. In addition, grafting experiments carried out first by DANIEL (1923) and later by RAZUMOV (1937) showed that the stimulus occurring in the leaves was not specific since tuberization takes place in tuber-forming species under the influence of leaves of non-tuberiferous plants.

More recently, grafting experiments have been carried out by NITSCH (1965), in which plants of short-day sunflower cultivar Russian Mammoth were grafted onto defoliated stocks of *Helianthus tuberosus*, cultivars Piedalla 17 and Vilmorin-D-19. Tubers were formed only in those grafts that had been maintained under short days. NITSCH (1965) concluded that under short days a non-specific photoperiodic stimulus formed in the leaves of sunflower which promoted tuber initiation in stocks of *H. tuberosus*.

In our experiments (CHAÏLAKHYAN *et al.* 1980, 1981, 1982) we used tobacco cultivars which differed in the character of their photoperiodic response, as experimental scions. The short-day *Nicotiana tabacum* cv. Mammoth, the long-day *Nicotiana sylvestris* and the day-neutral *N. tabacum* cv. Trapezond were grafted onto defoliated stocks of the potato species *Solanum andigenum*, *S. sparsipilum* and *S. polyadenium*.

Tuber initiation was found to depend on the appropriate photoperiodic conditions. In the grafts of short-day tobacco onto the stocks of these potato species, tuberization took place under short days only; in the grafts of *N. syl-*

vestris under long days only; and in the grafts of the day-neutral tobacco cv. Trapezond tuberization occurred both under short and long days. It was found that, with a few exceptions, the conditions favourable to flowering of various tobacco species were also favourable to the formation of a tuber-inducing stimulus in their leaves (Figs. 5, 6).

However, the question of the nature of the photoperiodic stimulus of tuberization remained unsettled; moreover two more questions arose concerning the nature of the mechanism governing tuberization in intact plants and of the mechanism functioning in grafted plants.

To settle these questions, we analyzed the available experimental data with respect to the function of phytohormones in the tuberization process. We followed two approaches: first, tuberization was regarded as a process consisting of two phases — the formation of stolons and the formation of tubers; second, we took into account the translocation of phytohormones, *i.e.* the sites of their origin and the ability to move throughout the plant as well as their levels in its various organs (CHAÏLAKHYAN 1980).

Marked effect of auxins was clearly shown in experiments (TURETSKAYA 1955) with cuttings from the potato cv. Epicur, taken from the subapical region of the shoot tip, and treated with indolylbutyric acid solution. The cuttings were found to develop roots instead of forming tubers. According to analytical data the content of natural auxins is always higher under long days.

Treatment of potato plants *Solanum tuberosum* with gibberellin solution had a marked inhibitory effect on tuberization. The same effect was obtained by the treatment of *Solanum andigenum* and *Helianthus tuberosus* with gibbe-

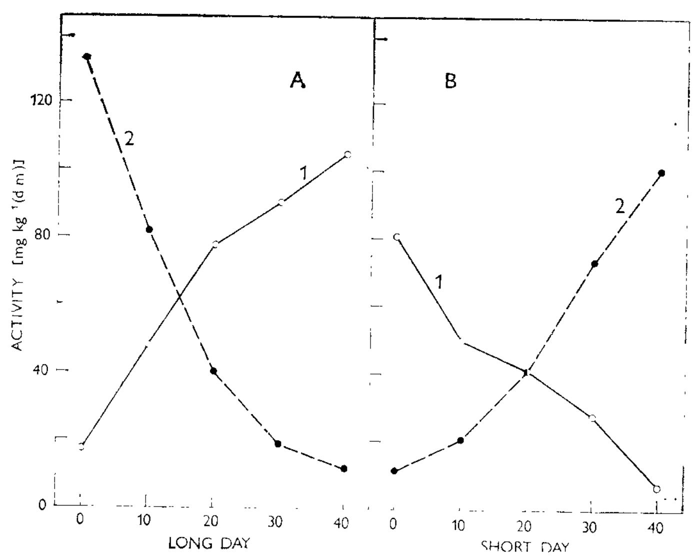

Fig. 7. Contents of gibberellins and abscisins in leaves of *Nicotiana sylvestris* (A) and Mammoth (B) under photoperiodic induction. Solid curve — increase in content of gibberellins under long--day induction of *N. sylvestris* plants and decrease under short-day induction of Mammoth plants. Dashed curve — decrease in content of abscisins under long-day induction of *N. sylvestris* plants and increase under short-day induction of Mammoth plants.

rellin (KUMAR and WAREING 1973, KHAZHAKYAN *et al.* 1979). The gibberellin content in leaves of a large number of plants is always higher under long days (LOZHNIKOVA *et al.* 1982).

