Effect of Some Growth Regulators on Growth, Flowering and Fruit-Setting of Tomatoes

By

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INTRODUCTION

The process of flowering represents a radical change in the physiology of higher plants. Suddenly the plant turns from producing stems and leaves to making the blooms that will yield fruit and the seeds of reproduction. Pioneer investigations to track down the physiological mechanism whereby a plant starts producing flowers have been carried out mainly along two lines using two different environmental tools to control flowering, namely vernalisation and photoperiodism. Such earlier experiments had shown that a plant begins to flower only after it has reached a certain maturity known as "ripeness-to-flower", and that the change over which causes a plant's stem tips to begin forming flowers instead of leaves is controlled by some substance(s) produced in its leaves and transported to the growing tips when the plant is subjected to certain photoperiods. On the other side of the same view, it has been established about 50 years ago in 1918 by the German plant physiologist Gustav Gassner (Romberger, 1963) for insensitive plants to photoperiods, but reactive to vernalization for its flowering, that buds itself are the preceptor to the signals which trigger-off this kind of development. Such plants are collectively known as day-neutral and seems to be experimentally very fruitful for acquiring deeper knowledge about the flowring nature.

However, one of the basic difficulties in understanding the biological control of flowering lies in our complete ignorance of the nature of the flowring hormone(s) due to the repeated failure in its isolation; thus our present knowledge of the biological control of flowering is still kept far from being perspicuous. For this, uncounted number of molecular biologists are now developing evidence that hormones such as auxins, phenols and other micromolecules (growth retardants, growth accelerants ...etc.) are the metabolic control agents through their modulation to different enzymatic reactions (Leopold, 1964; Bonner and Varner, 1965; van Overbeek, 1966; Galston *et al*., 1968; Palmer, 1968; Tillberg, 1970). The possibility that such biological agents are directly modifying the genetic potentiality of plants by altering the information transcribed by DNA molecules to various messenger RNA has been frequently considered (Silberger and Skoog, 1953; Patau and Skoog, 1957; Zeevaart, 1962; Heslop-Harrison, 1963; Searle, 1965; Mathur and Sharma, 1968). It has been postulated that the effect of such chemicals is confined to its interaction with the DNA chromatine, thus causing the DNA to be more or less co-operative in directing the synthesis of specific enzymes and other proteins.

It now seems likely that at least some hormones, some of the time, have their effects at the epigenetic level by activating groups of genes. Eventually, it seems that the response which leads to flowering is of this type, that there is a hormone(s) which can trigger release of genetic information that allows flowering if all other environmental conditions required for terminating juvenility are permissive.

For all this, a number of manipulating experiments were carried out in the present investigation to study some basic aspects contributing to flowering of the thermoperiodic tomato plants (Salisbury, 1963), its fruiting and yield as well. The regulating to tomato flowering, fruiting and yield effectiveness of chemically widely related phenols and auxins has been tested. Further biological tests were conducted for the determination of the changes in the levels of the growth promoters and inhibitors existed in stem and leaf extracts taken intervally prior to and concomitant with anthesis as affected by external additives. The role of different tomato organs in commencing the flowering process whether by acting as preceptors for the external stimulus and/or as providers of the needed for floral induction triggering material(s) was again, herein, of a major interest.

REVIEW OF LITERATURE

1. Introductory :

The state of our present knowledge of the biological control of flowering of many, if not all, of the higher plant groupings is far from being perspicuous. In a very general way one can say that even on good sites young plants do not flower until they have attained a certain minimum size, complexity of branching and physiological age. Such statement is not an explanation, but only an enumeration of conditions which usually, or sometimes, are prerequisites to the onset of flowering. It does not address itself to the problem of the means by which it is determined that a bud shall develop into a flower rather than a shoot, as well as it is not the trigger for fruit-set and yield. Physiologists who have attempted to analyse the problem of flowering are apt to find unconvincing any general statement about its control. This is because of the diversity, or even contradiction, of actual observations and the paucity of data from well-designed experiments. Discussion of the problem of flowering with reference to the literature is difficult without involving concepts of juvenility, ripeness to flower, correlations and hormonal regulation.

The view that correlation, or the influence that one part of a plant has on another part, is due to a specific chemical substance was clearly expressed about 1880 when Sachs proposed, on the basis of certain observations, that flower-forming substances are manufactured in different parts and, by moving in very low concentration through the plant, cause the development of such organ (Addicott, 1957). Moreover, data from certain experiments dealing with the flowering problem indicated that the flowering habit of various plants is brought about through the influences of a hormone-like compound which the Russian investigator Chailakhyan in 1937 suggested calling "florigen" (Heslop-Harrison, 1963).

