Regulation of Gynophore Elongation and Fructification in the Peanut *Arachis hypogaea* L.

By

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B.Sc.(Agr.) (Makerere University, Uganda) 1971
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DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Plant Physiology

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

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Committee in Charge

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TO

A. A. Chaula Mnzava

and

M. M. Kiure Mvungi

my parents

ACKNOWLEDGEMENTS

I register my appreciation for the guidance, inspiration and sincere cooperation of Professor William J. Flocker, my Major Professor. I am also thankful for helpful suggestions and prompt attention paid to my work by Dr. George C. Martin (Pomology Department) and Dr. Thomas L. Rost (Botany Department).

The study leave awarded to me by the University of Dar-Es-Salaam's Faculty of Agriculture (the People of The United Republic of Tanzania, alike), the financial support of the African-American Institute, and the Agency for International Development in liaison with the University of California, Davis which made my graduate studies possible, was a heartfelt honor.

To my patient wife, Marian, ever-cheerful sons Elsante and Eneza, and to Lorena and Haron Brown (Huntington, W. Va.) whose encouragement, sacrifice and perserverence had positive influence toward the successful completion of my mission, I express my eternal indebtedness.

I thank Moira Tanaka and Karen Murphy for figure and illustration preparations, Betty Perry for her expert typing and my many friends of the Vegetable Crops Department for their cooperation over the years.

The supply of certified seed from friendly individuals in Plains, GA is cordially appreciated.

ABBREVIATIONS AND NOMENCLATURE

Ancymidol = A-rest = -cyclopropyl- -(4-methoxyphenyl)-5-pyrimidine.

BA = 6-benzylamino purine; Benzyladenine

CCC = Cycocel; chlorocholine chloride = 2-chloroethyl trimethyl ammonium chloride.

CEPA = Ethrel; ethephon = 2-chloroethyl phosphonic acid.

CK = Cytokinin (interchangeably with BA)

GA = Gibberellic acid (GA_3) = 2,4a,7-trihydroxy-1-methyl-8-methylenegibb-3ene-1,10-carboxylic acid 1-4 lactone.

IAA = Auxin = Indol-3yl-acetic acid.

IM = Intercalary meristem.

Morphactin = Chlorflurenol = methyl-2-chloro-9-hydroxy fluorene.

TIBA = Regim-8 = 2,3,5-tri-iodobenzoic acid.

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GENERAL INTRODUCTION

The peanut or groundnut (Arachis hypogaea L.), crop is an important source of oil and protein in the low-land tropics (Rachie and Roberts, 1974) and warm temperate regions of the world (Woodroof, 1969). Together with several other Leguminosae, Cruciferae and Nyctaginaceae (Theune, 1916), it exhibits geocarpy, a mode of reproductive development in which the fruits develop and mature in the soil.

Prior to the study of Smith (1950), the reproductive development in Arachis was invariably misinterpreted. The majority of flowers are aerial but ovaries undergo two successive developmental stages: the aerial gynophoric and the subterranean fructification phases. Aerial gynophores have to elongate and enter the soil before radial ovary growth (to the fruit of commerce) ensues. These two phases are critical as they are ceteris paribus, the post-fertilizational determinants of the economic yield.

The two phases have been studied (Jacobs, 1947; 1951; Smith, 1950; 1956a; 1956b; Shibuya, 1935, Yasuda, 1943; van der Wolk, 1914; Amir, 1969; Ziv and Zamski, 1975; Zamski and Ziv, 1976), however, several problem areas for which present knowledge is meagre are of interest in this study.

Flower fertilization is followed by the initiation of gynophore elongation. Under certain conditions the gynophores fail to elongate, although fertilized ovules remain quiescent but otherwise functional for several weeks (see Gregory et al., 1973). It becomes important to elucidate the nature of the stimulus which evokes intercalary meristem (IM) activity at the base of the ovary and hence gynophore elongation.

From fertilization to conspicuous gynophore growth, a period of 5-7 days elapses during which the ovarian tissues perceive and positively respond to the gravity stimulus. Even under field conditions, any disturbance of plants tending to disorient the gynophores is counteracted by their readjustment to gravitation.

Peanut branching pattern in relation to gynophore growth is peculiar. Negatively geotropic, adiageotropic and positively geotropic aerial structures exist next to each other. Wetmore and Steeves (1971) noted that physiological mechanisms governing response of shoot growth to gravity deserve thorough investigation particularly where both horizontal and upright axes occur on the same plant. If future research should be directed towards attaining aerial fructification, it becomes mandatory that mechanisms of gynophore response to gravity be understood.

Once formed, gynophore elongation may cease prior to soil penetration, a usual phenomenon for those arising from flowers situated higher up on the stem (Amir, 1969), hence they do not fructify. A sustained high rate of elongation is vital for timely fruit enlargement. Some effects of exogenous growth regulators on gynophore elongation have been noted. Jacobs (1951) showed that auxin inhibited elongation while Amir (1969) and Zamski and Ziv (1976) reported that GA accelerated gynophore elongation but how these, together with other growth substances affect elongation and subsequent fructification, is only speculative (Ziv, 1976)[1]. There is no study done to determine gynophore sensitivity to growth regulator dosages except in the in vitro study of Ziv and Zamski (1975). It is not known which growth regulator(s) affect initiation of the IM, direct gynophore curvature and act as triggers of fructification.

In normal culture, the soil is the medium for fructification for several known reasons (see page 8). Apart from the study of Shibuya (1935), Zamski and Ziv (1976), and in the geocarpic Trifolium subterranea L. (Taylor, 1976) in which light was shown to inhibit fructification, the role of light on peanut fruit and seed growth is largely obscure. Yasuda (1943) and recently Zamski and Ziv (1976) noted the necessity for a physical stimulus for fructification. The mechanism by

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[1] M. Ziv, personal communication.

which darkness and mechanical stimulation would induce fructification has not been interpreted.

The control of some of the edaphic factors limiting peanut cropping during reproductive growth (which is a complex function of such soil variables as texture, structure, fertility and biota) (Garren, 1964) have not been attained. Even under the best crop managerial practices, approximately 30% of the crop is lost to the soil (as unrecoverable biological yield) imposing yet another disadvantage of geocarpy on a crop specie. Efforts to induce and maintain aerial fructification are few (van der Wolk, 1914; Yasuda, 1943; Waldron, 1918). Ziv and Zamski (1975) suggested that changes in growth substance balance during gynophore development affected pod formation. It is intended to induce aerial fructification in order to provide some clues on the regulation of the process.

The IM and the ovules are reported to compete for assimilates (Smith, 1956b) so that fructification only occurs after the cessation of IM activity. Similarly, the distal ovule is usually smaller than the proximal and Shibuya (1935) suggested that nutrition to the distal ovule is a limiting factor to its growth. The role of a cytokinin (BA) in the fructification process especially in relation to development of fruit components will be examined.

The gynophore as a unique reproductive structure (Brennan, 1961) has similarities to both stems and roots (Jacobs, 1947) although defined in sensu strictu as a fruit (Smith, 1950). Smith, however, failed to define fruit set and distinguished between elongation and fruit growth while maintaining the ovarian nature of the gynophore. Thus, the gynophore is still of ambiguous nature. Because of the phasic nature of its growth, conventional description of peanut fruit growth is confusing. In this study, a definition of fruit set will be suggested.

As opposed to the approach of Gorbet and Whitty (1975) who assessed various growth regulators for modifying growth habit of plants and effects on

their reproductive potential, the work reported here is at the organ level. The objectives are to study processes of gynophore initiation, response to gravity, elongation, fructification and fruit growth in relation to growth regulators.

LITERATURE REVIEW

A. THE PEANUT PLANT: REPRODUCTIVE DEVELOPMENT

With its origin in Latin America (Krapovickas, 1969; Purseglove, 1968; Rachie and Roberts, 1974), the peanut Arachis hypogaea L. is a papilionaceous hydiserae of the Leguminosae. Until recently, the floral and fruit morphology were misinterpreted (Smith, 1950). The plant as a crop has been a subject of symposia (Arant, et. al., 1951; St. Angelo, et. al., 1973) and a book (Woodroof, 1969).

The main shoot is orthotropic (vertical); in the runner types, the cotyledonery and other buds grow into adiageotropic (horizontal) branches while in erect (bunch) types they grow into plagiotropic (semi-erect) branches. The gynophores emerging from these branches are positively geotropic so that aerial parts of the same plant manifest drastically opposite orientation to gravity. This unique growth habit has an important bearing on fruit production although it has only recently been studied (Ziv, et. al., 1973) in an attempt to elucidate the physiological bases of branching pattern. Flowering is "inverted" in accordance to the geocarpic mode of fruit growth such that the bunch types bear fruits around the base of the plant from plagiotropic branches as flowering progresses towards the indeterminate apices. Although flowering parts are said to be pre-formed in the seed (Van Rossem and Bolhuis, 1954) so that there is no true juvenile phase (Wellensiek, 1977; Leopold and Kriedmann, 1975), there is a natural lag of flowering (see Gregory et. al., 1973) in what Bouffil (1947) referred to as "progression lente."

The flowering and fruiting patterns have been described (Umen, 1933) and mapped (Shibuya, 1935).

B. THE PHASIC DEVELOPMENT OF THE FRUIT

i. THE GYNOPHORE: TERMINOLOGY, STRUCTURE AND FUNCTION

Smith (1950), Jacobs (1947, 1951) and Brennan (1961) have given comprehensive accounts on the peanut gynophore. During this phase of growth, the fruit has been referred to as "gynophore" a term coined by Darwin (1884), literally meaning "gynoceum bearer," while others have used such terms as "carpopodium" and "fruchttrager" (see Smith, 1950). However, it is commonly and descriptively called a "peg" and the period of their formation by the plant is known as "pegging." Taxonomic literature refer to it as a "stalk" or "stipe" which supports the ovary of gynoceum in certain flowers. It is similar to, but not a scape. Its elongation is accomplished by the post-fertilizational formation of an "H" shaped intercalary meristem (Jacobs, 1947) located 2-5 mm proximal to the ovary (Jacobs, 1947; Yasuda, 1943).

Smith suggests that these technical terms are not appropriate when applied to Arachis since the peg-like phase of the fruit ensues from the elongation of the ovary itself. He then defines it as "the young fruit during the stalk-like phase of development which intervenes between syngamy and pod development." Other students of geocarpy hold different views. Thus, van der Wolk (1914) regards the subterranean fruit as "no true fruit but a rhizome within which the true pod is enclosed." He further states that the ovary is enveloped by a receptacle which becomes elongated and as the stalk shaped organ penetrates into the ground, the tip of the stalk then curves horizontally, begins to swell and forms the fruit. He refers to it as a stem. Marggraf, in 1648, first described the plant and figured it with fruits attached to the root system as though they arose therefrom. Other workers (see Smith, 1950) describe the pegs as "naked female flowers" and the showy flowers as being "male and sterile", an unfounded case for floral dimorphism of Bentham (1855). Smith is a proponent of the ontogenic ovarian nature of the gynophore, hence calling it a fruit at an early stage of

development. The definition of a fruit as given by Nitch (1962) and Coombe (1976) has to encompass both ontogenic and physiological aspects. The later aspects are least understood for the gynophore.

Both Jacobs (1947) and Brennan (1961) describe the gynophore anatomy to resemble that of a herbaceous dicot stem. The gynophore has both the features of stems and roots (see Jacobs, 1947). Functionally it is root-like in being able to absorb water and nutrients from the soil (Bledsoe and Harris, 1950; Buckhart and Collins, 1941) and possesses root hairs (Waldron, 1919; Ritcher, 1899).

Jacobs (1951) demonstrated the auxin relations in the gynophore and found its similarity to stems in this respect, however, Amir (1969) observed their ability to postpone senescence of the tops by possibly producing cytokinins and equated them to roots. Ziv and Zamski (1975) and Brennan (1964) studied gynophore behavior in vitro. The former noted their positive geotropism is not affected by light regime typical of roots while the latter found that they give rise to roots at their physiological bases manifesting similarity to shoots. It is normally held as a tenet in experimental anatomy to relate structure to function (and not vice versa). Esau (1969) outlines conceptual differences and similarities between roots and shoots, however, for the gynophore, structure is seemingly unrelated to physiological function and behavior.

ii. FRUIT GROWTH AND DEVELOPMENT

Peanut flower fertilization takes place above the soil followed by the development of a subterranean pod after gynophore has elongated and buried. The flowers are cleistogamous (Smith, 1956a) so that those near the soil grow into pegs without being externally visible. Subterranean flowers on fertilization develop into fruits with minimal gynophore elongation (Tetenyi, 1957), a feature that led Marggraf's misinterpretation of fruiting morphology. Under such conditions, fruit growth is rapid as opposed to when fruit growth is a result of gynophoric elongation. As a basis for cultural practice, covering plant bases with

soil at pegging facilitates earlier fruit growth despite disapproval by Acland. (1970).

Aerial flower fertilization is followed by withering of floral parts and the initiation of an intercalary meristem at the base of the sessile ovary to form the gynophore which elongates with the ovules at the tip (Jacobs, 1947; Brennan, 1961; Theune, 1916; Smith, 1950). Jacobs (1947) outlined the extent of the meristem and postulated how the elongation process is accomplished while the IM maintains a constant position behind the ovules.

Gynophore elongation in relation to fructification has been studied (Shibuya, 1935; Yasuda, 1943; Smith, 1956b), but there are disagreements as to the onset of embryo growth (see Schenk, 1961). Zamski and Ziv (1976) have reported that the proembryos control elongation although themselves remain dormant.

C. THEORIES FOR AND REQUISITES OF FRUCTIFICATION

Fruit enlargement rarely occurs above ground to the point where viable seeds are produced. Soil penetration is necessary to provide the necessary moisture (Shibuya, 1935; Yasuda, 1943; Badami, 1935) and darkness (Shibuya, 1935). Equally essential is calcium absorption and its role in pod formation (Mizuno, 1959; 1962; Bolhuis and Stubbs, 1955). Wiersum (1951) established that after soil penetration, the gynophore xylem system became functionally independent from the parent plant root system so that direct calcium absorption by them was afforded.

Light inhibits fruit development (Shibuya, 1935; Waldon, 1919; Zamski and Ziv, 1976). Gynophores from subterranean flowers lack the light induced inhibition of fruit enlargement. The mechanisms by which light inhibits fructification are not known, however, Shibuya (1935) reported the possible involvement of phytochrome when studying spectral dependency of this process. Other factors, i.e. pH changes, shifts in redox potential, basicity of embryo

protoplasm and moisture stress relating to fruitification processes have been reviewed (see Schenk, 1961).

Yasuda (1943) added pressure and mechanical stimulus as other factors necessary for fructification. The physiological basis for these factors have not been explained for the gynophore.

Smith (1956b) studied embryo and endosperm development in relation to fructification. In aerial pegs, ovules enlarge slowly and he attributed this to an insufficiency of nutrients which prevented seed development during rapid peg elongation. The IM, being proximal to the ovary, is thought to monopolize assimilates such that only after IM activity has stopped does fructification proceed. Linked to this assimilate monopoly hopythesis, Shibuya (1935) attributed the reduced growth of distal ovules to monopoly of assimilates by the proximal ovules.

D. ROLES OF HORMONES IN GYNOPHORE ELONGATION AND FRUCTIFICATION

The hormonal theory of fructification was first suggested by Badami (1935) whose studies implied that the embryo controls elongation probably by secreting a hormone which stimulates division and elongation of the tissue just basal to the ovules. However, Jacobs (1951) was first to show that auxin controlled gynophore elongation. He showed that auxin was produced by the ovary and moved polarly and basipetally across the active meristem. After soil penetration, he postulated that auxin levels increase and inhibit further elongation. Gynophore explant elongation was inversely related to exogenous auxin concentration. Yasuda (1943) reported that application of auxin to gynophore tip caused swelling of the ovary and unilateral curvatures when applied to one side. Sreeramulu and Rao (1971) found that auxin increased in the course of fructification.

The role of GA in promoting elongation of the gynophores was reported by

Amir (1969). Ziv and Zamski (1975) reported that 0.01 ppm kinetin and 0.1 ppm (and lower) of auxin promoted elongation whereas higher concentrations inhibited elongation and induced fructification. Response to kinetin and auxin was a function of gynophore age. Ziv (1976)[1] speculated that GA was responsible for elongation while CK and IAA controlled fructification.

E. INDUCTION OF AERIAL FRUCTIFICATION

According to Theune (1914) Treviranus, in 1863, was first to use the term geocarpy to refer to fruit development in soil. van der Wolk (1914) and Waldron (1919) first attempted to induce aerial fructification. Limited success was reported by Waldron under dark humid conditions while van der Wolk reported the necessity of a soil extract. Yasuda (1943) in an important quest on the problem wrote, "Peanuts can bear fruit only underground. Fructification in air, that is, the natural characteristic of other plants is quite impossible for this plant. But why?" Some of the factors necessary for fructification have been reported (see page 8) but no attempt has been made to put them together (and those known in other plant systems) to induce aerial fructification.

PART I

INITIATION, GEOTROPISM, AND ELONGATION OF GYNOPHORES IN RESPONSE TO GROWTH REGULATORS

INTRODUCTION

The structural features of the sexual reproduction in the peanut has been worked out and described with great precision (Smith, 1950, 1954) yet little is known of the physiological aspects of this phase. The concept that as a result of the gametic union growth is stimulated was first demonstrated in 1926 by Murneek and later elaborated by Murneek and Wittwer (1943) and Wittwer (1943). The presence of auxin in pollen was shown by Laibach (1932) and complete substitution of pollination by auxin to induce fruit set in some species is well documented since the studies of Gustafson (1936, 1937). Others (Muir, 1942; Lund, 1956) have shown that pollination results in the stimulation of auxin formation in the gynoceum. However, McLane and Murneek (1952) coined the term 'syngamin' to refer to the non-auxinic hormone resulting from the fertilization process in Zea. Various other hormones have been identified in fruits and seeds and participate in fruit set and growth (Crane, 1964; Nitch, 1962; van Overbeek, 1962; Weaver, 1973).

In the peanut, the stimuli for fruit set and growth are not known. With successful fertilization, a burst of growth of the otherwise erstwhile ovary occurs in a manner dissimilar to that of ovaries commonly encountered. The peanut ovary is sessile at anthesis (Smith, 1950) and growth in length occurs only after syngamy (Bolhuis, 1957). As described by Smith (1956b), the ovary proper remains quiescent and instead an 'accessory' tissue is produced by the activity of an IM.

Studying gynophore initiation and elongation is basically examining factors which regulate IM activity. Several studies on IMs have involved reproductive

structures (i.e. scapes) and vegetative parts in monocots. The techniques employed in studying the control of IM activity usually entail surgical removal of parts of the organ examined. The gynophore offers several advantages over other organs. It lacks complicating appendages, thus rendering surgical techniques unnecessary; the stimuli which evoke IM activity can carefully be eliminated making it possible for in vivo testing of specific growth regulating substances; the absence of parthenocarpy ensures that the role of ovules in fruit growth can be scrutinized; the floral structure lends itself to experimental design (see Methods); and the polarized gynophore growth affords linear measurements of IM activity. The positive geotropism of the gynophore necessary for geocarpy has received least research attention. Current theories of geotropism emphasize differential hormonal distribution (See Audus, 1969; Juniper, 1977). The use of inhibitors of certain hormone biosynthesis, transport or action is among the criteria by which a hormone may be implicated in regulatory phenomena (Jacobs, 1959). This study will examine the simultaneous effects on curvature development and growth of IAA, GA, BA and certain inhibitors, namely, ancymidol, morphactin, CCC and TIBA.