The role of abscisins in tuberization has been studied in considerable detail by WAREING *et al.* (EL-ANTABLY *et al.* 1967, WAREING and JENNINGS

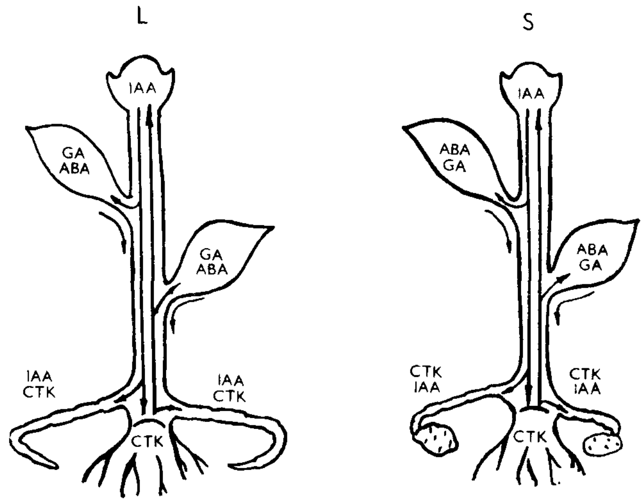

Fig. 8. Tuberization mechanism in tuberiferous plants forming tubers under short days. Left — plant under long (L), right — under short (S) days. In both cases circulation is of common character: gibberellins and abscisins are formed in leaves and move downwards to lower stem buds; auxins are formed in stem apex and move downwards to stem buds, cytokinins are formed and move upwards to stem buds. The ratio of hormones is different: on the left, under long days the relationship of hormones in leaves and stem buds shows the predominance of gibberellins (GA/ABA), in stem buds the predominance of auxins (IAA/CTK), formation and growth of stolons take place. On the right under short days the relationship of hormones in leaves and stem buds shows the predominance of abscisins (ABA/GA), in stem buds the predominance of cytokinins, (CTK/IAA) stolons are formed with subsequent tuberization.

1980). Abscisic acid (ABA) was found to have a stimulating effect on tuberization. The treatment of axillary buds with abscisic acid promoted tuberization even when the leaves were removed. Analytical data show that the levels of abscisins in plant leaves are always higher under short days (LOZHNIKOVA *et al.* 1982).

The ratio of gibberellin and abscisin contents in plant leaves under different day length seems to be of great importance. It has been established that when we add more induction by long days, the content of gibberellins increases and the content of abscisins decreases in *N. sylvestris*. When more induction is added by short days, the content of abscisins increases and the content of gibberellins decreases in Mammoth tobacco (Fig. 7).

Important results regarding cytokinin effect on tuberization were obtained using isolated stolons cultivated *in vitro* on a nutrient medium under aseptic conditions (PALMER and SMITH 1969, 1970). These authors found that by adding ABA to the medium the stolon growth was inhibited; introduction of ethylene led to their thickening, yet no tuberization was observed in either case. When, however, kinetin was added to the medium, thickening of stolons and actual tuberization were obtained.

Analytical data on the levels of endogenous cytokinins in the leaves oı plants are inconsistent. However, in tuber-forming plants the cytokinin level in roots and stolons rises under short days (MAUK and LANGILLE 1978).

All these findings directly account for the functional characteristics of phytohormones in the tuberization process. 1. Auxins are inducers of root formation. Produced in shoot buds and the adjacent young leaves, they are transported in the basipetal direction, stimulate root formation and inhibit tuberization. 2. Gibberellins are inducers of shoot formation. Produced in the leaves they are transported throughout the plant in both the up- and downward direction, promoting stolon growth and inhibiting tuberization. 3. Abscisins are inhibitors of root and shoot growth. Originating in leaves, they are transported throughout the plant in any direction and inhibit stolon growth, thus stimulating tuber formation. 4. Cytokinins are inducers of buds and tuberization. Produced in the roots they are transported throughout the plant in the acropetal direction resulting in stolon thickening and tuberization.