The genetic potentiality of a plant is a function of the information ecoded in the DNA of its chromatine. At any one time most of the DNA is masked or otherwise uncooperative in transcribing its information to various messenger RNA molecules able to direct the ribosomes in the synthesis of specific enzymes and other proteins. The stimulation, however, is limited by the metabolic systems and metabolites available at any one time. Consequently, molecular biologists are developing evidence that hormones, i.e., auxins, phenols and other micro-molecules, are perhaps only sometimes, metabolic control agents in the sense that they directly modulate enzymatic reactions at the epigenetic level. Actually, it is agreeable among most of the plant physiologits that the flowering response is controlled by certain hormonal chemicals that can turn-on certain genes to pass certain genetic information that allows flowering only under certain promising environmental conditions.

For this, flowering response is, at the epigenetic level, involving activation or inactivation of certain groups of genes. Thus, enzyme complements are changed and the dynamic texture and aspect of the interwoven fabric of metabolic reactions are also changed. New organism-level responses are then possible, i.e., flowering, fruit setting and fruit growth.

Based on the foregoing remarks, it seems that our present knowledge concerning the physiological and developmental aspects of flowering in plants is very inadequate. This inadequacy gives rise to confusion which makes the literature difficult to summarize and interpret.

II. Some factors affecting flowering :

A. Environmental factors.

One of the most impressive features about the response of plant to its environment is the direct modification of the organism by the surroundings which provide a synchronizing force for actions of which flowering is of chief importance. In tomato plants, however, 12 stages have been distinguished during the ontogeny of the reproductive organs; the duration of each stage was found to be a product of the interaction between the epigenetic factors and the environmental ones such as light, temperature, etc., (Polumordvinova, 1962).

1. Light and flowering :

Great number of investigations have been carried out to study the flowering response of tomato plants to different light conditions. Experimenting on the effect of day length on tomato flowering, Watanabe (1959) indicated that such treatment affected the flower buds and the degree of flower development, whereas it was ineffective in modifying number of leaves preceding the first inflorescence. However, Cooper (1961) noted that the age at which tomato flower bud first appeared was correlated with the day length; the greater the day length was, the younger the plant at the stage of flower bud appearance. Furthermore, a relation between leaf area at flower bud appearance and day length was established. The author indicated that flower buds appeared with minimal leaf area at a day length approximating to 12 hours; any increase or decrease in light duration was associated with an increase in the required leaf area. Moreover, an inverse relation was observed by Cooper between plant age at the time of the appearance of the inflorescence possessing the largest bud number and the mean day length of the growing period. There was no relation, however, between the age of the plant at the flower bud appearance and the total hours of light received. Similar results have been obtained (Saito and Ito, 1963) when tomato seedlings were subjected to photoperiods from 4 to 24 hours for 60 days from cotyledons expansion. It was shown that flower bud differentiation was earlier with more flower production as the photoperiod was increased up to 16 hours; photoperiods which exceeded 16 hours, however, delayed flowering and reduced flower number. Meantime, Wittwer (1963) found that tomato plants responded to a short (9 hours) photoperiod, given during the 2 weeks following cotyledons expansion. That was evidenced by earlier flowering as indexed by the number of nodes subtending the first inflorescence and by the time of first anthesis. It was added that widely different varieties in the type and earliness of flowering responded similarly to such photoperiod. Wittwer's result suggested that tomato is a facultative short-day plant. It was further observable by Cooper (1964) that the plant age at anthesis of glasshouse tomato plants was related to the mean-day length during the period from germination to anthesis. In line with such earlier observation, Young (1966) found that,16 hours photoperiods increased the number of flower clusters per plant, whereas 10 hours photoperiods promoted earlier flowering.

Conversely, Fölster (1964) did not detect any difference in the number of leaves produced before the first tomato inflorescence by varying day length from 12 to 16 hour photoperiods. Also, Calvert (1964) found that,in summer grown tomato, the reduction of the natural day length to 9 hours did not materially influence the number of days needed to anthesis. Thus, the insensitivity to photoperiods was re-emphasized.

