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Substances of Plant Flowering

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Abstract. The investigation of the hormonal nature of plant flowering in connection with their photoperiodic reaction has shown that flowering depends on a bicomponental system of hormones, gibberellins regulating stem formation and growth and substances of the anthesin type regulating flower-formation. In agreement with the division of the photoperiodic reaction into a leaf and a stem phase the study of the internal factors acting on plant flowering was carried out by means of leaf and stem (apex, bud and callus) models. The results obtained from work with leaf models proved the presence of two groups of hormones of flowering in plants. The data obtained from the application of stem models pointed to the localization of the action of gibberellin and anthesin in different zones of the shoot apices and characterized the potential capacity for flower formation of isolated callus tissue of neutral and photoperiodically sensitive species.

The study of the processes of floral initiation in plants has led us to the idea that flowering depends on the formation of physiologically active substances or hormones of flowering in the leaves. The complex of these active substances has been named florigen (CHAÏLAKHYAN 1937). Later it was suggested that the florigen complex might be formed by two groups of substances of hormonal nature, the gibberellins essential for the initiation and growth of stems and substances essential for flower initiation provisionally named anthesins (CHAÏLAKHYAN 1958). The analysis of the formation of flowering hormones in plants of different photoperiodic groups has shown that the genetic information of the flowering process is realized in two ways, directly through an internal hereditary program and independently on daylength and through an internal hereditary program but under the control of daylength. Thus, it was demonstrated that there are two types of regulation of flowering, an autonomous and a photoperiodic one (CHAÏLAKHYAN 1971, 1972).

In day-neutral species the formation of gibberellins and anthesins is entirely realized by autonomous regulation. Gibberellin synthesis of short-day species is connected with autonomous regulation and anthesin synthesis with photoperiodic regulation. Anthesin synthesis of long-day species is connected with

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autonomous regulation and gibberellin synthesis with photoperiodic regulation. In long-short-day plants and in short-long-day plants the formation of both groups of hormones is subjected to photoperiodic regulation. This scheme suggests the idea that the role of hormones in photoperiodic regulation manifests itself by the changes brought about in the leaves as organs susceptible to photoperiodic induction, while the role of hormones in autonomous regulation is realized through the changes brought about in the buds and stems as organs carrying the hereditary information.

It has been established long ago that the photoperiodic reaction of flowering proceeds in two phases, the leaf phase which is specific for photoperiodism and completely depends on daylength and the stem phase which is not specific for photoperiodism and does not depend on daylength (CHAÏLAKHYAN 1956a, SALISBURY and BONNER 1956, LANG 1965). For a long time research concerning the photoperiodic reaction of flowering was confined to the function of leaves, as at first a leaf model of flowering was elaborated (CHAÏLAKHYAN 1936, MOSHKOV 1936). Later attention was paid to apices, buds and stem segments and a stem model of flowering was elaborated in three forms, an apical one (LANCE 1957, BERNIER 1961, NOUGARÈDE *et al.* 1964), a bud model (LOO 1946, KAWATA 1957) and a callus model (SKOOG 1955, CHOUARD and AGHION 1961). The elaboration of these models led to considerable progress in our knowledge. At present it seems absolutely necessary to study the process of flowering on the basis of a complex application of all these models which permits a more rapid approach and brings us closer to an understanding of the physiological nature of flowering (Fig. 1).

In the present paper new data in favour of the bicomponental system of hormones and its role in photoperiodic and autonomous regulation of flowering are presented which were obtained by means of leaf and stem models. Data obtained from a bud model were published earlier (CHAÏLAKHYAN *et al.* 1961, BUTENKO and CHAÏLAKHYAN 1961).

Materials and Methods

Leaf Model

The investigation of hormones or substances of flowering by means of a leaf model was carried out in two fashions: in experiments concerning translocation of gibberellin and substances of the anthesin type in whole plants and in grafting experiments in which short-day scions were grafted onto long-day stocks.