All this provides a general picture of the hormonal regulation of the tuberization process in plants. Formation of stolon and tuber is a process which is entirely specific for tuber-forming species and takes place in the underground shoot buds of plants. These underground buds are the sites of accumulation of two complexes of phytohormones: 1) gibberellins and abscisins, the level of which are maintained and determined by their supply from leaves; 2) auxins and cytokinins, the level of the former being maintained and determined by the supply from the tip of the stem and the level of the latter by the supply from the roots. Under long days the gibberellin (GA): abscisin (ABA) ratio in the leaves and shoot buds is in favour of gibberellins and under short days in favour of abscisins. As regards the auxin: cytokinin ratio in the shoot buds, auxin tends to predominate under long days, and cytokinins under short days.

Thus, the general mechanism controlling tuberization in short-day tuber-forming species appears to be clear. The hormonal regulation of tuberization in these plants proves to be a two-phase process which is realized only under a favourable hormonal ratio.

Consequently, the question of the nature of the tuber-inducing stimulus which has been under study for the last fifty years can be answered as follows: the tuber-inducing stimulus which is formed in leaves of both the tuber-forming plants, and plants which do not form tubers, is a two-component hormonal complex consisting of gibberellins and abscisins (their nature being common to all plants). In the underground buds of tuber-forming species they regulate the first phase of tuberization, *i.e.* the formation and growth of stolons. The second phase, strictly speaking tuberization, is regulated by cytokinins coming from the roots and by auxins coming from the tops of the stems.

Thus, the mechanism controlling tuberization in both intact and grafted plants is based on the participation of all the components of the hormonal system and constitutes one of the most vivid manifestations of integration of all the organs in the whole organism (Fig. 8).

The identity of the photoperiodic conditions favourable to tuberization in stocks of tuber-forming species that tuberize only under short days, and the flowering in scions of certain tobacco species is not based on similarities of tuberization and flowering processes; the nature of these differs profoundly. The identity of those conditions can be explained by the identity of the conditions under which hormones (gibberellins and abscisins) are formed in leaves. These hormones regulate the first phase of both processes, *i.e.* stolon growth in tuberization and the growth of aerial shoots in the case of flowering.

Thus, the regulation of reproductive development of plants, both flowering and vegetative reproduction, involves the participation of a complex of hormones.

The data on the hormonal regulation of flowering and vegetative reproduction presented here provide evidence that our knowledge of these two processes is far from being equal. On the basis of the available data on phytohormones we can reconstruct the patterns, though not quite perfect, of the formation of the organs of vegetative reproduction, but we have not sufficient information for a similar reconstruction in the field of flowering.

In conclusion I should like to express the hope that in the nearest future many questions which have been not yet cleared up will be solved by common efforts of specialists working in this branch of science.

REFERENCES

Bernier, G., Kinet, J., Sachs, R.: The Physiology of Flowering. — CRC Press. Inc., Boca Raton 1981.

Chaïlakhyan, M. Kh.: Hormonale Faktoren des Pflanzenblühens. — Biol. Zentralbl. **77** : 641 to 662, 1958.

Chaïlakhyan, M. Kh.: [Flowering hormones in plants.] In Russ. — Bot. Zh. **55** : 913—930, 1970.

Chaïlakhyan, M. Kh.: [Integrity of the organism in the plant kingdom.] In Russ. — Fiziol. Rast. **27** : 917—941, 1980.

Chaïlakhyan, M. Kh., Grigorieva, N. Ya., Lozhnikova, V. N.: [The effect of extracts from leaves of flowering plants of tobacco on the flowering of sprouts and seedlings of *Chenopodium rubrum* L.] In Russ. — Dokl. Akad. Nauk SSSR **236** : 773—776, 1977.

Chaïlakhyan, M. Kh., Khazhakyan, Kh. K., Agamyan, L. B.: [Flowering of plants at mutual graftings of photoperiodically neutral and sensitive species.] In Russ. — Dokl. Akad. Nauk SSSR **230** : 1002—1005, 1976.

Chaïlakhyan, M. Kh., Khryanin, V. N.: Pol Rasteniï i ego Gormonal'naya Regulyatsiya. [Sex of Plants and Its Hormonal Regulation.] — Nauka, Moskva 1982.

Chaïlakhyan, M. Kh., Lozhnikova, V. N., Grigorieva, N. Ya., Dudka, N. D.: [The effect of extracts from leaves of vegetative plants of tobacco on the flowering of sprouts and seedlings of *Chenopodium rubrum* L.] In Russ. — Dokl. Akad. Nauk SSSR, in press, 1985.

Chaïlakhyan, M. Kh., Yanina, L. I.: [Regulation of flowering of shoots of *Bryophyllum daigremontianum* by means of graftings.] In Russ. — Dokl. Akad. Nauk SSSR **208** : 749—752, 1973.