Concerning effects of light intensity, Watanabe (1959) indicated that at low light intensities a longer time was required for flower bud differentiation. The number of flower buds and the degree of flower development, both were found to be affected by light intensity. It was further agreed upon that high light intensity reduced the number of nodes to the first inflorescences irrespective of any practiced photoperiod (Saito et al., 1963; Wittwer, 1963; Fölster, 1964; Verkerk, 1964). At higher light intensity, earlier flower bud differentiation was always obtained. Moreover, such treatment induced greater number of flowers with earlier development. Fölster (1964), however, pointed out that the reduction in the number of leaves to the first truss,due to high natural irradiation, was often followed by an increase in leaf number between the first and second produced trusses. More recently, Saito and Ito (1967) added that lower light intensities also retarded the morphological development of the flowers. Adverse results were obtained, however, by Greig and Al-Tikriti (1963) who indicated that the light intensity received in the seedling stage did not significantly affect the number of blossoms in any of the clusters.

2. Temperature and flowering :

The effect of temperature perse has been frequently cited. Lewis (1953) found that the first tomato flower could be brought down to a lower node by holding newly emerged seedlings at low temperature. Furthermore, Calvert (1957) indicated that the exposure of tomato seedlings to low temperature (16° to 10°C) for three weeks, lowered the first flower almost six nodes; seedling grown at higher temperatures (27°C) had the opposite effect by shifting the first flower to a higher node. Watanabe (1959) established a relationship between the number of leaves to the first inflorescence and low temperatures. He indicated that high temperatures, on the other hand, was ineffective on flower bud development in tomato seedlings. Temperatures higher than normal (18°C by night and 24°C by day) were cited by Anon (1961) to induce more leaves on tomato seedlings before the first truss was initiated; such truss was found to occur rather later than at normal temperatures (12°C by night and 18°C by day). However, it was shown that flowering was accelerated when the night temperature after transplanting was higher than normal (12° - 14°C compared with 10° - 12°C). Fujii and Ito (1962) indicated that high air temperatures resulted in the first flower truss occurring higher up the stem and also promoted the flowering. Saito and Ito (1962) ended to the same conclusion by obtaining earlier flower bud differentiation and development at high day temperatures. High night temperatures, however, induced reverse effects. Maximum flower formation occurred at day and night temperatures of 24° and 17°C, respectively.

The retarding to flowering of tomato plants by high night temperatures and /or low day temperatures, while the opposite holding true, was also noted by different investigators (Fukushima and Masui, 1962; Polumordvinova, 1962; Srinivasan and Hamner, 1962; Hussey, 1963; Fölster, 1964; Verkerk, 1964; Calvert, 1965; Dragonov et al., 1965; Komochi, 1965; Etzel, 1966; Saito and Ito, 1967). More recently, Frenz (1968) also obtained results which are in line with those earlier obtained. He indicated that a temperature regime of 24°C day and 18°C night resulted in the development of more leaves before the first inflorescence, whereas the number of leaves was depending on the variety. The most significant effect of temperature on flower number was observed by Frenz, only in the first inflorescence.

However, the effect of temperature on tomato flowering and its interaction with light has been frequently represented in the literature. Hussey (1963) who concluded that more leaves were formed before flowering at high night temperatures, indicated that the increase in leaf number was greater at lower light intensities. Moreover, Saito et al. (1963) who also agreed on that low day temperature retarded flower bud differentiation, showed that such treatment was effective in increasing flower numbers. They further emphasized that low night temperature accelerated flowering and differentiation. The effect of temperature on the period to flower initiation was believed by Calvert (1964) to be insignificant. He further showed that the inverse relationship between temperature and the period to anthesis was especially marked in low light intensity conditions. Same conclusion was also reached by Fölster (1964) who obtained flowering enhancement under unfavourable temperature conditions by the administration of extra light. Verkerk (1964), however, did not note any interaction between the applied light and temperature at which tomato plants were grown as flower development was considered. Krastina (1968) indicated that the reproductive development in tomatoes was inhibited most by either short or long light cycles if plants were subjected to low temperatures during short photoperiods, or to high temperatures during long ones. Calvert (1969), further exploring the interaction of temperature and light, showed that in low light conditions equivalent to those occurring naturally in mid-winter, an initial period of high temperature followed by low temperature induced a greater flowering capacity in tomatoes than did constant low temperatures.