Yasuda (1943) and Zamski and Ziv (1976) have indicated that the ovules (proembryos) regulate IM activity. Jacobs (1951) showed the retarding effect of auxin on elongation and Amir (1969) reported on the ability of GA to enhance upper nodal gynophore growth. Further study became necessary to establish the effect of certain inhibitors, hormonal interactions, effect of gynophore age on the response to GA and to re-examine the variation of the IM zone in time. The fate of the IM is not well understood and neither is the relationship between IM activity and fructification. Since depth of fructification is an important parameter in peanut agronomy, the effects of growth regulators on the onset of fructification was studied. A modification of gynophore growth on the plant would facilitate future studies on aerial fructification, therefore the effect of morphactin intact gynophore formation and growth was examined.

MATERIALS AND METHODS

(a) GENERAL

Peanut seeds (Spanish bunch cultivar) obtained from Plains, Ga were sown in plastic pots in a 3:1 Yolo sandy loam vermiculite mixture. To ensure erect root and shoot systems, the seeds were oriented at sowing such that the radicle-end pointed downwards (the seed has a straight embryonic axis and the radicle-end is discernible on inspection). The depth of sowing was kept uniform at 3 cm to ensure even emergence (hence flowering) and initial balance between hypocotyl and radicle growth (see Gregory, et al., 1973).

Plants were grown in a growth chamber at constant temperature (26.5°C) and a 12 hour photoperiod which favored fast growing plants and numerous gynophores as shown by Jacobs (1951b). Light intensity of 500 μ-Einsteins m^{-2} sec^{-1} was maintained by a combination of incandescent and flourescent lights placed a meter above the canopy. Relative humidity was about 90%.

Plants were watered alternately with half strength Hoagland's solution and distilled water. At flowering, floral buds, flowers and gynophores were tagged for the various experiments in Part I and Part II of this study. When gynophore explants were desired in some experiments, they were excised and treated as appropriately described. Because plants whose gynophores or floral buds were treated with hormone solutions were used only once (despite continuation of flowering), continuous planting became necessary to provide new experimental material.

(b) EXPERIMENTAL

A. INDUCTION OF GYNOPHORE ELONGATION BY GROWTH REGULATORS IN THE ABSENCE OF FERTILIZATION

At flowering, floral buds were tagged and groups of 8 were assigned to each of the treatments. After the hypantha (calyx tubes) had elongated to 4 cm before the floral bud had opened, the top part of the flowers were removed so

that the superior but uniquely positioned ovary, part of the style and the hypanthium portion ensheathing the ovary was left attached to the plant (Fig. 1a, 1b). To this natural chamber, 0.2 ml of GA of various concentrations (1, 5, 10, 15, 20 ppm); BA (10 ppm); Morphactin (10 ppm); IAA (1 ppm) and a combination of GA (10 ppm); BA (10 ppm) and IAA (1 ppm) were added with a micropippette. A drop of 0.01% Tween (Polyethylene sorbital), a surfactant, was added to the solutions during preparation. As controls, some buds with floral parts similarly removed were treated with equal amounts of distilled water and for some, fertilization was allowed to take place without such flowers being treated. Chemical treatment was done twice before termination of experiment after 14 days. Where hypantha had abscissed, the experimental materials were sprayed to dripping. These treatments were repeated on floral buds on new plants raised from seed. Since the peanut inflorescence is comprised of 3 flowers (Smith, 1950) (usually one or two developing to anthesis), only one per inflorescence and not more than 4 per plant were treated with any one chemical to avoid subsequent whole plant modification and/or interaction of growth regulators within one plant. To test the effect of CEPA and its antagonist, Ag^{+} ions on flower senescence and subsequent gynophore growth, groups of 8 flowers permitted to fertilize were twice sprayed with either CEPA (10 ppm) or $Ag\,NO_3$ (50 ppm) during a 14 day period after which all samples were excised from the mother plant and extent of IM activity was measured as growth in length of the gynophore. Other observations such as extent of curvature and degree of flower (or floral part) senescence were noted relative to the control. Unfertilized growth substance-treated ovaries were later buried in order to observe the significance of proembryo formation on the fructification process.

B. POST-FERTILIZATION ELONGATION OF INTACT GYNOPHORES FOLLOWING GROWTH REGULATOR TREATMENT

After gynophores had elongated to 1 cm (with display of positive geotropic

Fig. 1a. Peanut flower structure (Schematic longitudinal section). Note the position of the sessile ovary in relation to stamens and stigma.

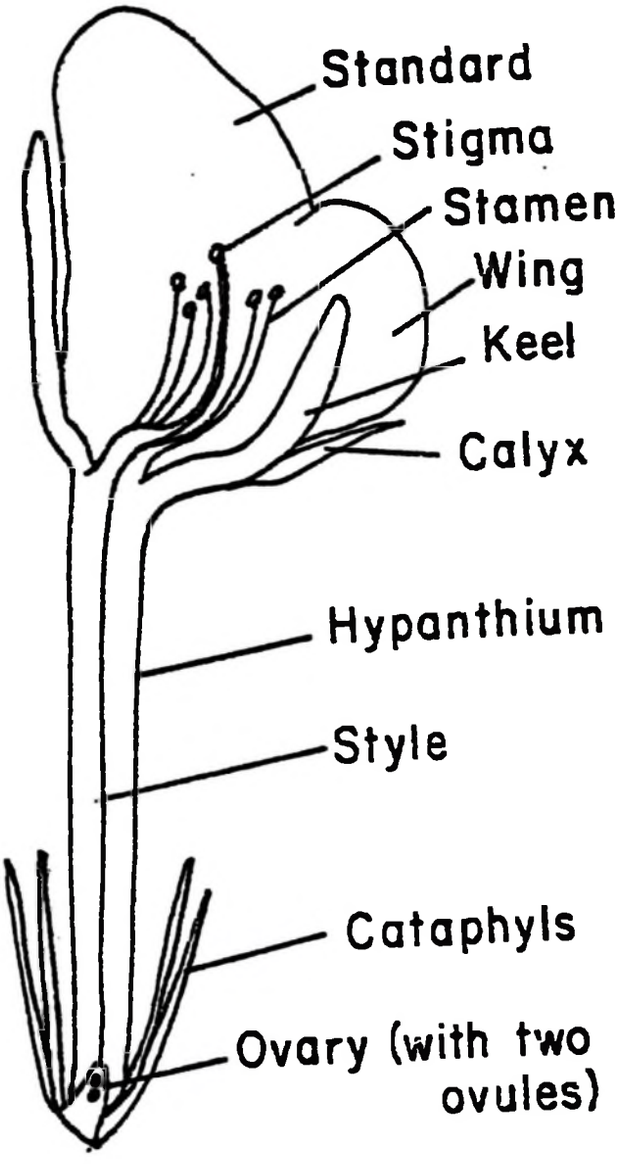
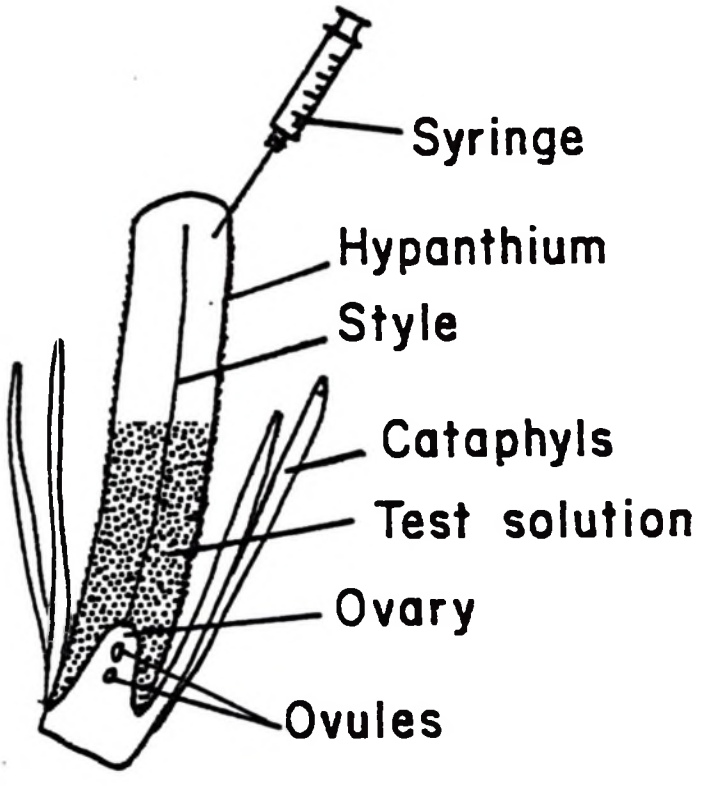

Standard
Stigma
Stamen
Wing
Keel
Calyx
Hypanthium
Style
Cataphyls
Ovary (with two ovules)

Fig. 1b. Technique permitting treatment of ovary with test growth substances in the induction of IM activity in the absence of fertilization.


Syringe
Hypanthium
Style
Cataphyls
Test solution
Ovary
Ovules

curvatures), groups of 10 were tagged and sprayed to dripping with growth regulator solutions as follows: GA (20 ppm); IAA (10 ppm); BA (20 ppm); TIBA (10 ppm); CEPA (20 ppm); CCC (10 ppm) and morphactin (15 ppm). The controls were sprayed with distilled water. To demonstrate the dependency of intercalary growth on ovules (proembryo), some gynophores had ovules (ovary) surgically removed without removing the IM. Gibberellic acid (20 ppm) was sprayed to such decapitated gynophores and the effects of these regulators on elongation were measured daily for a period of 15 days. The effects of BA and IAA on GA-promoted growth were studied. Forty tagged gynophores were sprayed with GA (20 ppm) and divided into two groups. After two days groups of 10 received either BA (20 ppm) or IAA (10 ppm). A similar treatment was done on previously GA-treated gynophores after 5 days. Elongation was measured daily. The effect of GA concentrations (50 and 100 ppm) on varying gynophore initial lengths (hence age) was examined for gynophores 1, 4 and 7 cm long. Ten of each gynophore length class were treated as above and their lengths were measured after 2, 4 and 8 days. The above treatments were applied twice during the experimental period and repeated on gynophores from plants raised from seed.

C. ZONE OF ELONGATION AND AGE OF GYNOPHORE IN RELATION TO FRUCTIFICATION

Aerial gynophores of initial lengths 2 and 6 cm were selected. Groups of 10 were marked with Indian ink at 2 mm intervals from the ovular end up to eight portions. Gibberellic acid (20 ppm) was sprayed once on a separate group of 2 cm long gynophores. After a week of elongation, gynophores were excised and lengths of marked portions measured. Due to growth, the intervals were remarked to correct for the distortion that occurred and to permit accurate measurements. Soil penetration by these gynophores was prevented.

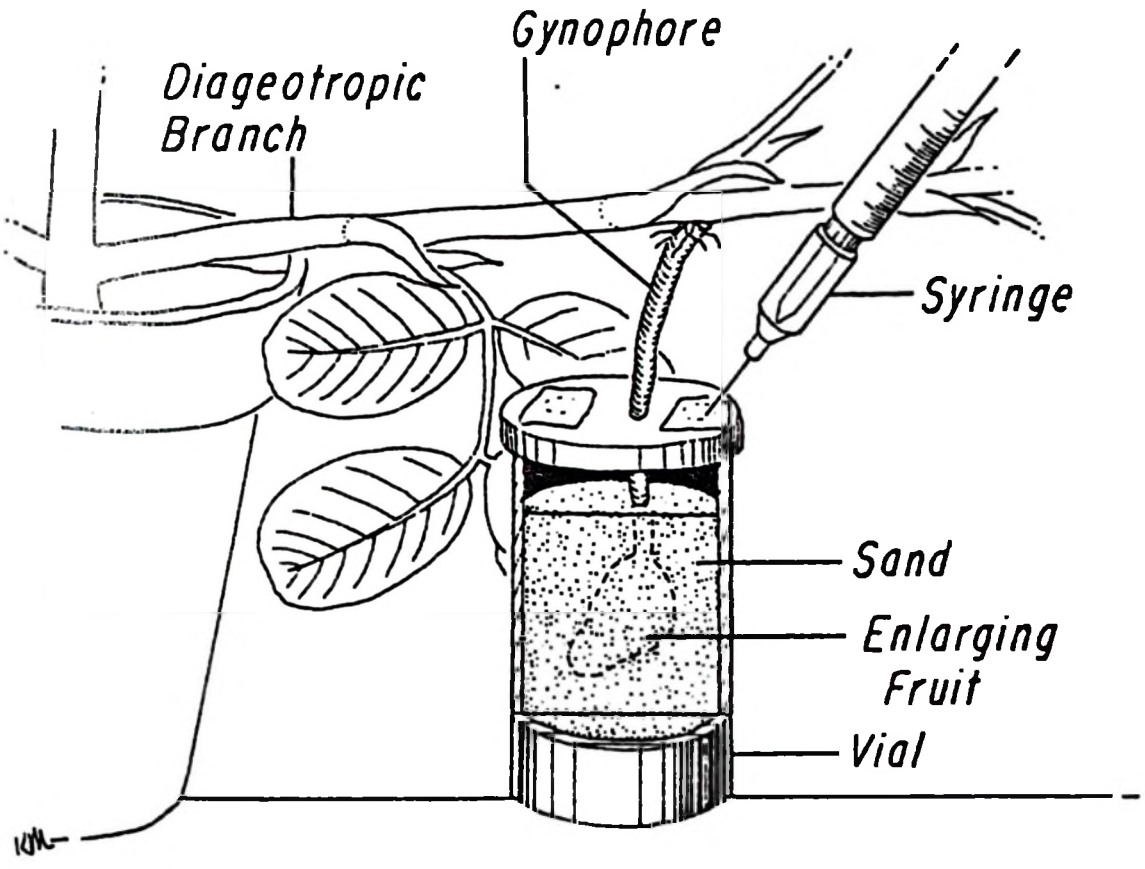
In another experiment, gynophores of initial lengths 2, 4, 6 and 9 cm were tagged and allowed to bury themselves in sand placed in black vials without cap

(Fig. 2). After 14 days, by which time fructification was complete, they were unearthed and depths of fructification determined by measuring the length of the etiolated portion. All the above treatments were duplicated.

D. GEOTROPISM AND ELONGATION OF EXCISED GYNOPHORES IN THE PRESENCE OF GROWTH REGULATORS

Aerial gynophores were excised when they were about 4 cm. They were immediately washed with distilled water to remove adhering debri and withered floral parts, surface sterilized with 1% Clorox (5% sodium hypochlorite) for 5 min and rinsed with generous amounts of distilled water. Five mm segments measured from the distal portion thus including the ovary with 2 ovules were excised with razor and placed horizontally on folded filter papers in petri dishes so that half the length of each gynophore protruded beyond the supporting papers. They were treated with five ml of distilled water or various concentrations of morphactin (0.01, 0.1, 1, 10, 30, 50 ppm); Ancymidol (0.1, 1, 2, 10, 20, 50 ppm); TIBA (0.01, 0.1, 1, 10 ppm); BA (10^{-5}, 10^{-3}, 10^{-1}, 1, 10 ppm); GA (10^{-6}, 10^{-4}, 10^{-2}, 10^{-1}, 1 ppm) and IAA (10^{-9}, 10^{-7}, 10^{-5}, 10^{-3}, 10^{-1}, 1 ppm). Neither surfactant nor buffer were used since preliminary observations did not show their necessity. Morphactin treated explants were, in a separate test, incubated with 0.1 ppm IAA, while Ancymidol treated explants were incubated with 0.1 ppm GA. The dishes containing all concentrations were incubated at room temperature including a water control and no special light conditions were maintained. Incubation time was 72 hrs by which time geotropic curvatures of 90^{o} for control were fully manifested. Each treatment was duplicated. Growth in length was measured with a finely graduated ruler to the nearest mm. The geotropic angle was determined by dipping each gynophore in ink and making imprints on lined paper. Curvature was measured by drawing a line on the imprint tangent to the growing point and relating it to the axis of the non-affected tissue (Fig. 3a).

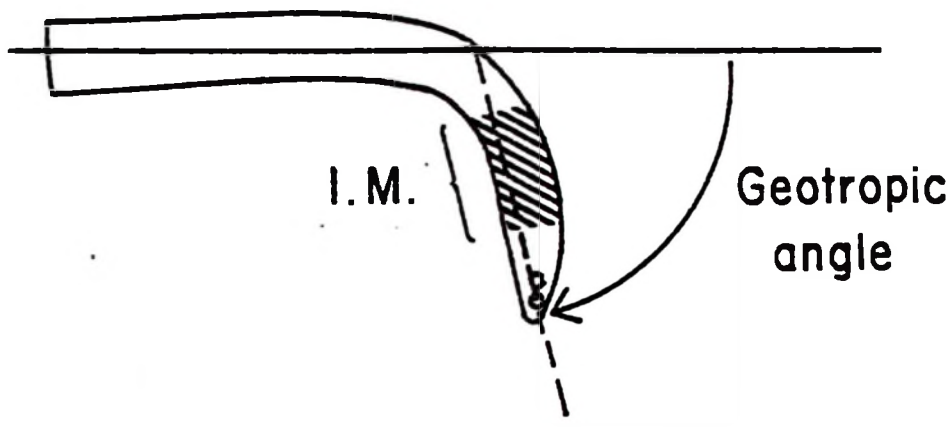
Fig. 2. Method of growth regulator treatment of gynophores buried in sand-containing vials in which depth of fructification was determined.

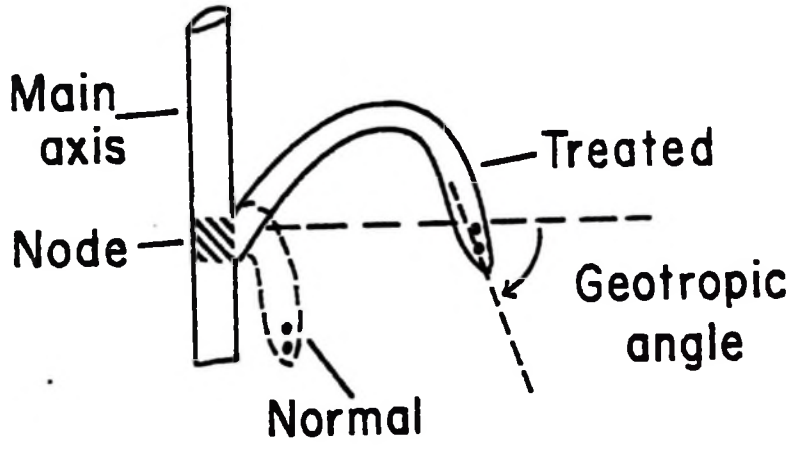

Gynophore
Diageotropic Branch
Syringe
Sand
Enlarging Fruit
Vial

To observe the effects of morphactin on intact gynophore geotropism, ten flowers at anthesis were sprayed once with 50 ppm morphactin to dripping. Their geotropic response was measured non-destructively after they had attained average length of 1 cm by tracing them on transparent paper placed in front of them. Angle orientation of the gynophore tip (with respect to the horizontal) was measured in the manner shown (Fig. 3b.) The measurement was discontinued when the gynophores had aligned themselves with the plumb line.