Chaïlakhyan, M. Kh., Yanina, L. I., Devedzhyan, A. G., Lotova, G. N.: [Induction of the tuberization in tuber-bearing plants in the interspecific and intergeneric graftings.] In Russ. — Dokl. Akad. Nauk SSSR **252** : 1276—1280, 1980.

Chaïlakhyan, M. Kh., Yanina, L. I., Devedzhyan, A. G., Lotova, G. N.: [Photoperiodism and tuber formation in tobacco graftings on potato.] In Russ. — Dokl. Akad. Nauk SSSR **257** : 1276—1280, 1981.

Chaïlakhyan, M. Kh., Yanina, L. I., Devedzhyan, A. G., Lotova, G. N.: [Photoperiodic control of the tuber formation in tobacco graftings on potato.] In Russ. — Dokl. Akad. Nauk SSSR **265** : 1276—1280, 1982.

Daniel, L.: Nouvelles recherches sur la migration de'inuline dans les greffes de Composées. — Compt. rend. Acad. Sci. (Paris) **177** : 1135—1137, 1923.

El-Antably, H. M. M., Wareing, P. F., Hillman, Y.: Some physiological responses to D, L-abscisin(dormin). — Planta **73** : 74—90, 1967.

EVANS, L. T.: Day Length and the Flowering of Plants. — W. A. Benjiamin, Menlo Park 1975.
KHAZHAKYAN, KH. K., DEVEDZHYAN, A. G., CHAÏLAKHYAN, M. Kh.: [Regulation of the topinambour tuberization using physiologically active compounds.] In Russ. — Dokl. Akad. Nauk SSSR 248 : 1021—1024, 1979.
KONSTANTINOVA, T. N., AKSENOVA, N. P., SERGEEVA, L. I.: [Interrelationship of tobacco stem explants differing in the type of morphogenesis.] In Russ. — Fiziol. Rast. 29 : 261—265, 1982.
KUMAR, D., WAREING, P. F.: Studies on tuberization in *Solanum andigena* I. Evidence for the existence and movement of a specific tuberisation stimulus. — New Phytol. 72 : 283—287, 1973.
LANG, A. G.: Physiology of flower initiation. — In: RUHLAND, W. (ed.): Encyclopedia of Plant Physiology, Vol. 15/1. Pp. 1380—1536. Springer Verlag, Berlin — Heidelberg — Göttingen 1965.
LANG, A. G., CHAÏLAKHYAN, M. KH., FROLOVA, I. A.: Promotion and inhibition of flower formation in day neutral plant in grafts with a short-day plant and long-day plant. — Proc. nat. Acad. Sci. USA 74 : 2412—2416, 1977.
LINCOLN, R. G., CUNNINGHAM, A., HAMNER K. C.: Evidence for a florigenic acid. — Nature 202 : 559—561, 1964.
LOZHNIKOVA, V. N., KREKULE, J., SEIDLOVÁ, F., BAVRINA, T. V., CHAÏLAKHYAN, M. KH.: [Balance between gibberellins and abscisins in tobacco in the course of photoperiodic induction of flowering.] In Russ. — Fiziol. Rast. 29 : 247—252, 1982.
MAUK, C. S., LANGILLE, A. R.: Physiology of tuberisation in *Solanum tuberosum* L. Cis-zeatin riboside in the potato plant. Its identification and changes in endogenous levels as influenced by temperature and photoperiod. — Plant Physiol. 62 : 438—442, 1978.
NITSCH, J. P.: Existence d'un stimulus photoperiodique non specifique capable de provoquer la tuberisation chez *Helianthus tuberosus* L. — Bull. Soc. fr. Physiol. vég. 112 : 333—340, 1965.
PALMER, C. E., SMITH, O. E.: Effect of abscisic acid on elongation and kinetin-induced tuberization of isolated stolons of *Solanum tuberosum* L. — Plant Cell Physiol. 10 : 657—664, 1969.
PALMER, C. E., SMITH, O. E.: Effect of kinetin on tuber formation on isolated stolons of *Solanum tuberosum* L. cultured *in vitro*. — Plant Cell Physiol. 11 : 303—314, 1970.
PHARIS, R. P., MORPH, W.: Precocious flowering of coastal and giant redwood with gibberellins A_3, $A_{4/7}$ and A_{13}. — BioSciences 19 : 719—720, 1969.
RAZUMOV, V. I.: [On localization of photoperiodic stimulation.] In Russ. — Tr. prikl. Bot. Genet. Selek. 27 : 249—280, 1931.
RAZUMOV, V. I.: [Tuberization in potato species not ready to form tubers.] In Russ. — Yarovizatsiya 4(13) : 76—88, 1937.
TURETSKAYA, R. KH,: [Root regeneration in potato cuttings in connection with their age and phases of plant development.] In Russ. — Proc. Inst. Plant Physiol. USSR Acad. Sci. 9 : 203—214, 1955.
WAREING, P. T., JENNINGS, A. M. V.: The hormonal control of tuberization in potato. — In: SKOOG, F. (ed.): Plant Growth Substances 1979. Pp. 293—300. Springer Verlag, Berlin — Heidelberg — New York 1980.
WELLENSIEK, S. J.: The floral hormones in *Silene armeria* L. and *Xanthium strumarium* L. — Z. Pflanzenphysiol. 63 : 25—30, 1970.
ZEEVAART, J. A. D.: Physiology and flower formation. — Annu. Rev. Plant Physiol. 27 : 312, 1976.
ZEEVAART, J. A. D.: Transmission of the floral stimulus from a long-short-day plant *Bryophyllum daigremontianum*, to the short-long-day plant *Echeveria harmsii*. — Ann. Bot. 49 : 549—552, 1982.