The experiments on hormone translocation were carried out in collaboration with L. P. Khlopenkova on adult plants of *Perilla nankinensis* which were grown under long-day conditions, then decapitated and divided into two groups. In the first group two large leaves and two shoots located two internodes above them were left on each plant. This variant served for investigating the translocation of substances from the leaves into shoots located above them. In the second group two large leaves and two shoots located two internodes beneath them were left. In this variant translocation of hormones from the leaves into shoots located beneath them was studied. In half of the plants of each group girdling of the stem was carried out between the leaves and shoots at the beginning of the experiment. The leaves were either moistened by means of cotton wool with water (var. 1 and 2) and with a 0.01% solution of gibberellin (var. 3 and 4), resp. for one month or they were induced by 8-h short days by covering them with light-proof paper cases (var. 5 and 6), or they were both induced by short days and moistened with gibberellin (var. 7 and 8). The experiments lasted two months. Gibberellin translocation was estimated from the growth response of the shoots and anthesin translocation from the flowering response.

The grafting experiments with adult plants of the long-short day species *Bryophyllum daigremontianum* were carried out in collaboration with L. I. Yanina. A part of the plants was grown in long day, another one in short day. In the first group plants from long day which served as stocks were decapitated and four large leaves were left on them. The apical part of plants from short day which served as scions was grafted into the split of the stem. After development of leaves on the scions they were decapitated and the newly formed shoots on the stocks were left. Thus, the plants had stocks with leaves growing in long day, scions with leaves growing in short day and shoots located between these two types of leaves. In the second group only leaves were grafted. Scions consisting of stem segments with two leaves exposed to short day were grafted onto decapitated stocks with two shoots and two leaves localized beneath them and growing in long day. Thus, in both groups components not induced to flowering were combined, which distinguished these experiments from those carried out earlier (ZEEVAART and LANG 1962).

Stem Model (apex and callus)

The study of hormones or flowering substances by means of the stem model was carried out in two fashions: in experiments studying the changes occuring in plant apices under the influence of a favourable daylength and gibberellin (apex model) and in experiments investigating the morphogenetic potentions of isolated pieces of stem callus derived from plants belonging to various photoperiodic groups (callus model).

The experiments concerning the changes occuring in the apices in connection with the effect of daylength and gibberellin were performed together with E. L. Milyaeva and I. A. Gukasyan on adult plants of the short-day species *Perilla nankinensis* and the long-day species *Rudbeckia bicolor*. Prior to the beginning of the experiment the plants were grown under unfavourable conditions of daylength. One group of the *Rudbeckia* plants was induced by increasing the number of long days in the single variants. The plants of the other group were treated with increasing quantities of a 0.01% gibberellin solution. One group of *Perilla* plants was induced by an increasing number of short days, the other one was treated with increasing quantities of gibberellin. The stem apices were fixed with Carnoi mixture, and stained according to Feulgen and Brachet. The mitotic index was determined in the central, medullary and lateral zones of the apices. At the some time the height of the plants was measured and their development was being observed.

The tests for studying the morphogenetic potentions of isolated stem callus tissue were carried out in collaboration with N. P. Aksenova, T. V. Bavrina and T. N. Konstantinova. Adult plants of three tobacco varieties served as test objects, the day-neutral cultivar 'Trapezond' (*Nicotiana tabacum*), the short-day cultivar 'Mammoth' (*Nicotiana tabacum*) and the long-day species *Nicotiana silvestris*. Prior to the experiments the plants were grown under long- and short-day conditions, respectively. Stem segments and callus pieces derived from them were cultivated under sterile conditions on the medium of MURASHIGE and SKOOG (1962) supplemented with mesoinositol and thiamine. The cultures were kept in growth chambers under optimal conditions of temperature and moisture and in an 18-hour day (light from luminescent lamps). As the callus cultures grew they were passaged. Growth of the callus cultures, their morphogenesis and their ability to form vegetative and flower buds was examined.