Fig. 3a. Geotropic angle measurement on excised gynophores. Note position of the l.M.

Fig. 3b. Geotropic curvature determination on intact gynophores arising from flowers treated with morphactin at anthesis. Note gynophore trajectory in comparison to the normal (untreated).


I.M.
Geotropic
angle


Main
axis
Node
Treated
Geotropic
angle
Normal

RESULTS

The ability of various growth regulators to induce gynophore elongation by evoking IM activity in the absence of fertilization and syngamy is demonstrated (Fig. 4). A mixture of GA, IAA and BA was most effective. Neither did BA, IAA or their combination cause appreciable elongation, however, morphactin was capable of stimulating IM activity. Fertilized ovaries showed high IM activity which was reduced by CEPA or Ag^{+} ion treatment. It was observed that Ag + ions profoundly delayed senescence of floral parts particularly the abscission of hypantha base while CEPA treatment reduced life span of the flowers. Gibberellic acid alone (Fig. 5) was effective in stimulating IM activity in the absence of syngamy although the dose-response curve indicates saturation as concentration is increased. It is demonstrated that the mother plant plays hardly any role in inducing IM activity.

The post-syngamic elongation of intact gynophores after the geotropic curvatures are manifested is accelerated by exogenous GA alone and inhibited by all other growth regulators tested (Fig. 6). The ovary proper controls the activity of the IM such that its surgical removal stagnates elongation. Treatment with CEPA, TIBA, and morphactin showed the most retardation as compared to CCC, BA and IAA effects, however, gynophores were capable of slow recovery. Gibberellic acid was effective in stimulating intact gynophore elongation but GA-induced elongation was inhibited by either BA or IAA (Fig. 7). This inhibition was accentuated by gynophore age so that both BA and IAA manifested drastic effects when applied at a later date. Auxin showed more inhibition of GA induced elongation for younger gynophores than BA. GA slightly promoted elongation of decapitated gynophores (i.e. without ovules). Gibberellic acid promotion of intact gynophore elongation is dependent on gynophore age and GA concentration (Fig. 8). Younger gynophores were the most responsive especially at the higher GA concentration while response diminished as they

Fig. 4. Induction of IM activity by growth regulators in the absence of fertilization. F = Fertilized, NF = Not Fertilized, MOR = Morphactin.

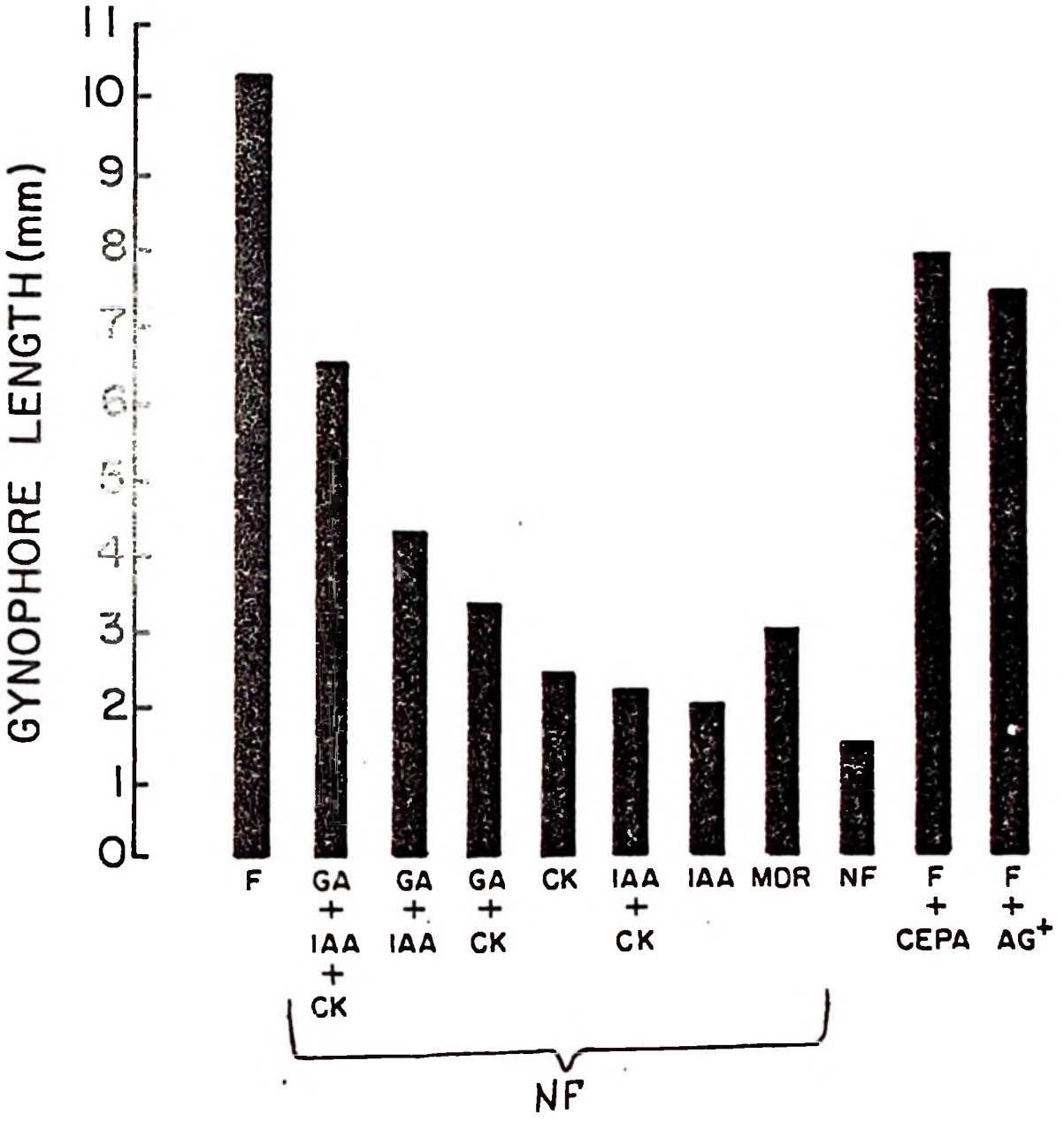

GYNOPHORE LENGTH (mm)
0
1
2
3
4
5
6
7
8
9
10
11
F
GA + IAA + CK
GA + IAA
GA + CK
CK
IAA + CK
IAA
MDR
NF
F + CEPA
F + AG+
NF

Fig. 5. Dependency on GA of IM activity in the absence of fertilization. A dose-response relationship. GA concentration in μg/flower.

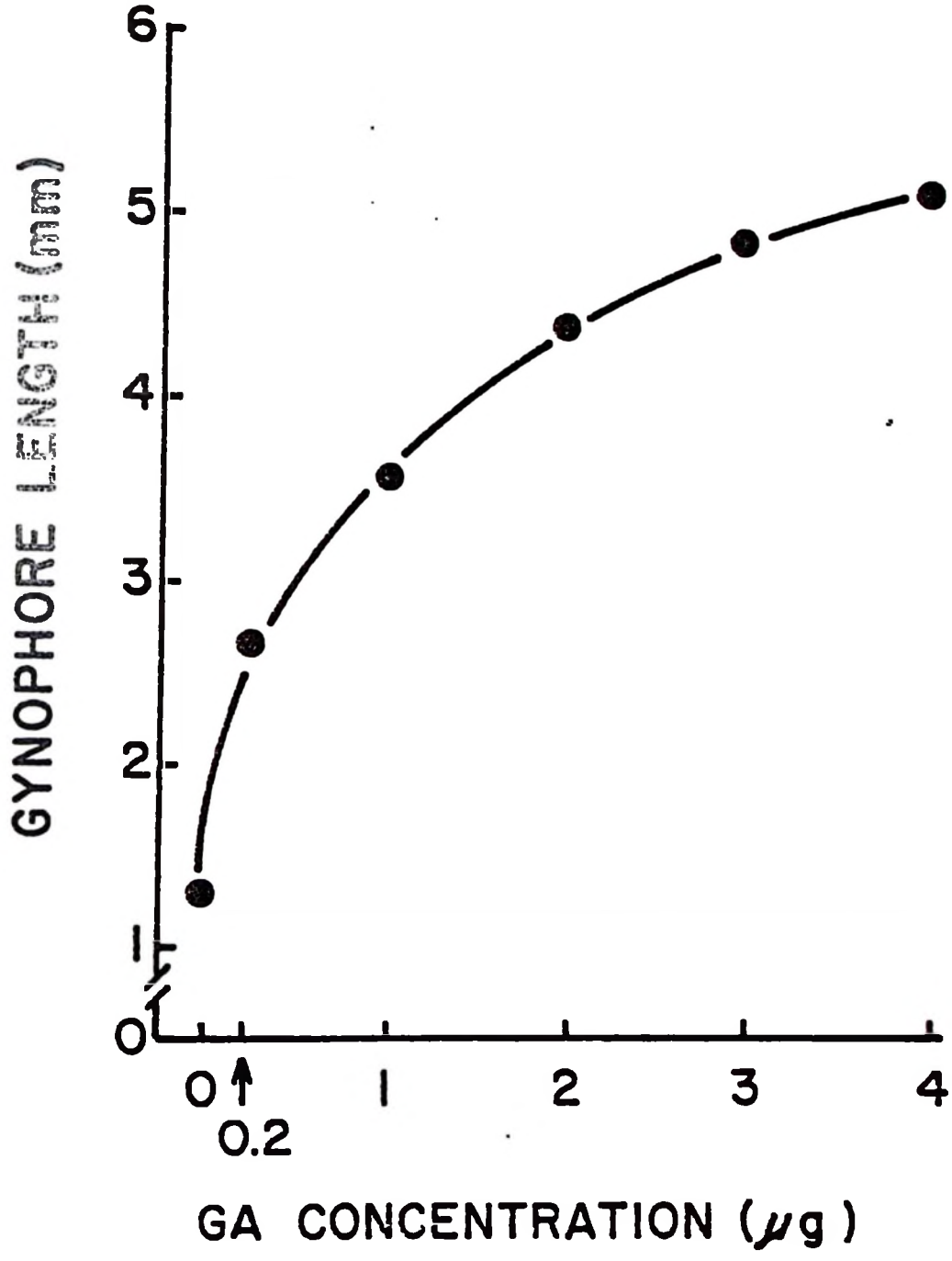

GYNOPHORE LENGTH (mm)
6
5
4
3
2
1
0
0
0.2
1
2
3
4
GA CONCENTRATION (µg)

Fig. 6 Post-fertilization elongation of intact gynophores by various growth regulators. Note .the effect of ovule removal. ETHR = Ethrel, MORPH = Morphactin.

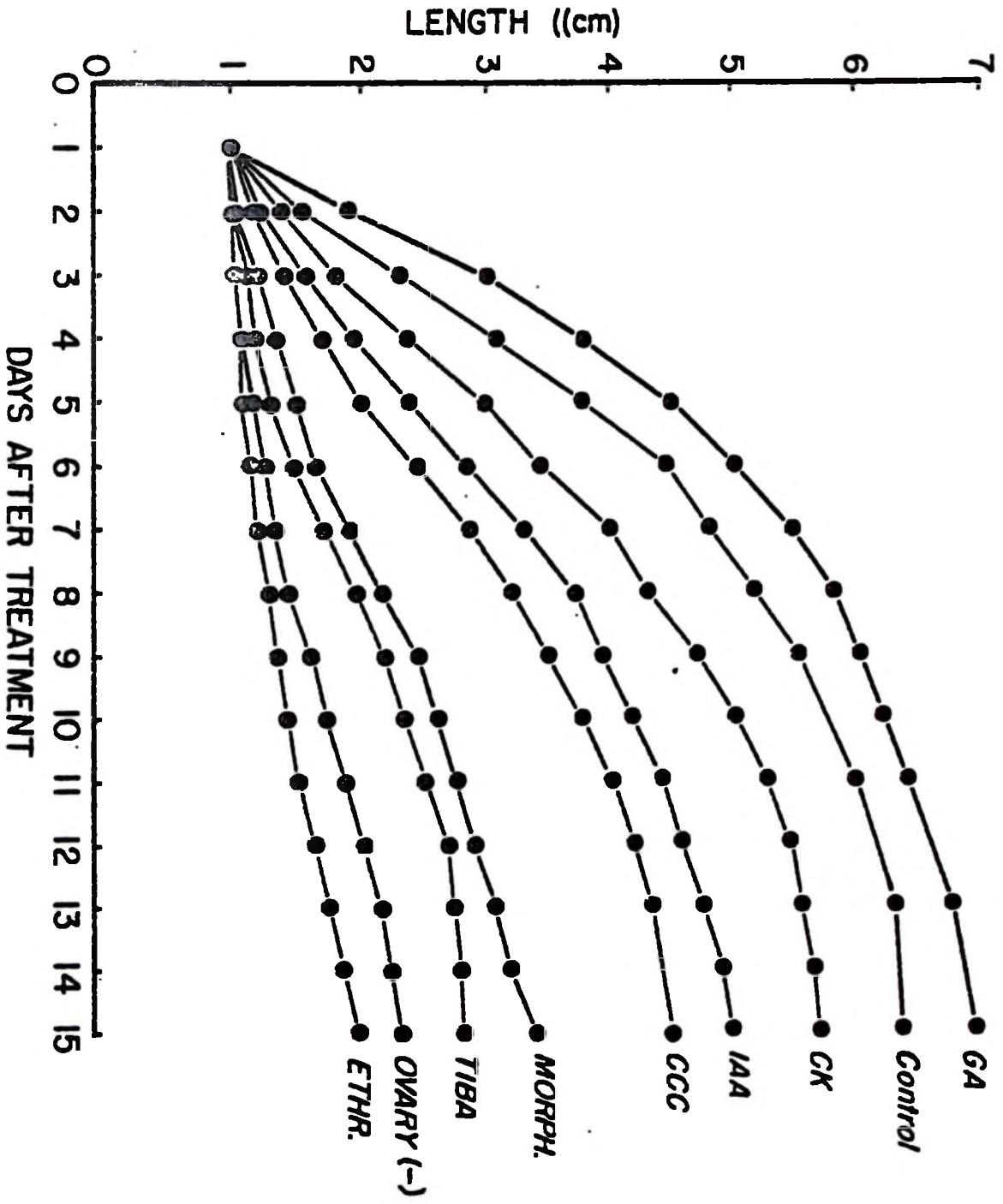

LENGTH ((cm)
0
1
2
3
4
5
6
7
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
DAYS AFTER TREATMENT
GA
Control
CK
IAA
CCC
MORPH.
TIBA
OVARY (-)
ETHR.

Fig. 7. Inhibition of GA-promoted elongation of intact gynophores by IAA and BA in relation to gynophore age, and the effect of GA on subsequent elongation of decapitated gynophores. Arrows indicate time of treatment application.

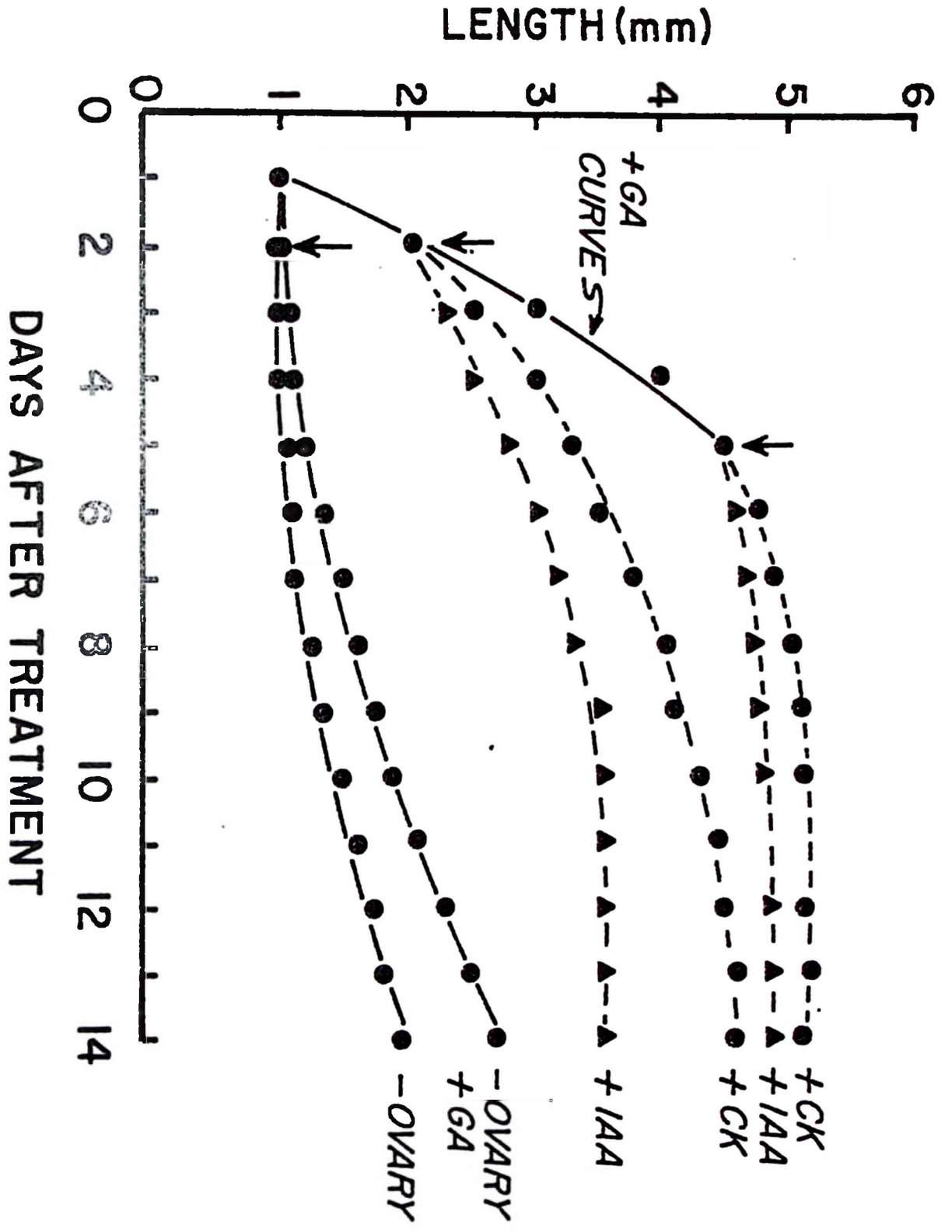
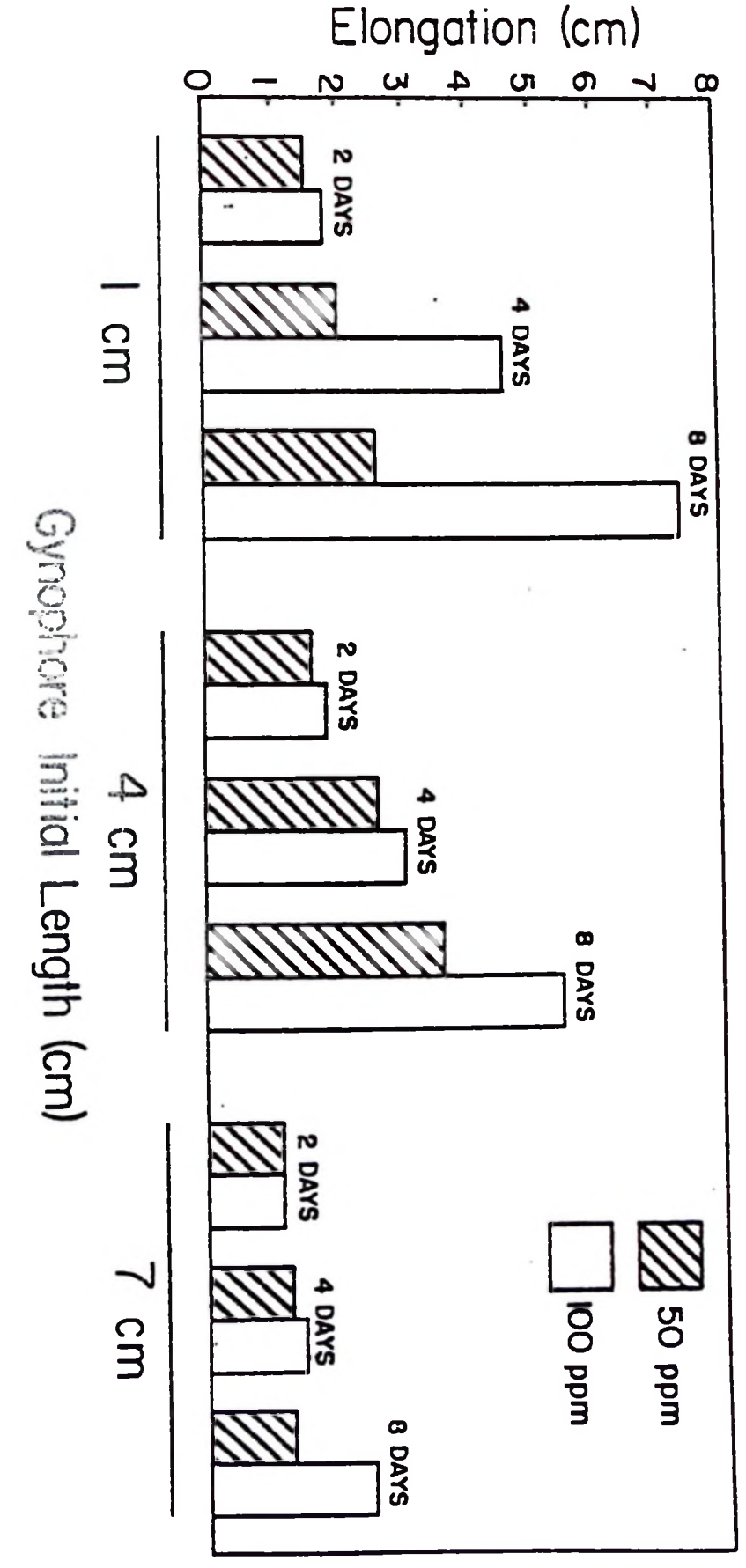