Differential temperature exposure of tops and roots of tomato seedlings has been experienced by Phatak _et al_. (1966). Such treatments revealed that top temperatures determined the position (as node number) of the first inflorescence, whereas root temperatures influenced the number of flowers in the first inflorescence. Top temperatures of 50° to 55°F significantly reduced the number of nodes below the first inflorescence as compared with 60° to 65°F or 65° to 70°C. Conversely, with root temperature of 50° to 55°F the number of flowers was significantly increased as compared with 60° to 65°F or 65° to 70°F. Phatak _et al_. further showed that the effects of root temperature on flower numbers were graft-transmissible. Hurd and Cooper (1967) provided evidence that the most beneficial effect of low temperature on enhancing flowering in the first truss was restricted to exercising that treatment shortly after transplanting and that the optimal timing for such treatment varied by only a few days over most of the year; in summer, flower number could be doubled, but in winter increases of only 30-40 % were obtained. Chilling, however, was found to delay anthesis by up to 10 days. This delay was shown to be proportional to the duration of chilling.

B. _Some chemical factors_.

1. _Effect of auxins on flowering_ :

Several sources of evidence have lead to the conception that different chemically unrelated groupings play a direct or indirect role in modifying the major physiological phenomenon, namely flowering; thus affecting the overall morphogenesis in higher plants. Such sources were only available via the great achievements accomplished by pioneer investigators, as well as by great number of recent workers in the fields of plant morphology and physiology. One major group of naturally present, as well as artificially synthesized, chemicals which received a great deal of attention, as is logically expected, is the so-called auxins since it has been first discovered in 1928 by Went.

Consequently, the effect of auxins upon flowering was reported by Dostal and Hosek (1936) who found that Indole-acetic acid (IAA), applied to presumptive flowering shoots of <u>Circaea lutetiana</u>, caused their reversion to vegetative growth (Heslop-Harrison, 1963). It was further indicated that such kind of response was commonly observed in plants whose flowering is usually accelerated by exposure to short days. In line with such retarding to flowering response for several plant species by auxin application, Thurlow and Bonner (1947), Bonner and Thurlow (1949), Leopold and Thimann (1949) indicated that the effects of photoperiodic induction in Xanthium were partly annulled by spray application treatments with IAA and NAA given during the daily dark periods. Lockhart and Hamner (1954) reported that when Xanthium plants were treated with IAA solution (50 mg/1) at the beginning of a second dark period (greatly inhibiting to flowering), the effectiveness of this period was greatly enhanced, and suggested that the second dark period and/or the IAA acted either to destroy the flowering stimulus or to prevent intermediate reactions in the production of the stimulus. Consequently, for acquiring deeper knowledge, careful timing experiments were carried out by Salisbury (1955) in which the auxin was applied to the leaf of Xanthium at various times during the inductive dark period and the subsequent light period. Such experiments revealed that flowering in Xanthium was inhibited when auxin was applied before the complete translocation of the flowering stimulus from the leaf. However, when translocation was completed, auxin application promoted flowering and this effect acted independently from the leaf. Furthermore, removal of active buds during or after induction caused dormant buds to remain vegetative. Based on such findings Salisbury and Bonner (1956) deduced that auxin interferes with reactions normally occurring during the photo-inductive dark period.

Different from hindering hormonal translocation as an earlier given explanation for the retarding effect of auxin on flowering, was later offerred by Salisbury (1957) working with various growth active substances in relation to photoperiodic induction of flowering of Xanthium pennsylvanicum. He indicated that IAA, NAA and low concentrations of 2,4-D most likely caused a destruction of the flowering hormone in the leaf in either light or darkness. Similar flowering retardation in other plant species, i.e., chrysanthenum has also been reported by Tsukamoto and Harada (1957) who found that NAA sprays at 50 ppm delayed the flowering in chrysanthemum,and it was only effective if applied before flower bud differentiation. Later Tsukamoto and Tanok (1964) confirmed such findings and further indicated that tryptophane at 100 and 200 ppm inhibited flower bud differentiation, but such chemical did not have any appreciable effects when applied as combined spray with ascorbic acid.

Since the discovery of the group of chemicals which was characterized as specific anti-auxins, based on their biological competition with auxins on the same active sites, effects have been centered around the acceleration of flowering using such competitors. This was based on the hypothesis of lowering the native concentration and/or effectiveness of the flowering retardants (auxins). Promotion of flowering by the use of such chemicals has been reported by Glaston (1947) and Bonner (1949) who found that 2,3,5-triiodobenzoic acid (TIBA)