Results and Discussion

Transport of Flowering Hormones in Whole Plants

The main results from the experiments investigating the transport of hormones in whole plants are represented in Fig. 2. They indicate that the transport of gibberellin and substances of the anthesin type, resp. in whole plants is different. Moistening of the leaves with gibberellin (var. 3) led to more rapid growth of the indicator-shoots located above then as compared with the controls (var. 1). This supports the assumption that gibberellin is transported free in the acropetal direction. Girdling of the stem (var. 4) showed that gibberellin moves not only through the phloem but through the xylem, as well. Moistening of leaves located above the indicator-shoots with gibberellin (var. 3) did not enhance their growth, girdling remaining without effect, too (var. 4). This points to a retardation of gibberellin transport in the basipetal direction. Induction of leaves located beneath the shoots led to budding and flowering which points to free translocation of anthesins in the acropetal direction (var. 5); girdling entirely inhibited the translocation of anthesins in the acropetal direction (var. 6). Induction of leaves located above the shoots by short day (var. 5) led to budding and flowering of the shoots which indicates that anthesin is translocated free in the basipetal direction, as well. Girdling (var. 6) completely inhibited translocation. Induction of the leaves by short day and simultaneous moistening with gibberellin yielded the same results as found in experiments in which both treatments were applied separately. These findings confirm earlier work on gibberellin transport (Konovalov *et al.* 1960, Evtushenko 1961) and on translocation of anthesin-like substances (Chaïlakhyan 1956, Chaïlakhyan and Butenko 1957). They support the conception of the presence of two different groups of hormones in the florigen complex.

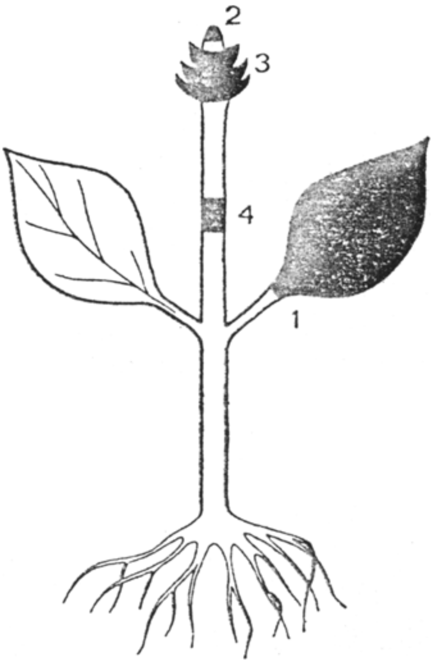

Fig. 1. Models of plant flowering: 1: leaf, 2: apex, 3: buds, 4: callus.

Action of Hormones on Flowering of Shoots in Grafted Plants

The experiments with grafted *Bryophyllum* plants showed that when stocks bearing leaves are constantly exposed to long days and scions bearing leaves to short days the shoots located between these two types of leaves form buds and flowers irrespectively of whether they are exposed to long or short days. In control plants in which both stocks and scions were exposed either to short or to long days the shoots remained vegetative (Fig. 3*A*). The same results were obtained when leaves only were grafted. When scions bearing two leaves grown in short days were grafted onto stocks with two leaves grown in long days the shoots located on the stocks between the leaves from