LENGTH (mm)
0
1
2
3
4
5
6
0
2
4
6
8
10
12
14
DAYS AFTER TREATMENT
+GA CURVES
+CK
+IAA
+CK
+IAA
-OVARY +GA
-OVARY

Fig. 8. Intact gynophore elongation as a function of GA concentration and gynophore age at application.


Elongation (cm)
0
1
2
3
4
5
6
7
8
2 DAYS
4 DAYS
8 DAYS
2 DAYS
4 DAYS
8 DAYS
2 DAYS
4 DAYS
8 DAYS
50 ppm
100 ppm
1 cm
4 cm
7 cm
Gynophore Initial Length (cm)

became older irrespective of GA concentration.

The IM occupies a broad zone behind the ovary and this region varies with gynophore age (Fig. 9). As gynophores become older, the IM zone becomes less active and is confined to a small area at the ovary base. When young, practically the entire gynophore is elongating with the exception of the ovary proper and there is gradual maturation towards the gynophore tip. The effect of applied GA appears to be on increasing the length of cells of the IM zone and to a lesser extent the length of older portions of the gynophore. The elongation of the gynophore is basipetally polarized so that the IM maintains a constant position proximal to the ovary. The elongating portions of the gynophores as a function of initial length (age) is depicted (Fig. 10a) to influence the eventual depth of fructification; and an inverse relationship exists between their initial lengths and depth of fructification (Fig. 10b).

When intact gynophores were treated with morphactin after syngamy, gynophore trajectory (locus) became remarkably altered (Fig. 11). The circumnutation indicates typical morphactin effect (Compare with Fig. 3b) on gynophore morphogenesis which appear to be only transient.

Aerial gynophore explants continue their growth and manifest geotropic curvatures even when placed in distilled water. It was observed that excision of the ovules without removing the IM delayed but did not prevent curvature development although elongation was much reduced, therefore, the IM region appears to be the region of stimulus perception and response as well as the region of maximum elongation. The effects of morphactin on elongation and geotropism were unique. Growth was enhanced by all concentrations with optima at 0.1 and 10 ppm (Fig 12). Morphactin was very effective in altering geotropic curvature, even at 0.1 to 1 ppm. At 50 ppm morphactin, the gynophores were rendered completely insensitive to geotropic stimulus (ageotropic). There was an inverse relationship between the anti-geotropic effect and growth stimulation.

Fig. 9. Variation of IM zone with gynophore length (age) and GA effect on the elongation of marked portions in young gynophores.

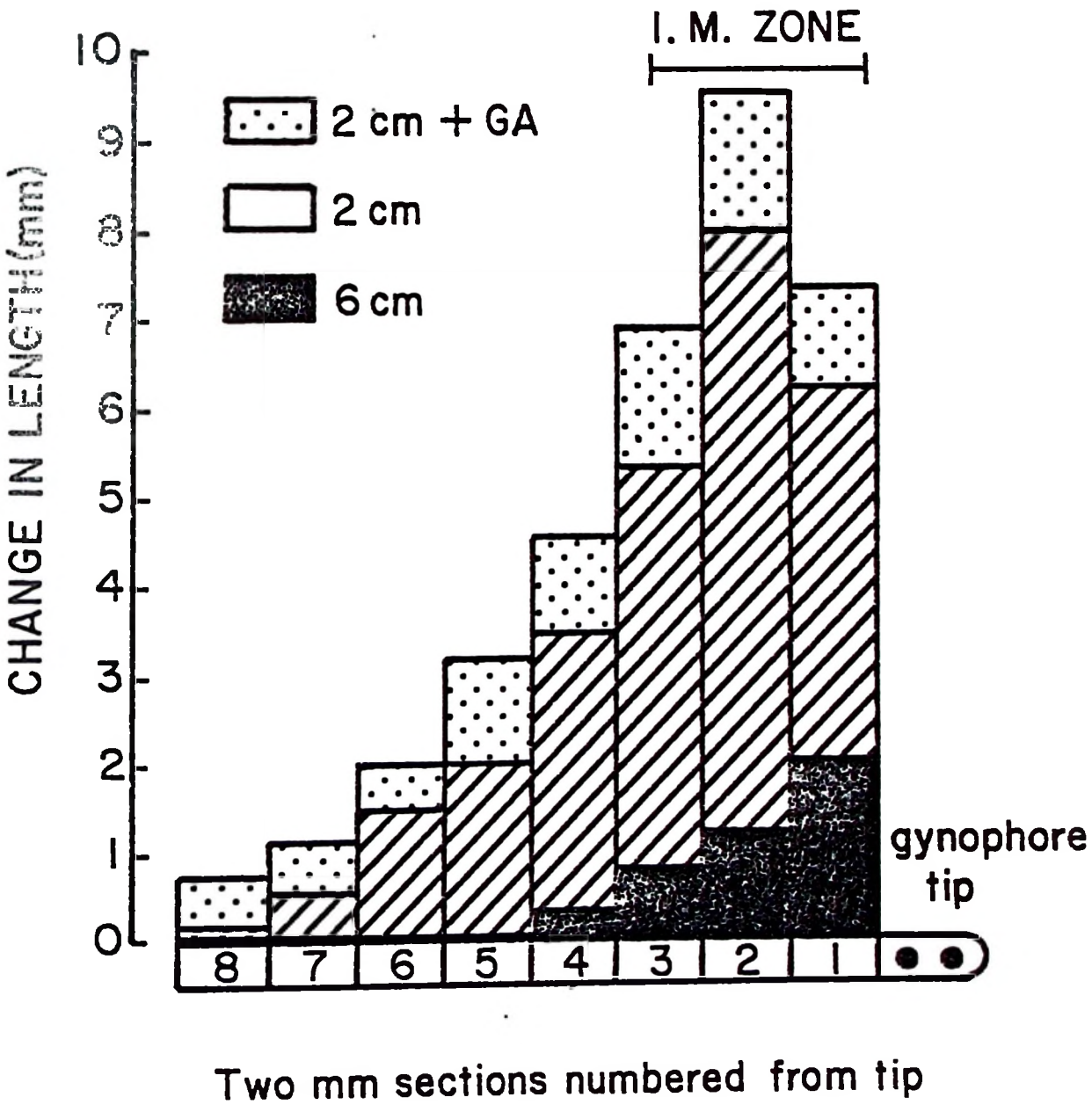

I. M. ZONE
2 cm + GA
2 cm
6 cm
CHANGE IN LENGTH (mm)
0
1
2
3
4
5
6
7
8
9
10
8
7
6
5
4
3
2
1
gynophore tip
Two mm sections numbered from tip

Fig. 10a. Relative sizes of IM zone in gynophores of varying lengths (ages) (Schematic).

Fig. 10b. The depths of fructification in relation to respective (Fig. 10a) gynophore initial lengths (ages) after burial.

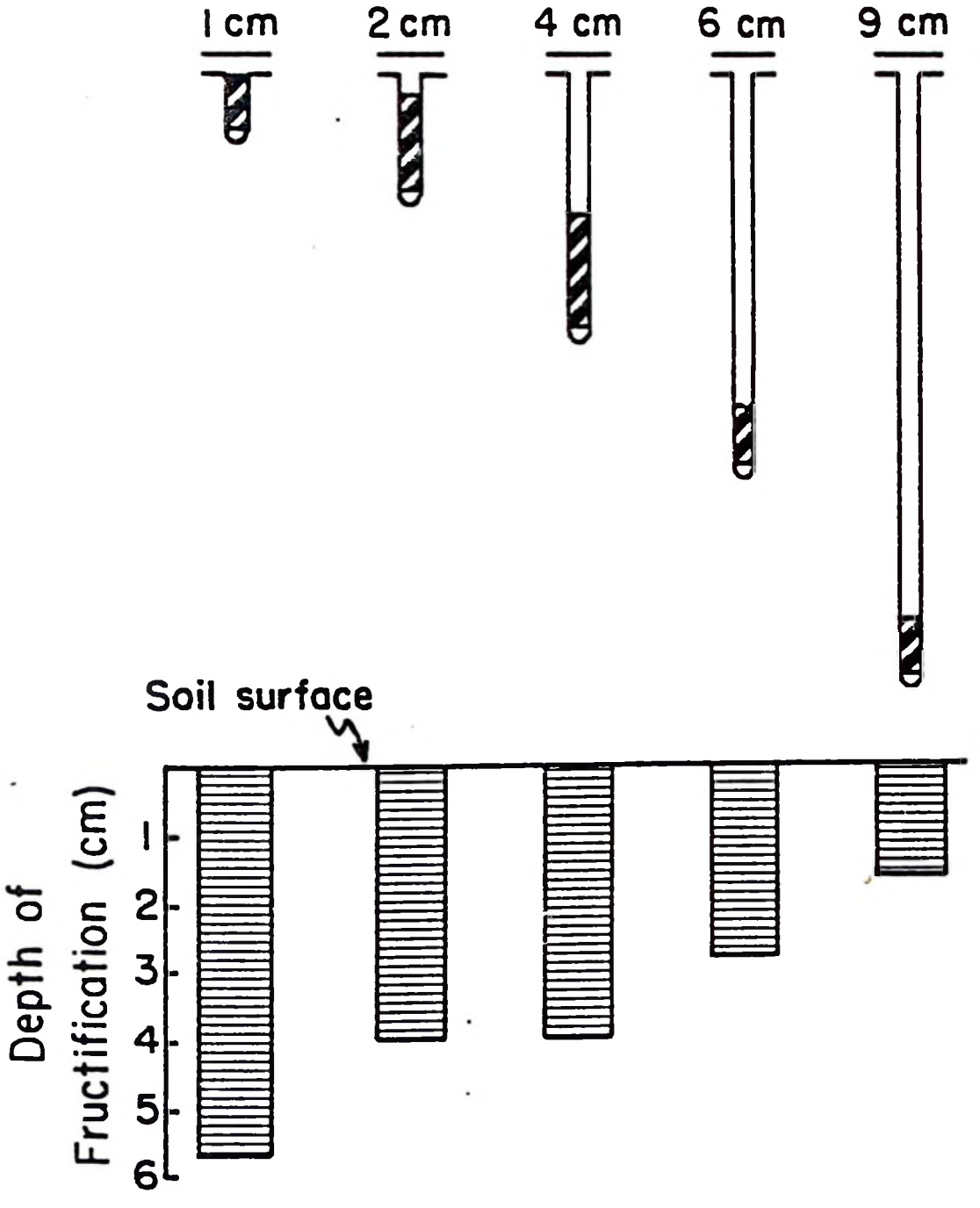
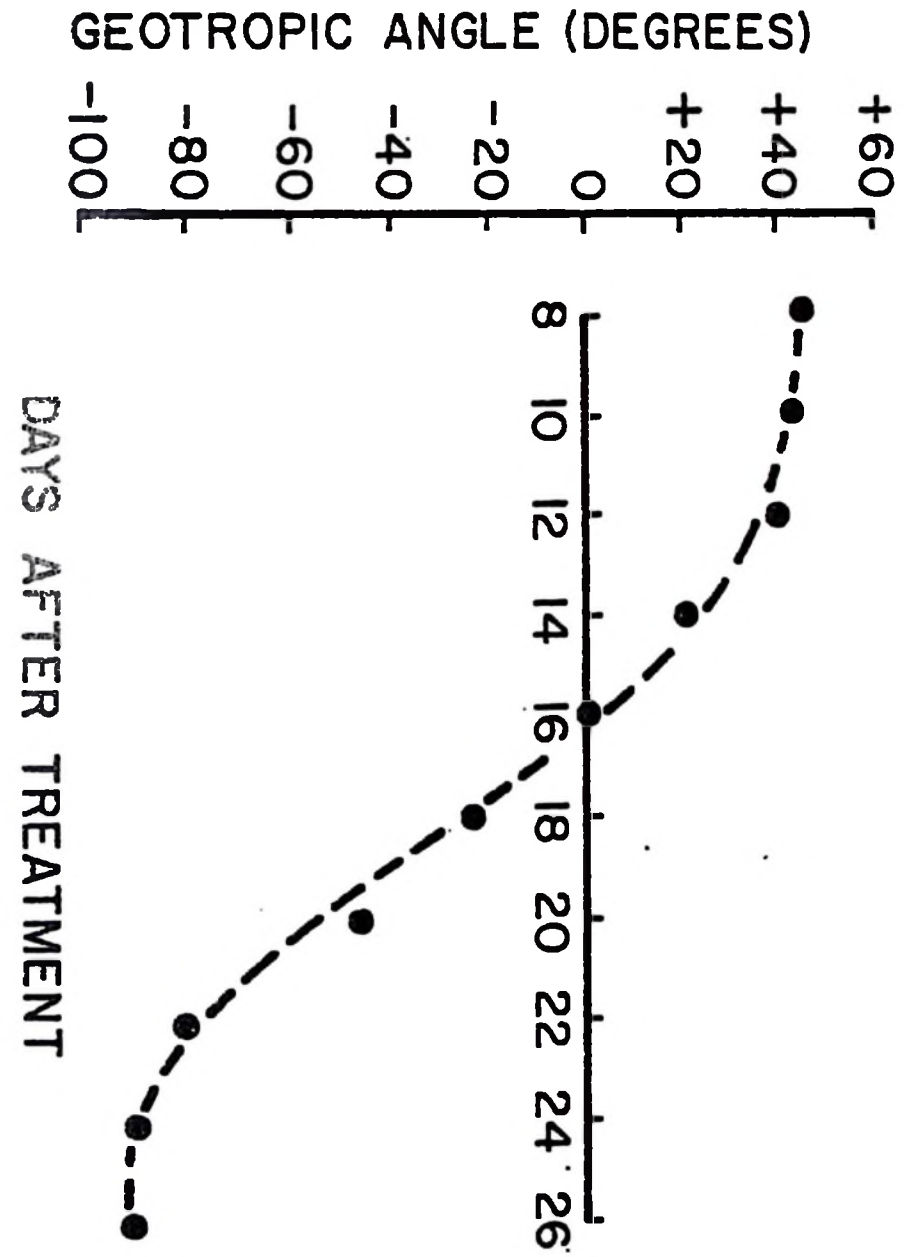

1 cm
2 cm
4 cm
6 cm
9 cm
Soil surface
Depth of Fructification (cm)
1
2
3
4
5
6

Fig. 11. Change of geotropic angle with respect to time (measured non-destructively) on gynophores arising from morphactin treated flowers at anthesis. The positive and negative angle values reflect orientation of ovary above or below the horizontal. Note--a zero degree angle shows gynophore tip is aligned with horizontal.


GEOTROPIC ANGLE (DEGREES)
-100
-80
-60
-40
-20
0
+20
+40
+60
DAYS AFTER TREATMENT
8
10
12
14
16
18
20
22
24
26

Morphactin failed to stimulate growth in the presence of added auxin, (Fig. 13), and auxin partially reversed its effects on geotropic curvature.

An examination on the effect of auxin on elongation of excised gynophores (Fig. 14) reveals that auxin does not stimulate elongation for all concentrations and progressively reduced the degree of curvature. A similar effect was evident for TIBA treated gynophore explants (Fig. 15) in which the reduction of curvature and growth were more drastic. While GA promoted both geotropic curvature and stimulated growth (in length), BA had the effect of reducing both of these parameters (Fig. 16). The effects of BA were more pronounced as its concentration increased. Ancymidol reduced elongation and curvature (Fig. 17) for all concentrations tested, however, in the presence of GA, there was partial reversal of inhibiton of these processes.

Fig. 12. Effect of morphactin concentration on growth in length and geotropic curvature of gynophore segments. The abscissa is in logarithmic scale.