Figs. 5, 6 are at the end of the issue.

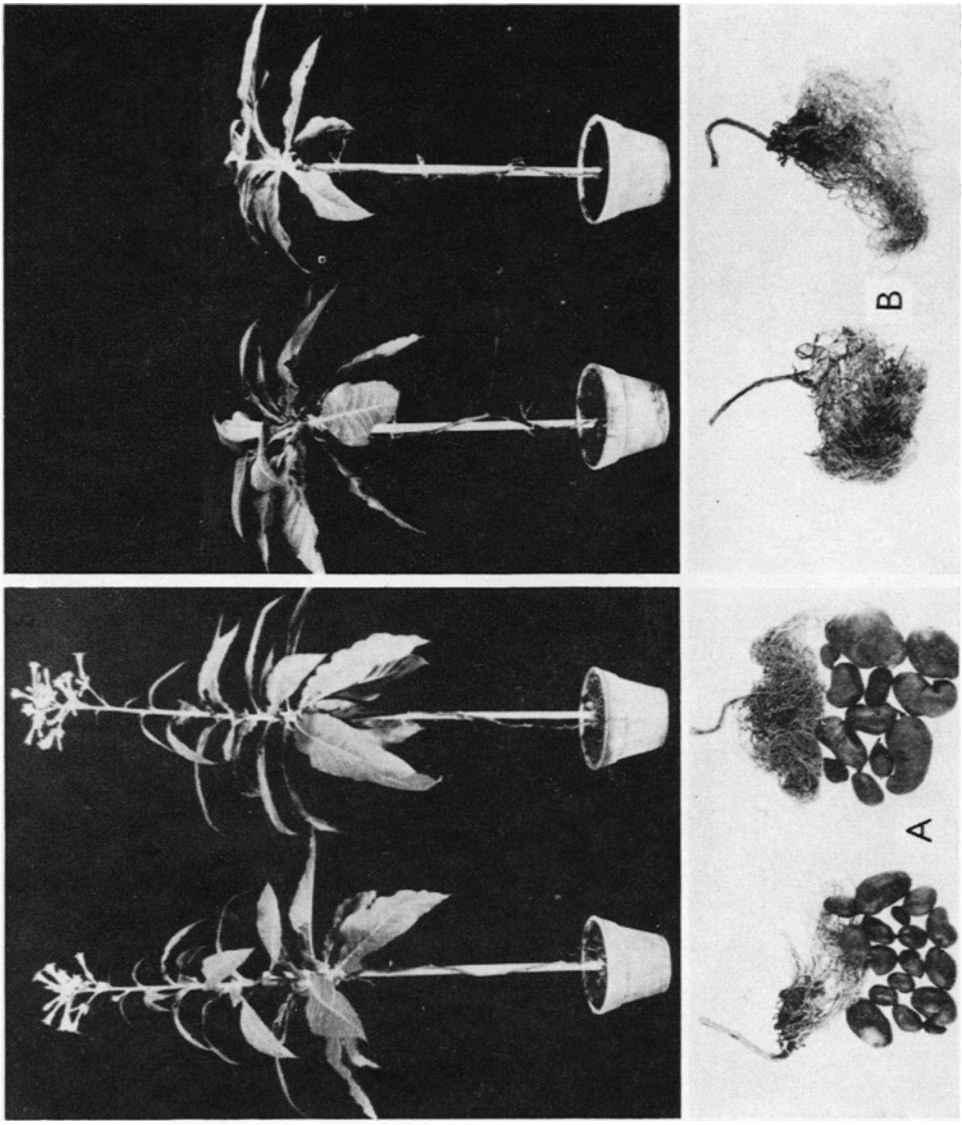

Fig. 5. Grafted plants on short-day tobacco Mammoth onto potato *S. andigenum* under short (A) and long (B) days. Flowering in tobacco scions, tuberization in potato stocks under short days; vegetation in tobacco scions, tuberization in potato stocks under long days.

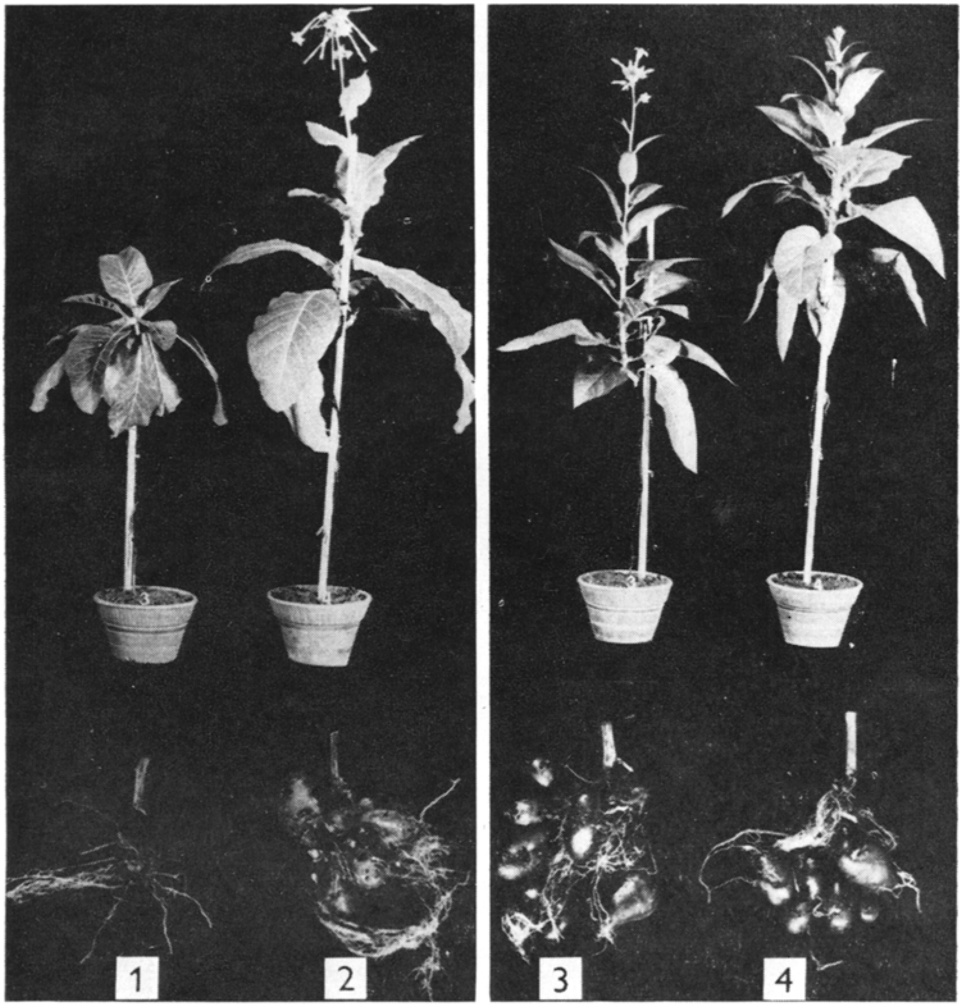

Fig. 6. Grafted plants of long-day *Nicotiana sylvestris* (left) and neutral tobacco Trapezond (right) onto potato *S. andigenum* under short (1,3) and long (2,4) days. In graftings of *Nicotiana sylvestris* on the potato under short days (1) rosette in tobacco scion, no tubers in potato stock. Under long days (2) flowering in tobacco scion, tuberization in potato stock. In graftings of Trapezond onto potato under short (3) and long (4) days flowering in tobacco scions, tuberization in potato stocks.