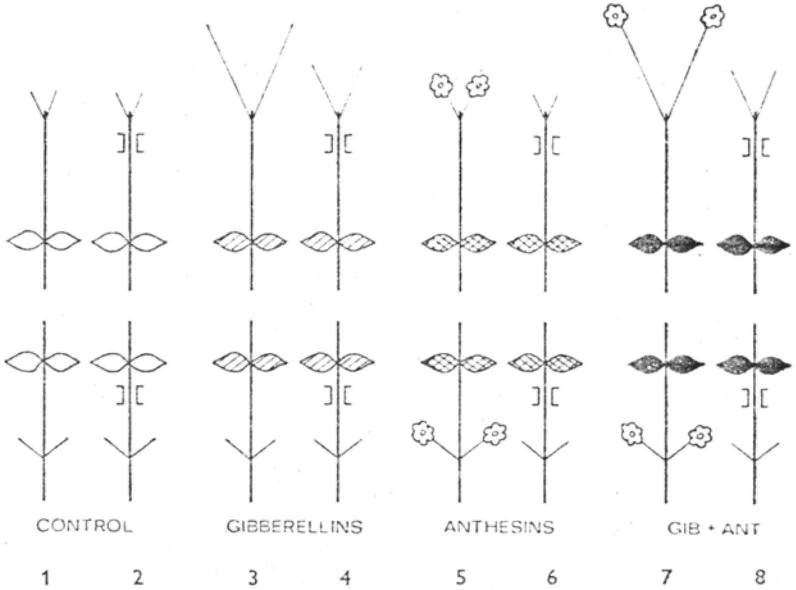

Fig. 2. Transport of gibberellins and anthesins in whole *Perilla nankinensis* plants. Upper row: transport from leaves located beneath the shoots; lower row: transport from leaves located above the shoots. 1, 2, control; 3, 4, gibberellins, 5, 6, anthesins; 7, 8, gibberellins + anthesins. The sites of stem girdling and of flower formation on the shoots are indicated.

long and short days started flowering. In control plants exposed to long or short days the shoots remained vegetative (Fig. 3*B*). These experiments as well as those carried out earlier with grafted *Bryophyllum* plants (CHAÏLAKHYAN and YANINA 1971 1973) indicate that substances formed in the leaves from both long and short days are equally essential for flowering.

It was demonstrated earlier that the substances formed in *Bryophyllum* leaves under long-day conditions are gibberellins (BÜNSOW and HARDER 1956, RESENDE and VIANA 1959, PENNER 1960). The substances formed in the leaves under short-day conditions are substances of the anthesin type (CHAÏLAKHYAN 1964). As *Bryophyllum* forms flowers if long days are followed by short days it may be assumed that at first gibberellins are formed in the leaves in long days and later anthesins are formed in short days. The grafting experiments show that such a successive formation of the two groups of substances separated in time can be substituted by their simultaneous formation separated in space. These tests also prove the existence of a bicomponental hormones system regulating flowering.

Localization of the Action of Hormones of Flowering in the Shoot Apices

In experiments with *Rudbeckia bicolor* and *Perilla nankinensis* the dynamics of mitotic activity of different zones of the shoot apex was compared with the dynamics of growth and flowering as related to induction by favourable daylength and to treatment with gibberellin. It was shown that the activation of the medullary zone brought about by the application of gibberellin or by treatment with long days finally leads to an intensification of stem growth and to slower flowering in *Rudbeckia* or to complete absence of flowering in