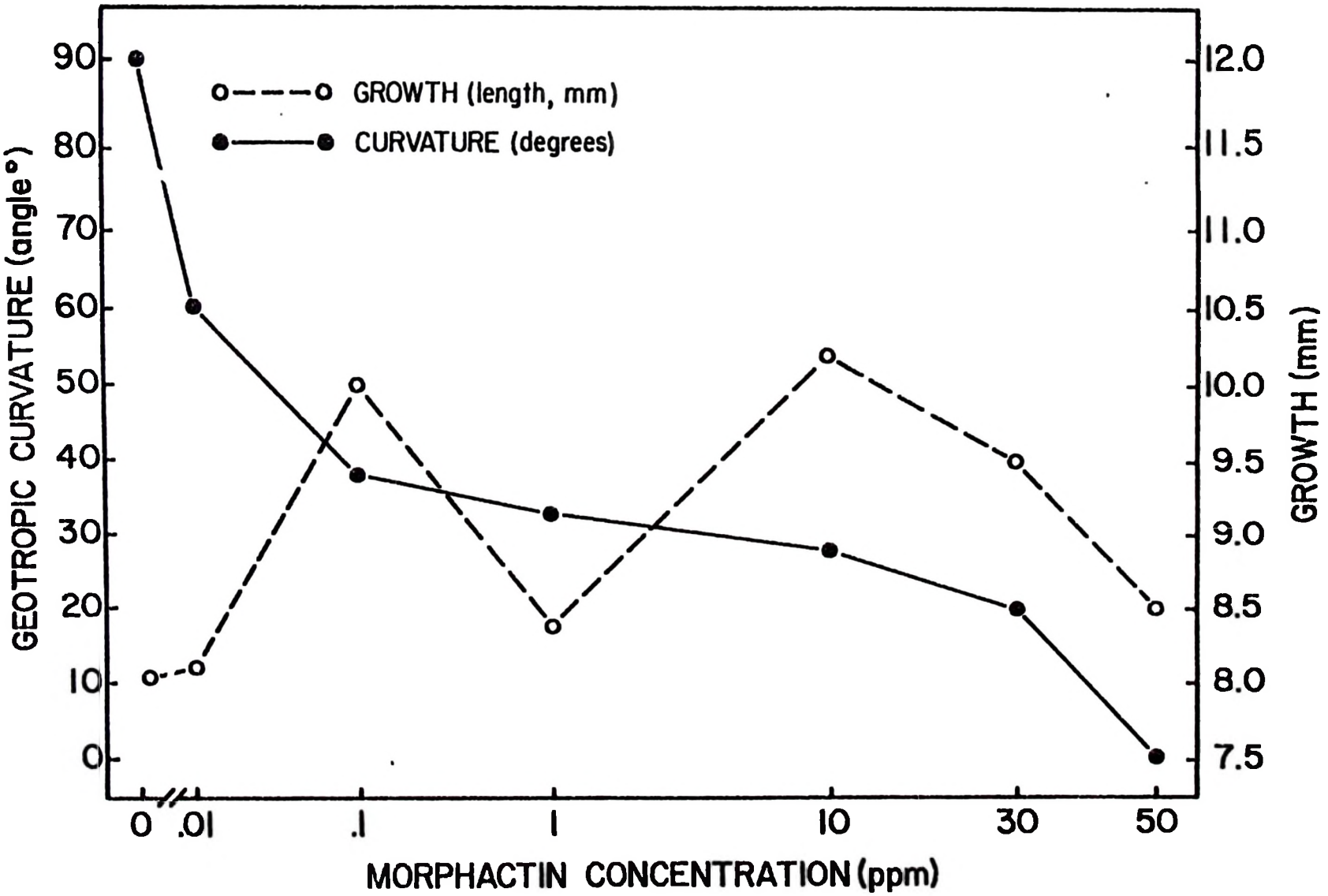

GROWTH (length, mm)
CURVATURE (degrees)
GEOTROPIC CURVATURE (angle°)
GROWTH (mm)
90
80
70
60
50
40
30
20
10
0
12.0
11.5
11.0
10.5
10.0
9.5
9.0
8.5
8.0
7.5
0
.01
.1
1
10
30
50
MORPHACTIN CONCENTRATION (ppm)

Fig. 13. Effect of morphactin concentration on growth in length and geotropic curvature of gynophore segments in the presence of auxin(0.1 ppm)

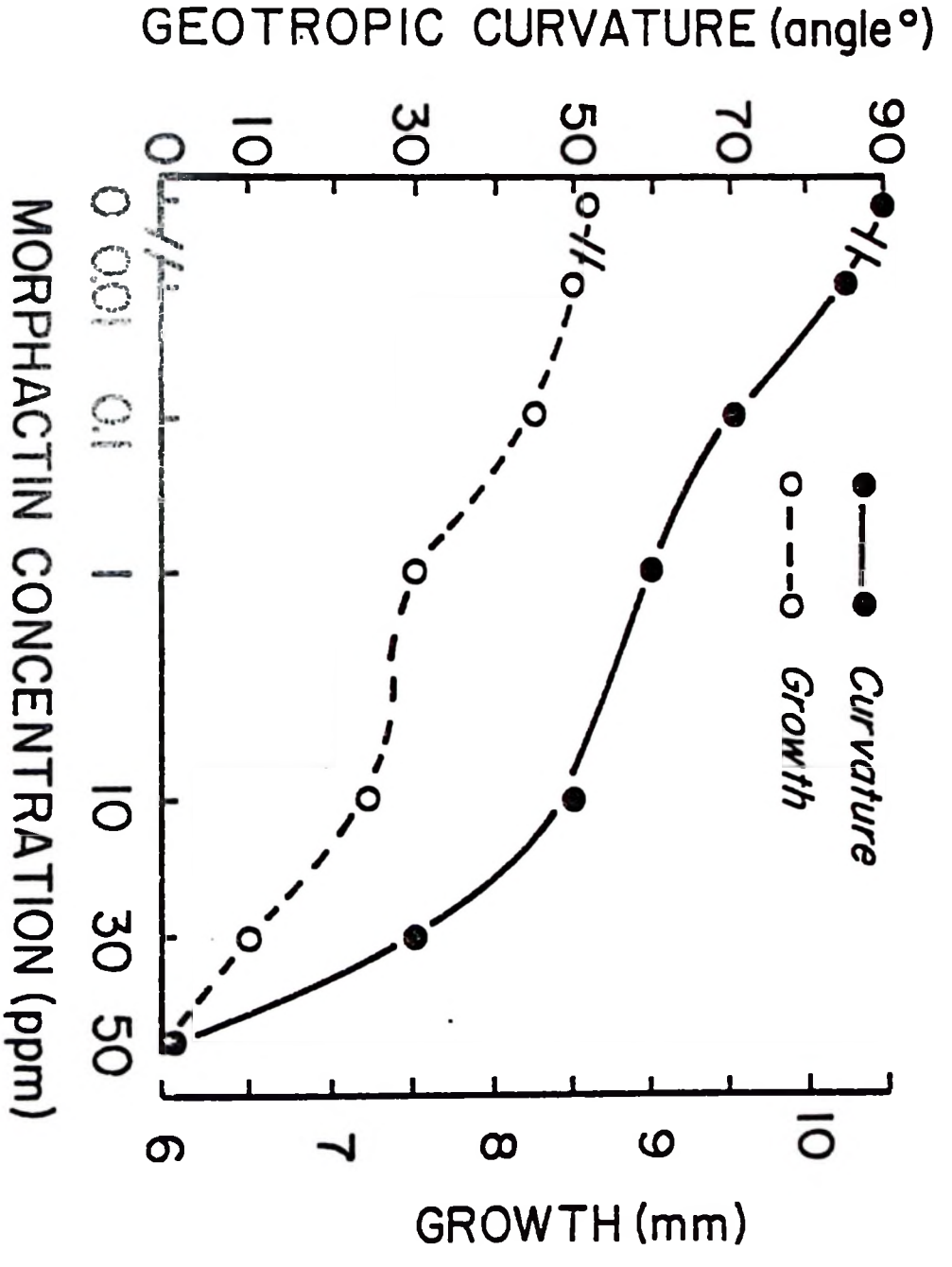

GEOTROPIC CURVATURE (angle°)
0
10
30
50
70
90
MORPHACTIN CONCENTRATION (ppm)
0
0.001
0.01
0.1
1
10
30
50
6
7
8
9
10
GROWTH (mm)
Curvature
Growth

Fig. 14. Effect of IAA concentration on geotropic curvature development and elongation of gynophore segments. Arrow indicates the water control.

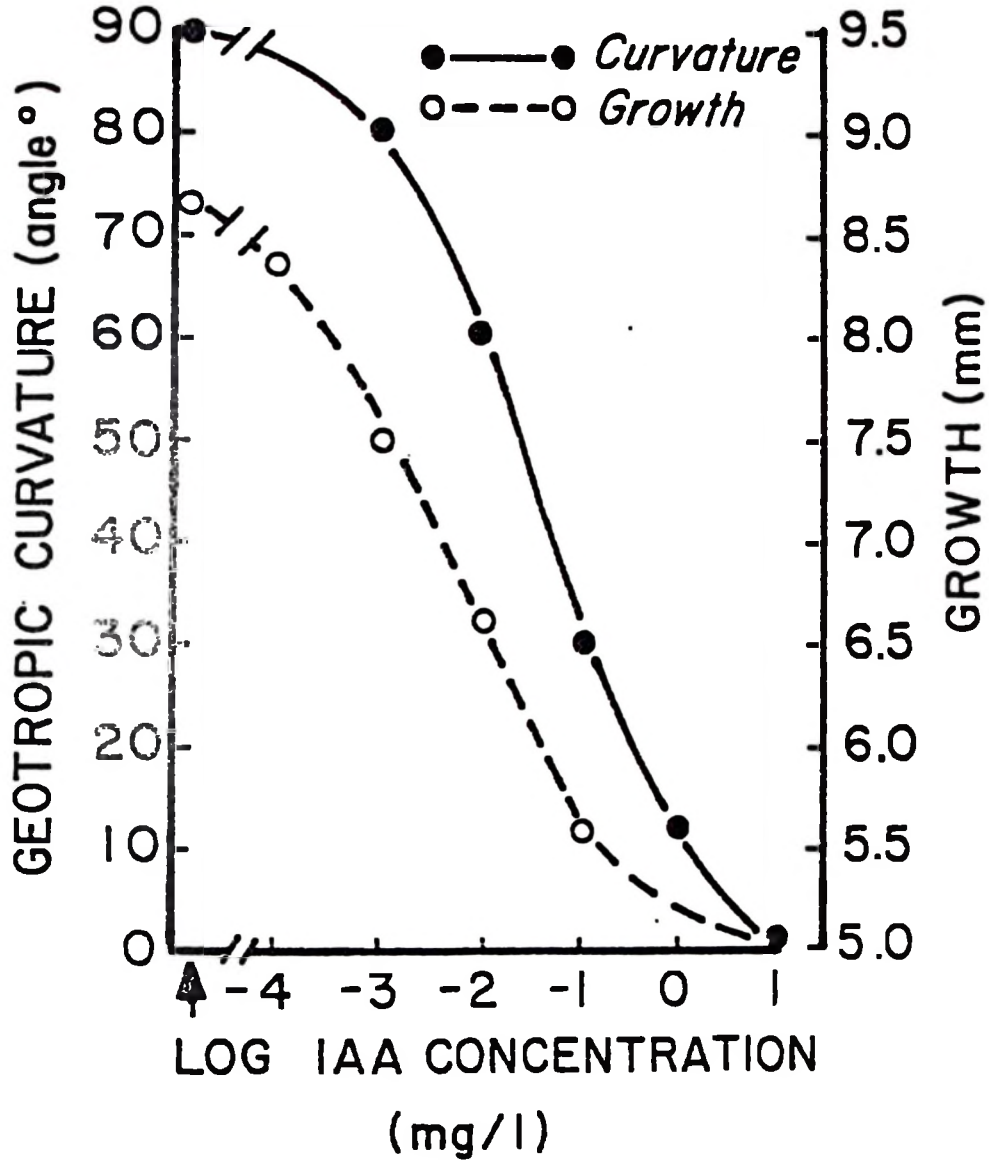

Curvature
Growth
GEOTROPIC CURVATURE (angle°)
GROWTH (mm)
90
80
70
60
50
40
30
20
10
0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
-4
-3
-2
-1
0
1
LOG IAA CONCENTRATION
(mg/l)

Fig. 15. Inhibition of geotropic curvature development and elongation of gynophore segments by increasing TIBA concentration. Arrow indicates the water control.

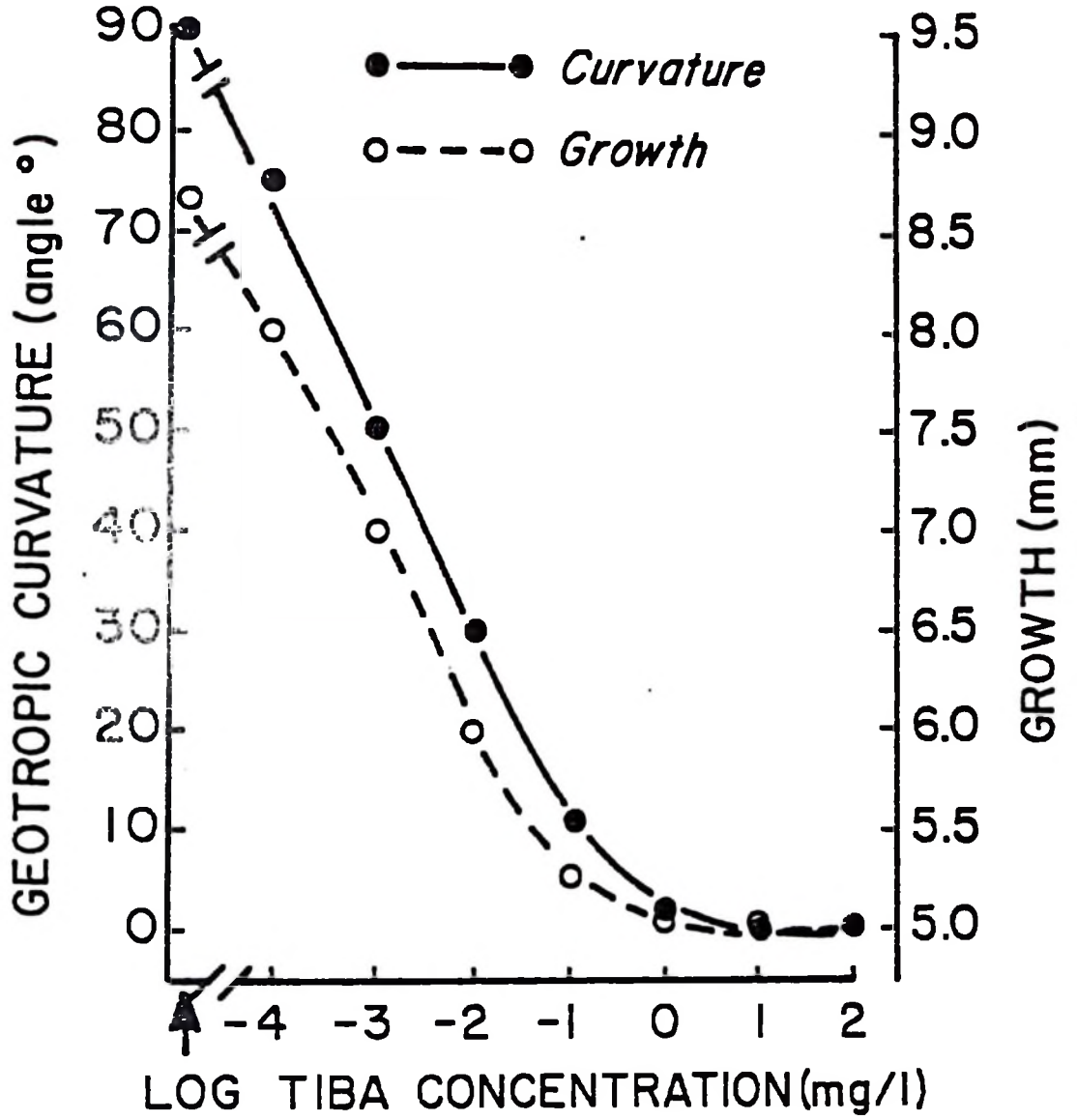

Curvature
Growth
GEOTROPIC CURVATURE (angle °)
GROWTH (mm)
LOG TIBA CONCENTRATION (mg/l)
90
80
70
60
50
40
30
20
10
0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
-4
-3
-2
-1
0
1
2

Fig. 16. Effects of GA and BA concentrations on geotropic curvature development and elongation of gynophore segments. Arrow indicates the water control.