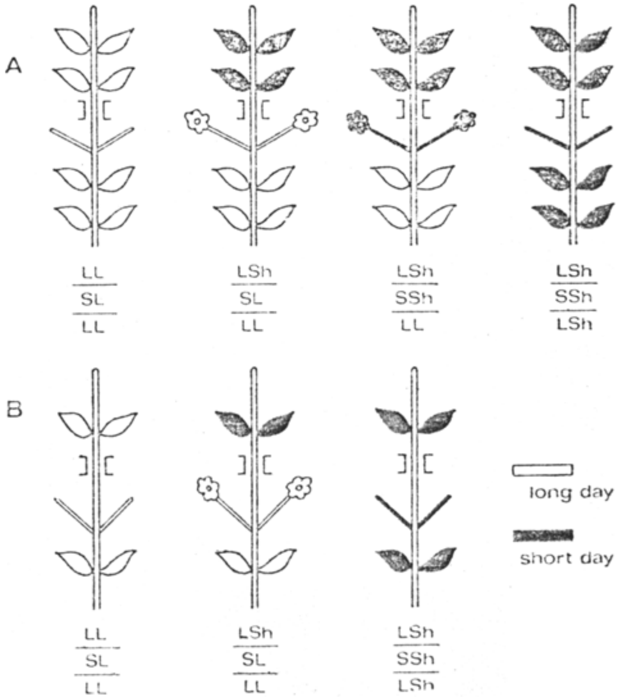

Fig. 3. Flowering in grafted plants of *Bryophyllum daigremontianum*. A: Apical parts grafted onto decapitated stocks. From left to right: control grown in long day, experimental grafted plant with shoots grown in long days, experimental grafted plant with shoots grown in short day, control grown in short day. B: Grafted leaves. From left to right: control grown in long day, experimental grafted plant with shoots grown in long day, control grown in short day. LL: leaves grown in long day, LSh: leaves grown in short day, SL: shoots grown in long day, SSh: shoots grown in short day.

Perilla. The activation of the central zone brought about by substances transported to the apices from leaves growing under favourable daylength leads to a slowing down of stem growth and a stimulation of flowering (CHAÏLAKHYAN *et al.* 1969 GUKASYAN *et al.* 1970). This justifies the assumption that the action of gibberellins is localized in the medullary zone and this of anthesins in the central zone of the shoot apex (Fig. 4).

Rudbeckia plants grown in short days form rosettes and the central and medullary zones of their apices are not active (A 1). If the apex is treated with gibberellin an activation of the medullary zone may be observed at first (A 2) and later an activation of the central zone occurs under the influence of endogenous anthesins (autonomous regulation) (A 3). During induction by long days gibberellins newly formed in the leaves are transported to the medullary zone and lead to its activation, thereupon an activation of the central zone begins under the influence of endogenous anthesins (A 4). *Perilla* plants grown in long days contain endogenous gibberellins (autonomous regulation) and therefore the medullary zone of their apices is active (B 1). After treating the apex with gibberellin the activation of the medullary zone is enhanced but the central zone remains inactive (B 2). After induction by short days anthesins newly formed in the leaves are transported to the central zone and lead to its activation (B 3). Simultaneous application of gibberellin and induction by short days increases the activation of both the medullary and the central zone of the shoot apices (B 4). This localization of the hormones of flowering in the apices and the sequence of their action is reflected by the two-phase character of flowering. Stem formation and growth occur at first and are followed by formation of flowers (CHAÏLAKHYAN 1964, MILYAEVA and CHAÏLAKHYAN 1974).

Morphogenesis of Isolated Stem Callus Cultures and the Hormonal Complex of Flowering

The experiments with isolated stem callus cultures indicated that callus tissue of stem segments derived from young vegetative plants of the day-

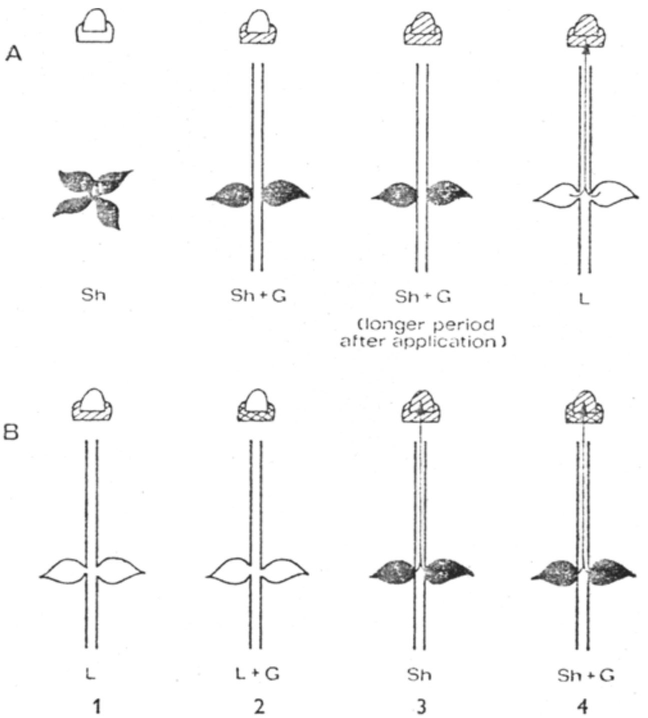

Fig. 4. Localization of the action of gibberellins and anthesins in shoot apices. A: *Rudbeckia bicolor*, from left to right: Sh: after treatment with short day (1), Sh + G: a short time after treatment with short day and application of gibberellin to the apex (2), Sh + G: a longer time after treatment with short day and application of gibberellin to the apex (3), L: after treatment with long day (4). B: *Perilla nankinensis*, from left to right: L: after treatment with long day (1), L + G: after treatment with long day and application of gibberellin to the apex (2), Sh: after treatment with short day (3), Sh + G: after treatment with short day and application of gibberellin to the apex (4).

neutral tobacco cultivar 'Trapezond' regenerate vegetative buds only and never form flower buds. Callus tissue obtained on stem segments derived from the upper part of flowering plants form generative buds with developing flowers. Such a difference in the formation of vegetative and generative buds is observed during three passages the tendency to form vegetative buds gradually increasing. Callus cultures on stem segments derived from both vegetative and reproductive plants of the short-day tobacco cultivar 'Mammoth'' and the long-day species *Nicotiana silvestris* formed vegetative bud only (KONSTANTINOVA *et al.* 1969). Thus the data obtained earlier with various tobacco species (CHOUARD and AGHION 1961, AGHION-PRATT 1965) were confirmed and additionally it was shown that isolated callus cultures preserve the potencies of stem callus tissue cultivated together with the original stem segments (AKSENOVA *et al.* 1972).