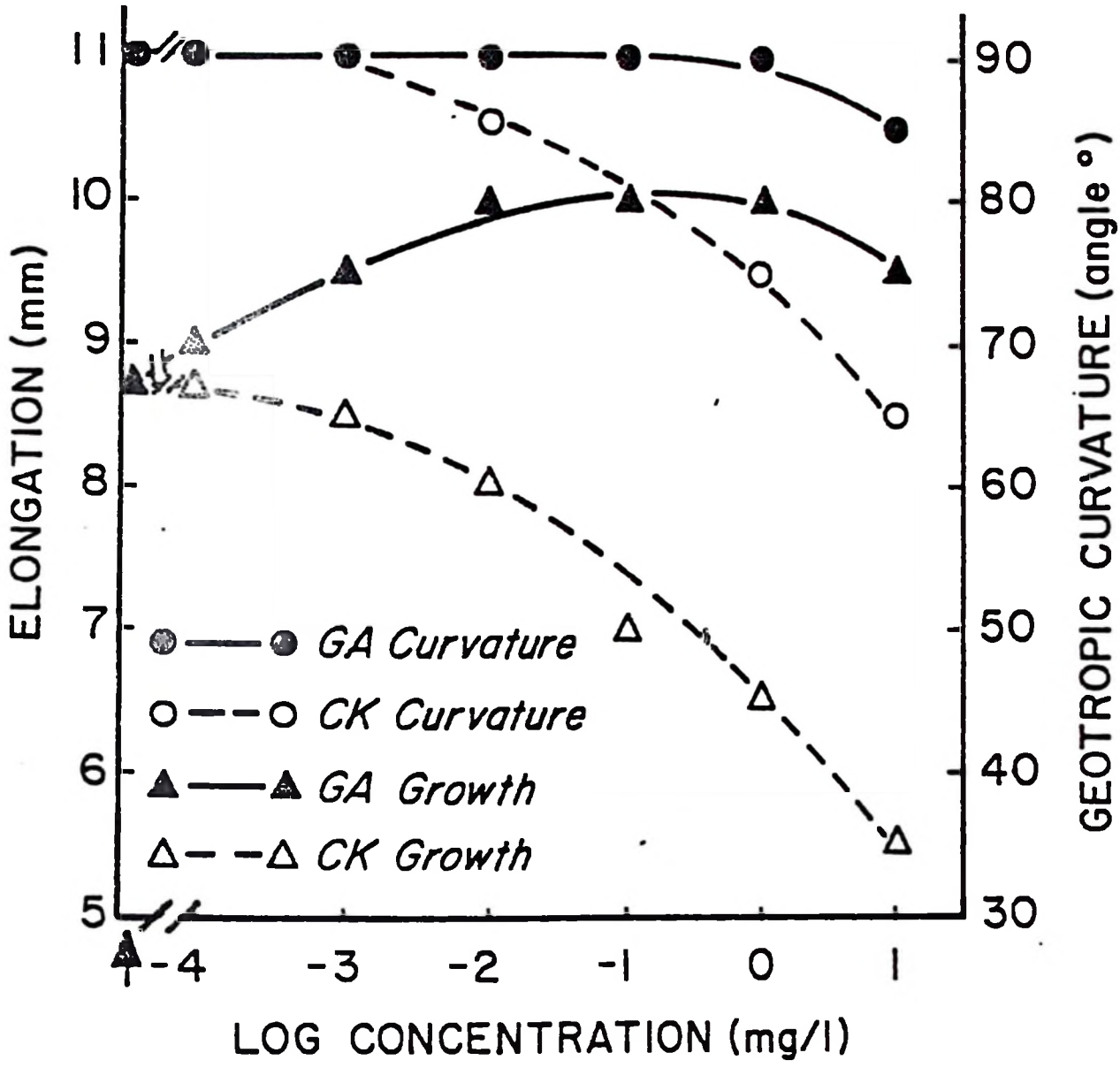
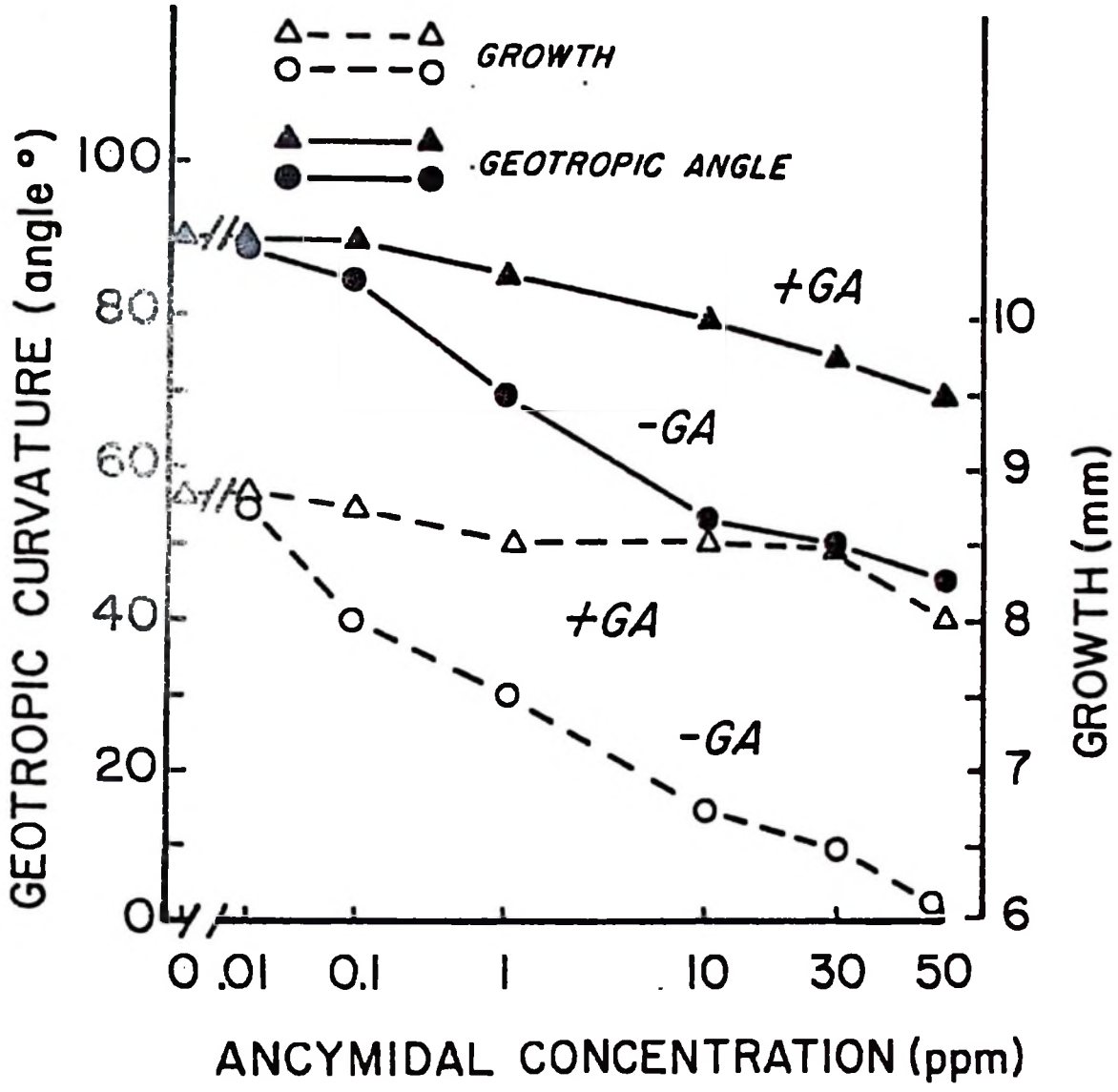

ELONGATION (mm)
GEOTROPIC CURVATURE (angle °)
LOG CONCENTRATION (mg/l)
GA Curvature
CK Curvature
GA Growth
CK Growth
11
10
9
8
7
6
5
90
80
70
60
50
40
30
-4
-3
-2
-1
0
1

Fig. 17. Effect of ancymidol concentrations on geotropic curvature and elongation of gynophore segments in the presence or absence of exogenous GA. Abscissa is in logarithmic scale.


GROWTH
GEOTROPIC ANGLE
+GA
-GA
+GA
-GA
GEOTROPIC CURVATURE (angle °)
GROWTH (mm)
100
80
60
40
20
0
10
9
8
7
6
0
.01
0.1
1
10
30
50
ANCYMIDAL CONCENTRATION (ppm)

DISCUSSION

The development of the peanut gynophore which is a consequence of syngamy, effects the transition between the sessile aerial flowers and subterranean fruit (Smith, 1950; Shibuya, 1935). Because typical ovary growth frequently encountered in higher plants is radial rather than longitudinal, fruit set which is a post-fertilization phenomenon in which rapid growth of the ovary into a young fruit ensues (except under parthenocarpy) is difficult to define in peanut. In a physiological analogy to other angiosperms, the initiation of gynophore development could conveniently be termed fruit set. Like in many other fruits, the syngamic stimulus can be substituted for by exogenous growth regulators. The developing ovules regulate IM activity (gynophore growth) and there exists anatomical continuity between the tissue surrounding the ovules and the IM at their base (see Jacobs, 1947; Zamski and Ziv, 1976). The definition of a fruit being a mature ovary with associated parts overshadows some of their similarities when fruits are young (see Coombe, 1976). Nitch (1952, 1962) defined fruits as structural entities that develop from tissues that support the ovules. In the peanut, the gynophore is derived from the activities of the IM which, as results show, is proembryo-directed and functions in ensuring growth of ovules in their natural environment. The concept of the fruit is physiological rather than morphological (Nitch, 1962) and the development of the gynophore can be interpreted as a case where there is a sequential influence of the proembryos first causing cell division and elongation of the IM region (while themselves remaining in suspended growth) and later, promoting growth of the tissues surrounding them (fructification). The phasic development of the peanut fruit is in response to the immediate physical environment at the onset of gynophore initiation, for in subterranean flowers fructification occurs without substantial gynophore elongation (Tétényi, 1957). It is suggestive that gynophore growth in length thus represents an alternate course of fruit development. The

entire gynophore is basically a fruit as previously emphasized by Smith (1950). In keeping with its physiological and anatomical anomally, it is suggested that the gynophore be treated as a unique fruit. Although the ovule-end becomes the 'ovary proper' at maturity, the rest of the gynophore appears as an accessory tissue of ovarian origin manifesting both stem- and root-like properties (see Jacobs, 1947). From this analysis, it is proposed that future work with this organ, whole or excised, should acknowledge it as a fruit or its part.

The results in this study show that the initiation of the IM, defined as a region of rapid but limited growth occurring between zones of differentiated primary tissue (Salisbury and Parke, 1965) is induced by the act of fertilization. The mother plant plays no role in this phase in agreement with the tenet that the mother plant is only a prerequisite and not a cause of fruit set (Weaver, 1973). The nature of the induction and regulation of its activity is hormonal. Gibberellic acid stimulates its initiation in the absence of fertilization and together with BA and IAA, IM activity is enhanced. The induced IM activity is, however, short lived showing that there must be continual supply or synthesis of these hormones in order to effect the amount of growth that normally takes place. Thus the secondary stimuli appear to originate from the ovules as indicated (Fig. 6). Tukey (1936) and Wittwer (1943) showed that the ovules are vital for fruit growth possibly as sites of hormonal synthesis. In the peanut gynophore, these hormones would possibly move basipetally to influence IM activity (see Jacobs, 1951a). The effect of GA in inducing IM activity is in conformity with its reported effects on plants (Linser, 1966) and on fruit set (Crane, 1964). Auxin or BA alone were less effective in inducing IM activity, however, the presence of auxin appeared to be essential for the development of geotropic curvature in accordance with its regulatory function in geotropism (Audus, 1969). Cytokinin which induces cell division and organ differentiation would seem necessary in IM induction, however, higher concentrations have been

reported to inhibit growth by increasing cell enlargement (Fox, 1969). In peanut fruit set (here defined as IM induction), the stimulus appears to be GA, IAA and CK and other factors which could be termed 'Syngamin' in accordance with work of McLane and Murneek (1952) and GA plays a predominant role.

Morphactin has been reported to induce cell division (see Schneider, 1970; 1971) and it is capable of initiating limited gynophore IM activity. This may indicate that it has an independent effect on growth. Application of CEPA to fertilized flowers retards gynophore elongation. The inhibitor of endogenous ethylene action, Ag + ions, were ineffective in accentuating elongation. This is explained by the differed senescence of floral parts it caused. A morphological observation indicated that unabscised hypantha remained attached at the ovarian base. Thus longitudinal gynophore growth would be delayed. It is apparent that normal senescence of floral parts (which occurs within 24 hrs in peanuts) is an essential process for aerial gynophore elongation.

When gynophores initiated without fertilization (by growth regulator application) were buried, they failed to fructify confirming the essential role of ovules in this process. This is consistent with the results of Dennis (1966) on apple fruit growth. Although GA, CK and IAA appear to regulate gynophore initiation, their differential localization and action at the ovular base, i.e., physiological differentiation of the gynophore, is unclear.

The promotion of intact gynophore elongation by GA confirms previous results (Amir, 1969; Zamski and Ziv, 1976), however, the effectiveness of GA depends on its concentration and gynophore age (Fig. 8). The IM is traversed by vascular tissue supplying the ovules (see Brennan, 1961) and as the gynophore ages, elongation ceases due to the lignification of this zone. Thus, GA effect on young gynophore tissues appears to be consistent with IM internal structure. It is shown in this study that the IM size decreases with gynophore age. This pattern is similar to that described by Barley and England (1970) for Trifolium

subterraneum L. From the study of the effect of GA and the elongation of marked gynophore segments at various ages, the mechanism by which the IM retains a constant position proximal to the basal ovule supports the suggestion of Jacobs (1947). GA enhances IM-mediated elongation of various plant parts (Hank and Rees, 1975; Dicks et. al., 1974; Kaufman et. al., 1971), however, in Cyperus IM (Fisher, 1971) exogenous GA and BA promoted elongation while in Gerbera (Sachs, 1968), GA and IAA substituted for the excised hormonal sources in these plants. Although the concentrations applied and type of plant studied would account for the diversity in results reported by the various investigators, the retardation of elongation of intact gynophores by the growth retardant CCC would imply the regulatory role of GA. Similarly, the effect of auxin transport inhibitors TIBA, CEPA and morphactin indicate a possible requirement of IAA for normal gynophore elongation. When applied to flowers after anthesis, morphactin effectively postponed gynophore geotropic curvature development (Fig. 3b), however, the continued growth is evidence for the gynophore's ability to metabolize morphactin. This observation further supports the suggestion that the presence of auxin is essential for early curvature development.

Geotropism is the plant response to gravity manifested as a curvature of an organ when its orientation is deviated from that normal to gravity. The gynophore is suited for studies on geotropism because its IM is not complicated by appendages, its growth is strictly polarized and for young gynophores the geotropic response is autonomic. The ability of gynophore explants to elongate, respond to gravity and even fructify has been reported (Ziv and Zamski, 1975). This would occur if the IM is retained during excision. The observation that upon ovule removal curvature still develops indicates that once the IM is formed, it can independently act as the zone of stimulus perception and response.

Morphactin renders roots and stems insensitive to geotropic stimulus (Bopp, 1971; Schneider, 1970). The results in this study agree with previously published

data on various plant organs (Bopp, 1971; Khan, 1967; Krelle and Libbert, 1968a; Zeigler, 1970). The effect on gynophore geotropism is striking at very low concentrations and parallels the reported effects on roots (see Schneider, 1970). Morphactins have been implicated in growth inhibition, however, results show that they stimulate growth at low concentrations which is in agreement with reported results on coleoptiles by Krelle and Libbert (1968a). Several studies (Parups, 1970; Krelle and Libbert, 1968; Pilet, 1970; Naqvi, 1971; Bopp, 1971) have shown that morphactin inhibits auxin transport. In the presence of auxin, the growth stimulation by morphactin is annulled and the concentration dependent curvature suppression is partially reversed. According to the classical Cholodny-Went theory, gravity induces an assymetrical distribution of auxin, more accumulating on the lower than the upper side of the organ. In view of the different sensitivities of roots and shoots to auxin, the negative and positive curvatures respectively could be explained. Because gynophores are more root-like than stem-like in physiology, auxin may control geotropic response by acting differentially on the IM. Yasuda, (1943) induced lateral curvature on vertical gynophores by unilateral application of auxin. If curvature is affected by auxin, then morphactin could be used to test the Cholodny-Went hypothesis. The results show that growth of gynophore is stimulated by morphactin while curvature is suppressed so that the "anti-geotropic effect" and growth regulating activity seem to be coupled.

Auxin does not stimulate excised gynophore elongation at any concentration, a pattern of inhibition similar to that on Lepidium roots (see Audus, 1969). This result further emphasizes the root-like physiological nature of gynophores in accordance with the criterion of Thimann (1937) and supports the suggestion by Jacobs (1951) that endogenous auxin in gynophores may be in supra-optimal levels. Thus with increasing IAA concentration, curvature is inhibited parallel with growth in agreement with results on wheat roots (Keitt,

1960). The ability of TIBA to inhibit curvature development is consistent with its mode of action (see Winter, 1968) and reported effects on roots (see Torrey, 1956; Audus, 1975), however, its inability to stimulate growth may imply some other mode of action not directly involving auxin transport as suggested in several studies (Aberg, 1953; Pohl and Ochs, 1953; Kandler and Fink, 1955).

Benzyladenine (BA) retarded elongation of excised gynophores and reduced curvature with increasing concentration. Similar effect on geotropism of soybean hypocotyls has been reported (Krul, 1968). It is evident from this study that GA has no appreciable effect on curvature development and appears to stimulate excised gynophore elongation. El-Hinawy, (1975) reported the ability of GA to stimulate excised tomato root growth. The suppression of both curvature and elongation of gynophore explants by ancymidol and their partial reversal by GA is suggestive of a possible role of GA in regulating gynophore geotropism. As reported by El-Antably and Larsen (1974) and El-Antably (1975), GA becomes redistributed in roots, more on the upper portion than the lower. The effect of ancymidol on the gynophore IM would possibly be on inhibiting GA action, thus upsetting the balance of hormones participating in differential growth in response to gravity.

PART II

GROWTH REGULATOR EFFECTS ON THE FRUCTIFICATION PROCESS

INTRODUCTION

Peanut ovaries exhibit a period of arrested radial growth (fructification) during the gynophoric phase, the duration of which depends on how far they are formed above the soil medium (Smith, 1950; Amir, 1969) and the nature of the edaphic physical conditions (Shibuya, 1935; Yasuda, 1943; Zamski and Ziv, 1976). Although the physical requirements have been elaborated since the early studies of Waldron (1919), light and mechanical stimulus have received inadequate attention. The regulatory roles of phytohormones on this process have not been delimited despite reports of their possible key functions (Badami, 1935; Yasuda, 1943; Jacobs, 1951a). For instance, auxin has been shown to increase in the ovary at the onset of fructification (Sreeramulu and Rao, 1971) and its exogenous application induces ovary swelling (Yasuda, 1943). Thus the effect of auxin parallels research findings on other fruit types (see Luckwill, 1959; Nitch, 1962; Leopold, 1962; Van Overbeek, 1962). Further work with auxin and other hormones appear necessary in order to possibly explain some of the mechanism relating to fructification.

It is suggested (Brennan, 1961; Smith, 1950) that gynophore elongation must cease prior to the onset of fructification and no satisfactory explanation has been given for the opposing effects of these processes. Jacobs (1951a) concluded that auxin from the ovary inhibited further IM activity after soil penetration, however, Zamski and Ziv (1976) reported abnormal ovary growth in mist treated gynophores in which there was a resumption of IM activity in the isthmus separating the ovules. Auxin effects have not been interpreted in relation to the influence of other hormones whose effects on the process are likewise not documented.

Wiersum (1951) showed that although xylem continuity between the root system and the ovary exists, after soil penetration gynophores become independent with regard to Ca^{++} and water, absorption, and meet their requirements directly from the soil (Bolhuis and Stubbs, 1954). Since the ovary is separate from the root system with respect to water and nutrient supply, CKs believed to be supplied from the roots (Kende, 1965; Carr and Reid, 1968; Weiss and Vaadia, 1965; Sitton et al., 1967) would likewise be unavailable to the developing ovules and would have to be synthesized there. Cytokinins play a regulatory role in plants in promoting cell division (Letham, 1968), inhibiting elongation of stem sections (Fox, 1969) stimulating growth by swelling (Katsumi, 1962), an effect which may participate in the formation of such natural swellings as tubers (Esashi and Leopold, 1968; Palmer and Smith, 1969) and roots (Radin and Loomis, 1971) where they act as assimilate mobilizers to the physiological sinks (see Mothes, 1964). Smith (1956b) showed that cell division in endosperm and embryo is arrested until the gynophore is buried thus indicating the dormancy of the proembryo in the light.

A typical characteristic of two seeded peanut pods is the size difference between the distal and the proximal seeds in which the former is always smaller and begins to grow later than the latter. Incidences of poorly filled or empty distal seeds usually called 'pops,' though linked to Ca^{++} nutrition (see Reid and Cox, 1973) is a consequence of competition for assimilates as suggested by Smith (1950) and Brennan (1961). The possible influence of BA on development of peanut fruit components and seed size within the pod has not been reported.

The need for a mechanical stimulus (Yasuda, 1943; Zamski and Ziv, 1976) and darkness (Shibuya, 1935; Zamski and Ziv, 1976) on fructification pose constraints towards aerial fructification. These aspects deserve further study in order to elucidate possible mechanisms from a regulatory standpoint.

The multiple effects of ethylene in plants (see Abeles, 1973; Zamski and

Ziv, 1976) 1969) include growth inhibition, promotion of radial cell expansion and alteration of geotropism. Beyer, (1976) reported the effectiveness of Ag^{+} to inhibit endogenous ethylene action and can be used in verifying the participation of this hormone in physiological processes. Aerial fructification has been reported to occur in a misted chamber in the dark (Zamski and Ziv, 1976) and to a limited extent in light (Harris[2]) where supraoptimal boron was supplied to gynophores. The effects of CEPA, which generates ethylene in plant tissues (Warner and Leopold, 1967, 1969; Yang, 1969) in combination with other chemical and physical factors on this process was investigated. The influence of various exogenous growth substances on fructification is reported.

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[2]H. C. Harris, personal communication.

MATERIALS AND METHODS

A. OVARY DEVELOPMENT AS INFLUENCED BY GROWTH REGULATORS

Groups of eight uniform gynophores were allowed to grow into black plastic vials containing evenly compacted moist sand into which 2 ml of growth regulator solutions were added. The various treatments included GA (50 ppm); IAA (25 ppm); GA (25 ppm); CEPA (50 ppm); Morphactin (50 ppm) and a distilled water control. The sand in all vials had previously received 2 ml of half strength Hoagland's solution. All vials were loosely covered to prevent excessive evaporation and no additional water was necessary (Fig. 2). After 7 days by which time ovary swelling was evident in the control, all treated gynophores were unearthed and ovary length, diameter and depth of fructification were measured. The treatments were duplicated.