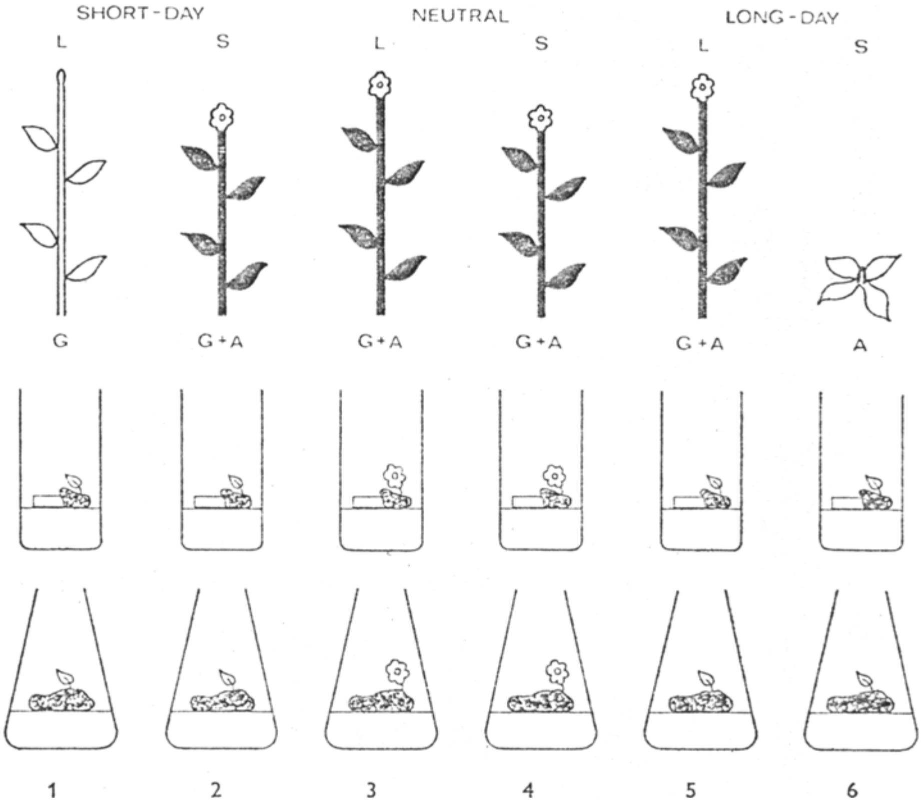

Fig. 5. Morphogenesis of isolated stem callus cultures from different cultivars of *Nicotiana*. Upper row: plants from which stem segments were derived. From left to right: short-day cv. 'Mammoth' (1, 2), day-neutral cv. 'Trapezond' (3, 4), long-day species *Nicotiana silvestris* (5, 6), exposed to long (L) and short (S) days, resp. G: gibberellins, A: anthesins. Middle row: growth and morphogenesis of callus cultures on stem segments. Lower row: growth and morphogenesis of isolated callus cultures. From left to right: 'Mammoth', 'Trapezond', *N. silvestris*.

The striking fact that callus cultures derived from photoperiodically sensitive plants form only vegetative buds may be explained by the fact that flowering in these plants is determined by autonomous as well as photoperiodic regulation while in the day-neutral cultivar 'Trapezond' flowering depends on autonomous regulation only (Fig. 5). In photoperiodically neutral species both components of the hormonal complex of gibberellins and anthesins are formed irrespectively of day length and are probably present in all parts of the plants including stems and apices. Therefore stem callus cultures derived from flowering plants of 'Trapezond' (3, 4) form floral buds. On the other hand, in photoperiodically sensitive species only one component of the hormonal complex is formed, gibberellins in 'Mammoth' and anthesins in 'Silvestris'. Therefore, callus cultures derived from flowering plants of the cultivar 'Mammoth' (1, 2) are unable to form flowers because of a lack of anthesins and of the cultivar 'Silvestris' (5, 6) because of a lack of gibberellins. In the entire plants of these species the deficient hormones are formed in the leaves under favourable conditions of daylength and are translocated to the stem buds.

The above-mentioned assumption shows further possibilities for the use of the callus model of flowering stem callus tissue not only from neutral but also from photoperiodically sensitive plants.

Conclusion

In conclusion it is necessary to dwell on two questions of great importance demanding consideration in connection with a problem of substances or hormones of plant flowering.

Science knows many effects and various compounds causing the induction of flowering of short-day and long-day species under those conditions of environment, when they fail to flower. The existence of great number of substances influencing plant floral initiation does not condition a great deal of internal reactions preceding this process. Apparently, it would be true to suppose that these substances effect on general endogenous system which we imagine to be bicomponent system of hormones of flowering.

Some approaches or methods taken separately are highly fruitful and valuable in the study of such an integral process as plant flowering. However, these are only tactical operations in guessing one of the most interesting riddle of biology. It is strategy in the organization of scientific researches that we need now and such strategy, in our opinion, is complex usage of different models of plant flowering.

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M. CH. ČAJLACHJAN, (Moskva): **Růstové látky kvetení.** — Biol. Plant. **17** : 1—11, 1975.

Studium kvetení z hlediska jeho fotoperiodické podmíněnosti ukázalo na hormonální povahu tohoto procesu. Kvetení je spojeno s dvoukomponentním systémem růstových látek — s gibereliny, jež regulují tvorbu a růst stonku a s anthesiny, jež regulují tvorbu květu. V souhlase s tímto rozdělením fotoperiodické reakce na listovou a stonkovou fázi byly studovány vnitřní faktory kvetení na listových a osních (apikální vrcholy, pupeny a kalusy) modelech. Výsledky s listovými modely prokázaly přítomnost dvou skupin hormonů kvetení. Údaje získané na osních modelech ukazují na lokalizaci účinků giberelinů a anthesinů v různých oblastech vzrostných vrcholů a umožňují charakterizovat potenciální schopnost ke kvetení u isolovaných kalusů získaných z neutrálních a fotoperiodicky citlivých druhů.