In another experiment to study the effect of several inhibitors on ovary development, a similar set-up consisted of sand in vials treated either with 2 ml of ancymidol (10 ppm); CCC (50 ppm); TIBA (10 ppm) and Ag^{+} (50 ppm) as $AgNO_3$. Similar measurements were made after 7 days of fructification.

B. CYTOKININ (BA) EFFECTS ON FRUIT (POD) DEVELOPMENT

Fifty uniform gynophores were simultaneously buried into moist sand to which BA (25 ppm, 10 ml/pot) was previously added. The controls were watered daily with half strength Hoagland's solution. The BA treated sand was watered likewise two days after treatment. During the course of pod development, 5 gynophores were unearthed weekly for a period of 10 weeks. The pods were separated into pericarp (shell) and seed (kernel). Their fresh and dry weights were determined as well as those of the controls. The incidence of single-seededness or poorly filled pods (pops) and the sizes of seeds within the pods at maturity were observed. From the fresh and dry weights, the water content of pods in the course of their development as influenced by BA treatment was determined.

C. EFFECT OF POST-FRUCTIFICATION EXPOSURE TO LIGHT ON THE DEVELOPMENT OF POD COMPONENTS

Fifty uniform gynophores were simultaneously buried and allowed periods of subterranean fructification ranging from 7, 14, 35, and 70 days. After each duration, ten fruits were carefully unearthed and prevented from touching the soil or other media. To prevent undue dessication, all exposed fruits were alternately sprayed daily to dripping with water and half-strength nutrient solution. The experiment was terminated at 100 days after which the fruits were harvested and separated into their components whose fresh and dry weights were then determined.

D. INDUCTION OF OVARY GROWTH IN AIR

In an attempt to induce aerial fructification by providing ovaries with various chemical and physical environments in vivo, 30 gynophores averaging 4 cm in length were prevented from entering the soil. Ten tagged gynophores were grown in darkness provided by sealed black vials whose relative humidity was about 100% and an equal number remained in the light 12 hrs/day. All received chemical treatment in sequence as follows: dipping in nutrient solution; dipping in 3% boric acid; coating with $CaCO_3$ powder; dipping in CEPA (50 ppm) and then in BA (25 ppm). The liquid treatments were done an hour apart. Those kept in the dark were treated under low light intensity. A control included an equal number of aerial gynophores which received only a nutrient solution spray. The treatments were done once daily for 14 days after which all gynophores were observed for ovary swelling as a measure of the extent of fructification and compared with those grown normally in soil for the same duration.

RESULTS

Subterranean elongation of gynophores and ovary growth were invariably affected by exogenous growth regulators (Fig. 18a). Ovary length was increased by CEPA, IAA and morphactin but was reduced by GA in comparison to the control. Morphactin increased ovary diameter and GA reduced it while CEPA and IAA treatment effects were similar to the untreated controls. The depth of fructification was increased notably by GA but Morphactin, IAA and CEPA equally reduced it. BA and the tested growth inhibitors (Fig. 18b) reduced the depth of fructification and with the exception of Ag^{+} ions, they increased ovary diameter over the control; however, Ag^{+} ions, TIBA and BA increased ovary length while CCC and ancymidol were less effective in this regard.

The course of pod component development and the influence of BA on them is depicted (Fig. 19a, 19b). Fruit pericarp shows drastic fresh weight increase with the onset of fructification. Fresh weight decreases gradually as the fruit matures. Seed (kernel) fresh weight increase shows initial lag behind that of the pericarp. Exogenous BA increased both seed and pericarp fresh weight. The seed showed a steady accumulation of dry matter which was increased by BA while the pericarp whose dry matter increase commenced earlier than that of the kernel did not show much change after the first two weeks of fructification (Fig. 19b). The effect of BA was more pronounced in the seed than in the pericarp with respect to dry weight and fresh weight accumulations. Water content of fruit (Fig. 20) which closely followed the fresh weight increase in the pericarp was increased by BA treatment but progressively declined after the second week of fructification. The BA treatment improved distal seed filling more than in normally grown pods and reduced the incidence of 'pops' and single-seededness (Fig. 21).

The effect of exposure to light on growth of fruit components of previously subterranean pods as a function of length of permitted fructification is indicated

Fig. 18a. Effects of various growth regulators on the fructification process of buried gynophores. Ordinate in mm.

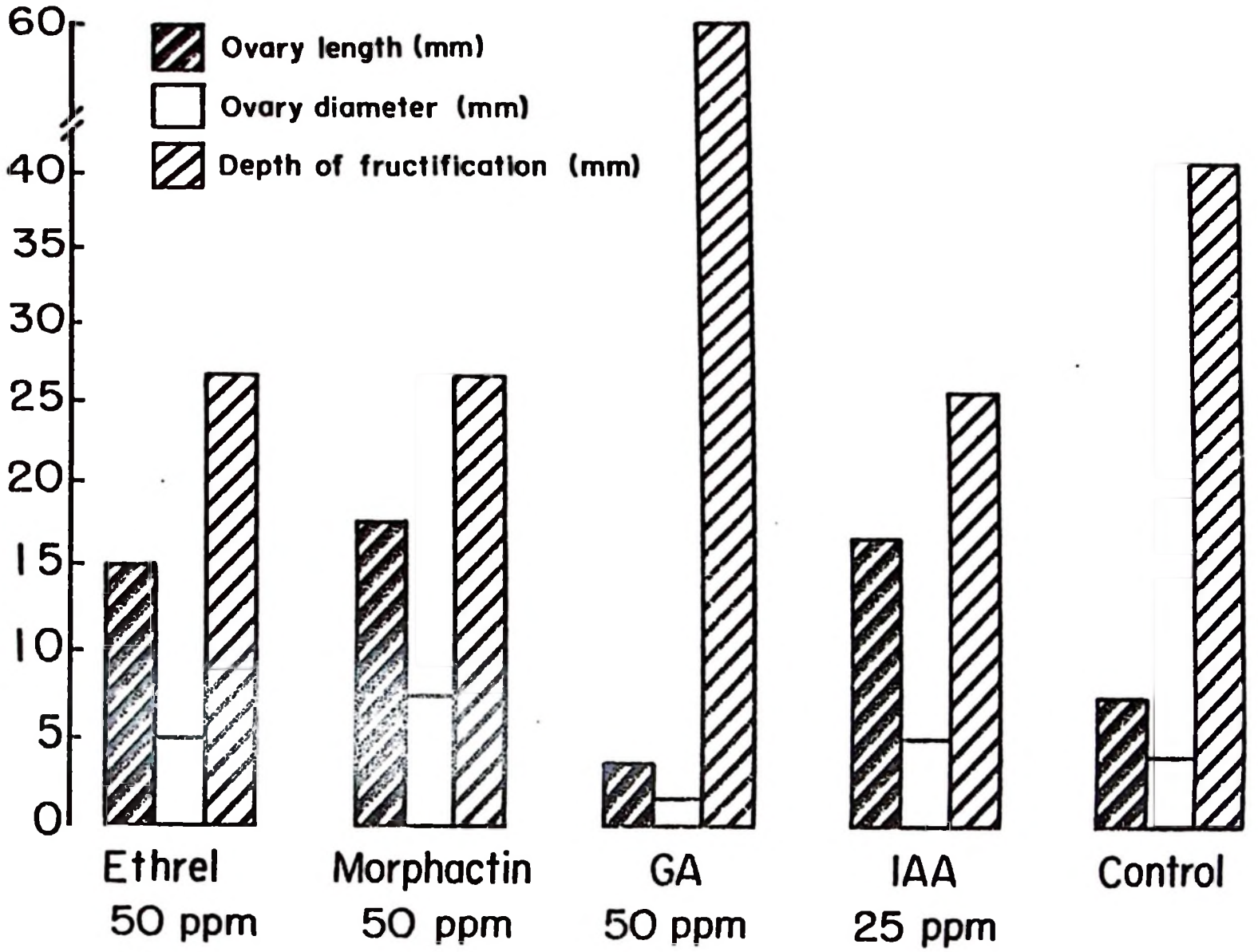

60
40
35
30
25
20
15
10
5
0
Ovary length (mm)
Ovary diameter (mm)
Depth of fructification (mm)
Ethrel
50 ppm
Morphactin
50 ppm
GA
50 ppm
IAA
25 ppm
Control

Fig. 18b. Effects of various growth regulators on the fructification process of buried gynophores.

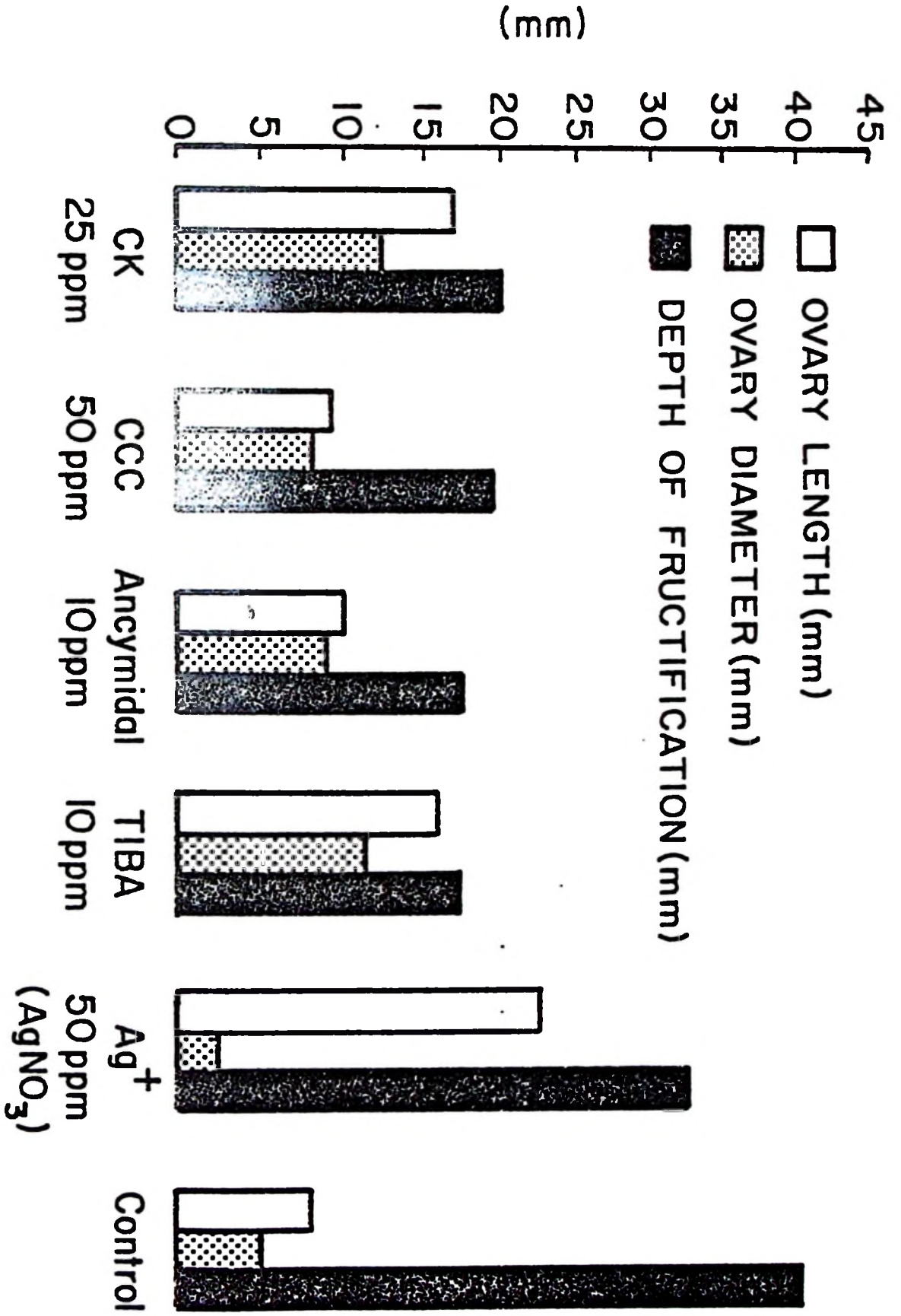

(mm)
0
5
10
15
20
25
30
35
40
45
OVARY LENGTH (mm)
OVARY DIAMETER (mm)
DEPTH OF FRUCTIFICATION (mm)
CK
25 ppm
CCC
50 ppm
Ancymidal
10 ppm
TIBA
10 ppm
Ag+
50 ppm
(AgNO3)
Control

Fig. 19a. Effect of cytokinin (BA) on fresh weight of fruit components in the course of fructification.

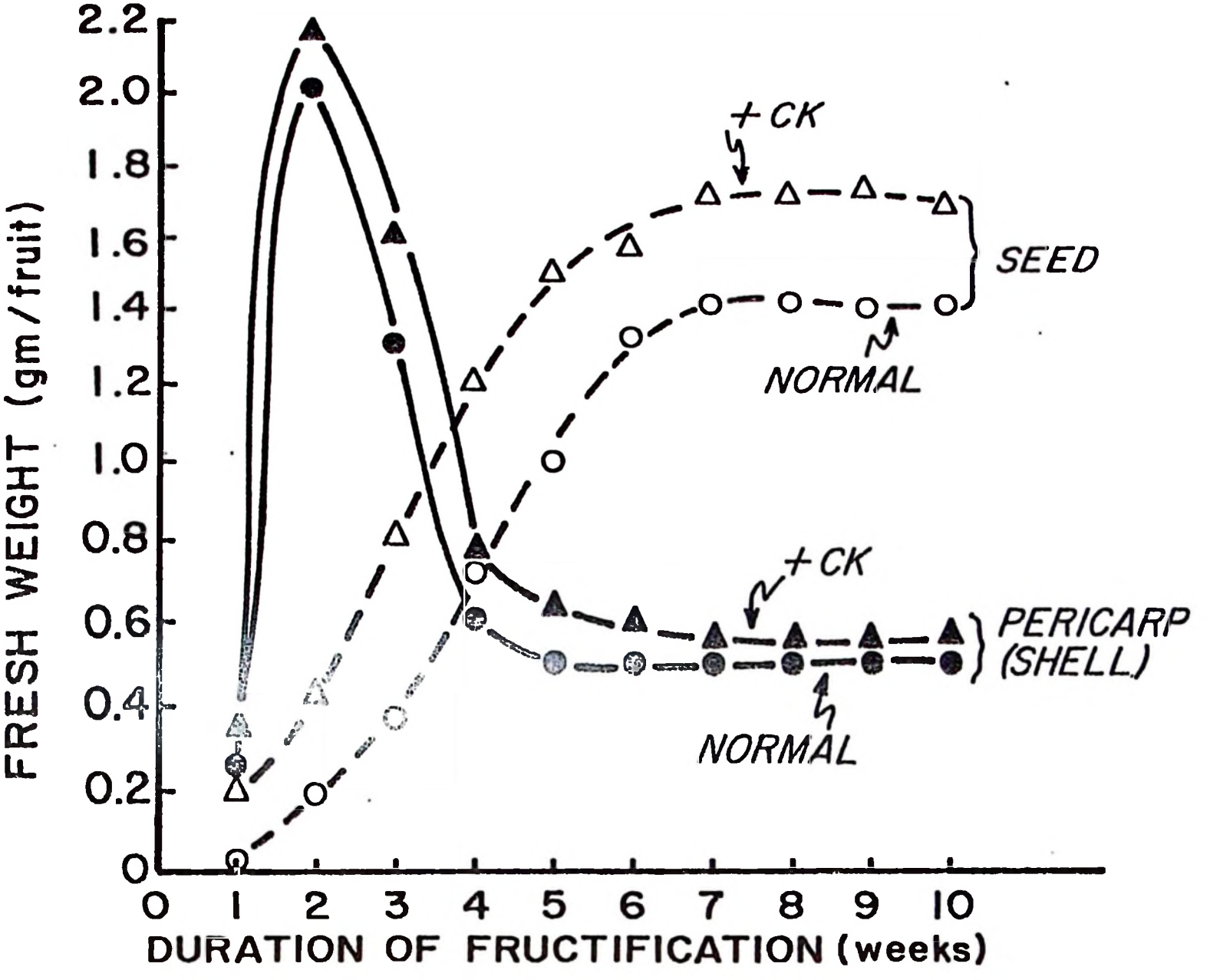

FRESH WEIGHT (gm/fruit)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10
DURATION OF FRUCTIFICATION (weeks)
+CK
SEED
NORMAL
+CK
PERICARP
(SHELL)
NORMAL

Fig. 19b. Effect of cytokinin (BA) on dry weight accumulation of fruit components in the course of fructification.

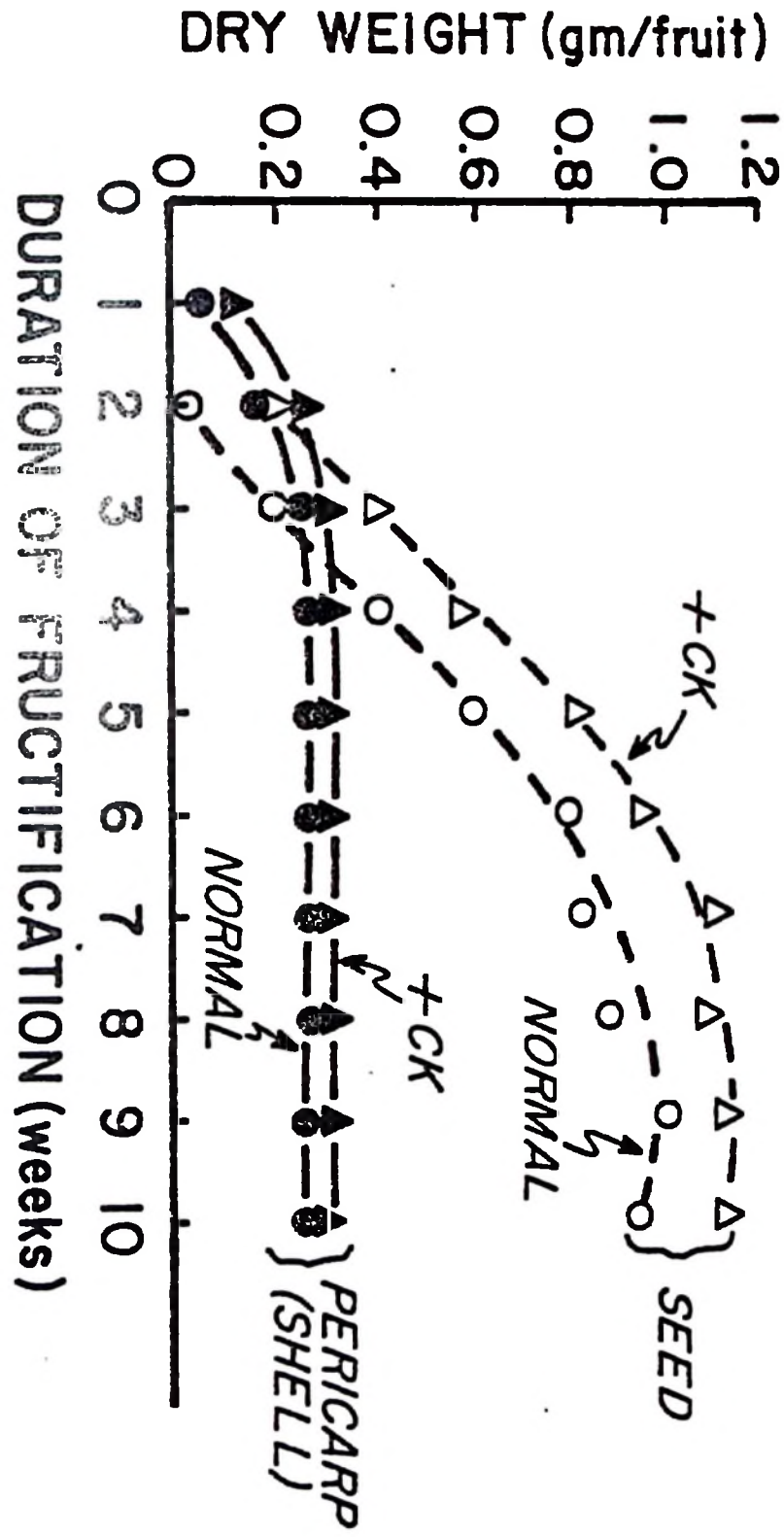

DRY WEIGHT (gm/fruit)
0
0.2
0.4
0.6
0.8
1.0
1.2
0 1 2 3 4 5 6 7 8 9 10
DURATION OF FRUCTIFICATION (weeks)
+CK
NORMAL
+CK
NORMAL
SEED
PERICARP (SHELL)

Fig. 20. Fruit water content as affected by CK (BA) during fructification.

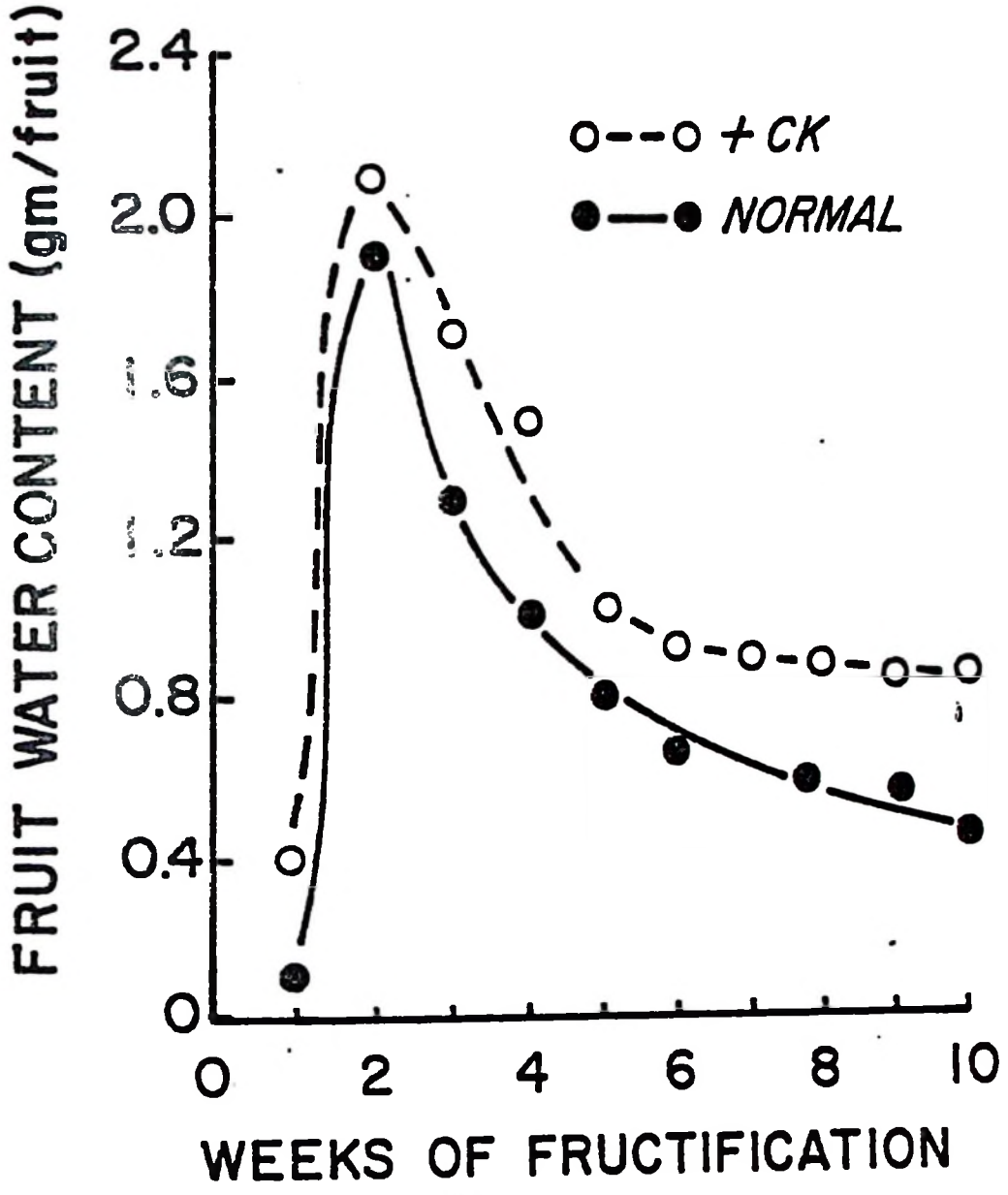

FRUIT WATER CONTENT (gm/fruit)
2.4
2.0
1.6
1.2
0.8
0.4
0
+CK
NORMAL
0
2
4
6
8
10
WEEKS OF FRUCTIFICATION

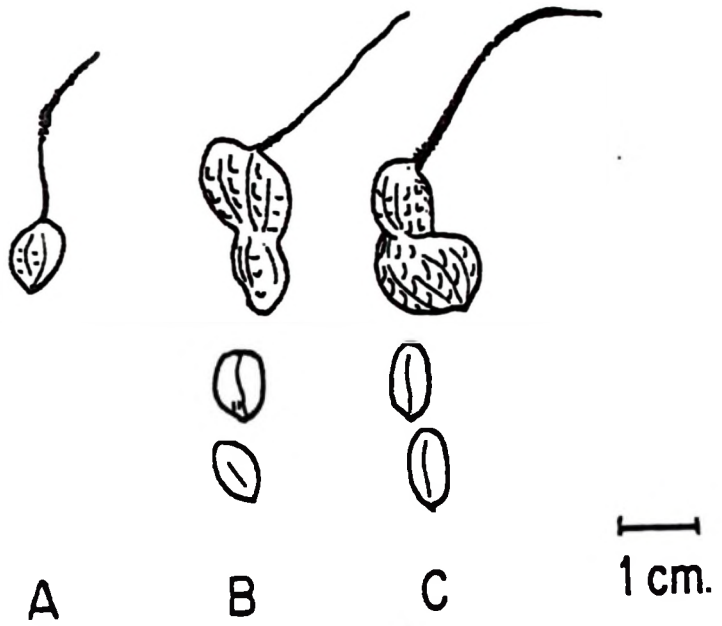
Fig. 21. Cytokinin (BA) effects on distal seed development and incidence of 'pops' and single seeded-ness. Traced from photograph.

A. A single seeded pod.

B. Normal pod (not treated) = 20% 'pops' and single seeded-ness.

C. BA treated pod at maturity = 5% 'pops' and single seeded-ness.

Note - comparative distal seed size between normal and treated.


A
B
C
1 cm.

(Fig. 22). Light preferentially inhibited pericarp growth over that of the seed. Dry weight in the seed, however, was characteristically checked by early exposure although there was a progressive increase of both fresh and dry weights of fruit components the longer the subterranean growth prior to exposure up to 70 days, by which time exposure had practically no effect. It was observed that when fruits were unearthed early, exposed and left to 'mature' on the plant, the pericarp became harder than normal and its thickness was reduced as a result of the higher relative seed growth within. When unburied, the ovary remains small while that in a moist dark atmosphere enlarges (Fig. 23). When exposed after 35 days, the further fruit growth is arrested even when moisture and nutrients were provided (Fig. 23) as compared to the control.

Aerial fructification in light was stimulated by a 14 day chemical treatment comprising of BA, CEPA, water, and supplemented mineral nutrients (excess Ca^{++} and B^{+}). This treatment was more effective for gynophores treated in the dark. The untreated dark controls had ovary diameters of same magnitude as those treated in light, however, gynophores left untreated in air (light) had shrivelled by the end of the experimental period (Fig. 24). Discontinuation of the treatment after 14 days halted further ovary growth in all treated categories. It was observed that gynophores in the dark (treated or untreated) showed loss of chlorophyll and development of root hair-like outgrowths while those treated in light depicted excessive intumescence.

Fig. 22. Fresh and dry weight accumulation by fruit components (partitioning) as influenced by exposure to light following various durations of subterranean ovary development.

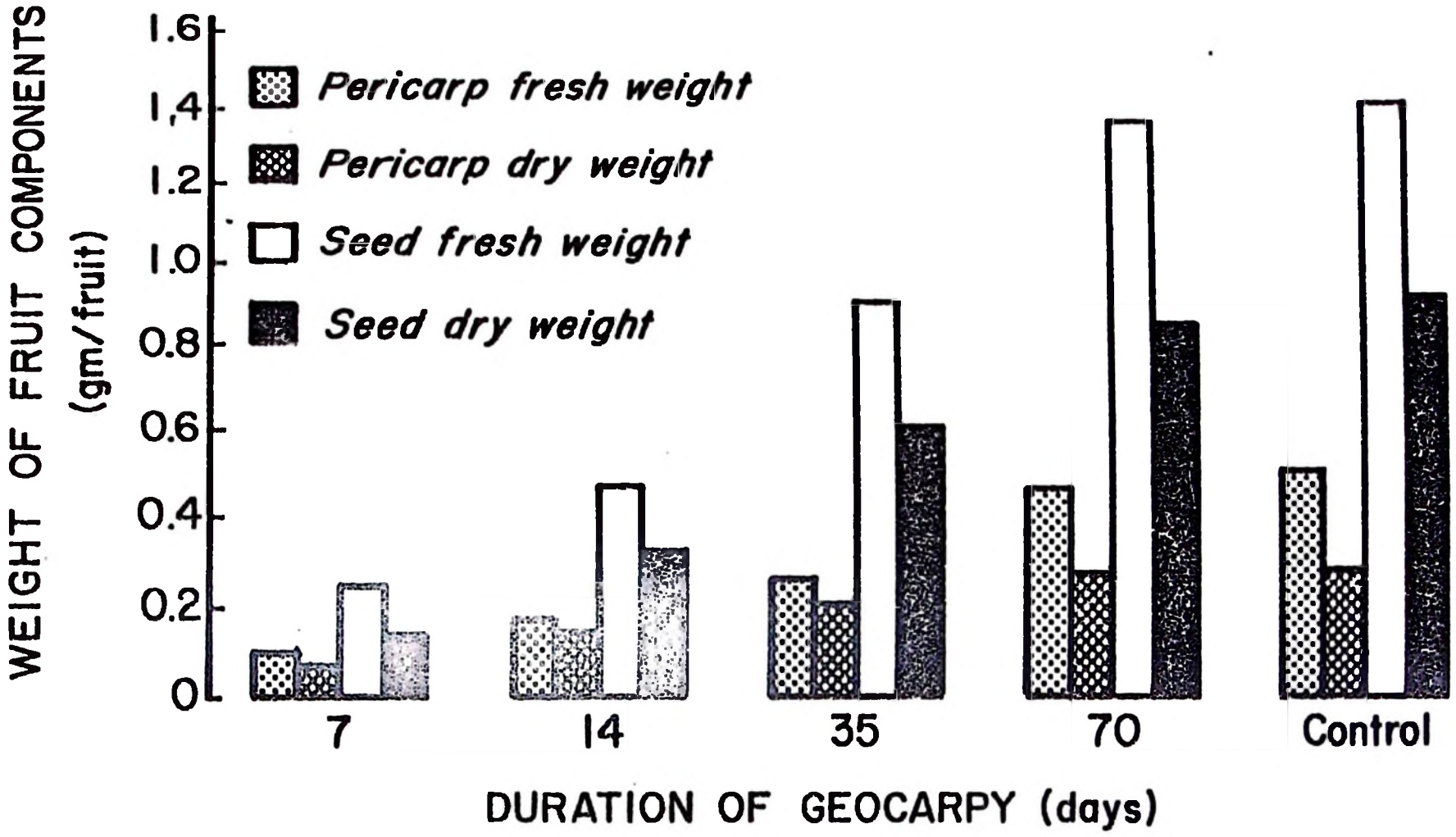

WEIGHT OF FRUIT COMPONENTS
(gm/fruit)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
Pericarp fresh weight
Pericarp dry weight
Seed fresh weight
Seed dry weight
7
14
35
70
Control
DURATION OF GEOCARPY (days)

Fig. 23. Geocarpy Illustrated. The treated (buried) and untreated (aerial) gynophores are of same age. Insert: A-pod exposed after 35 days of fructification compared to B. (normal) at maturity.

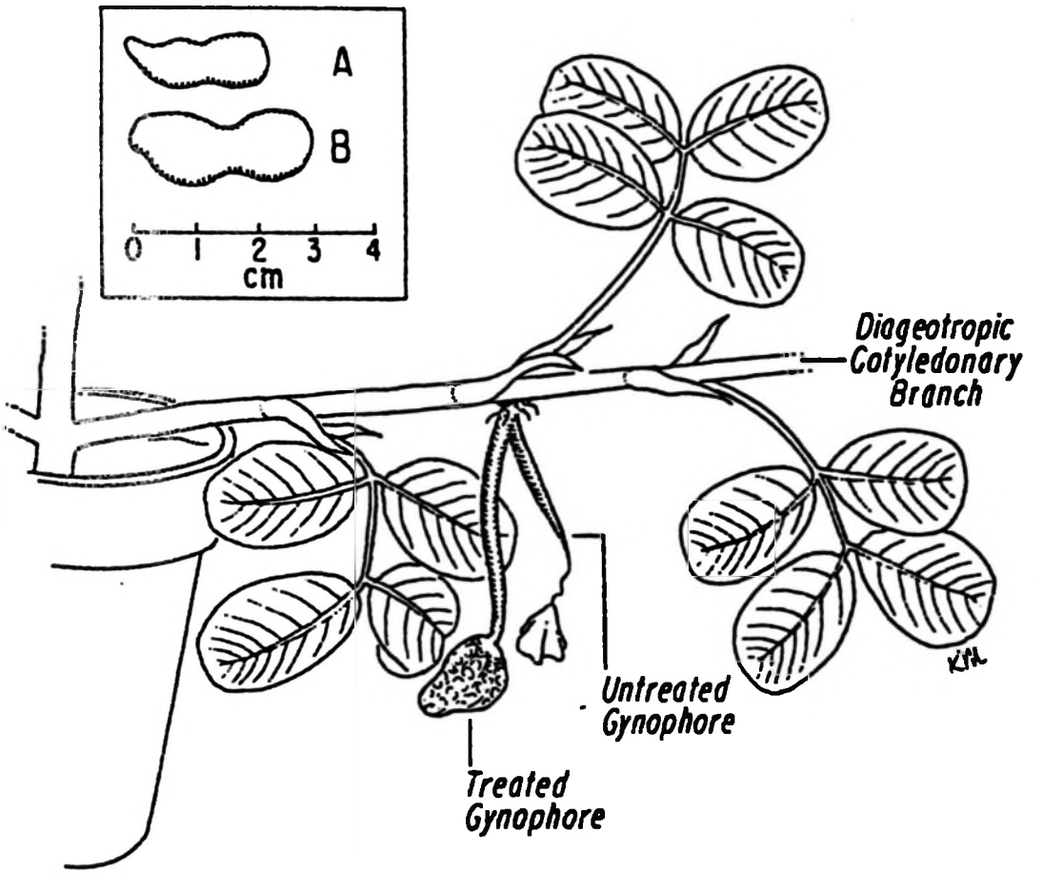
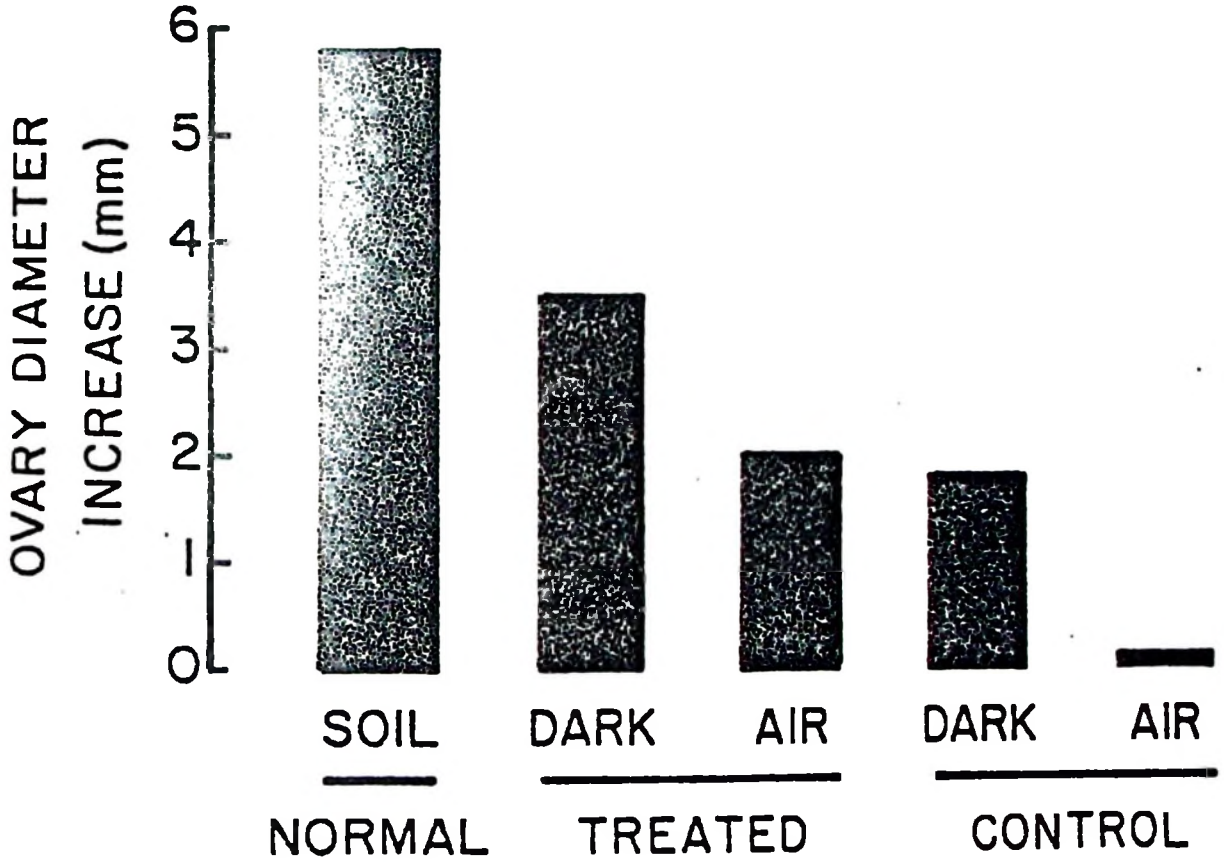

A
B
0 1 2 3 4
cm
Diageotropic
Cotyledonary
Branch
Untreated
Gynophore
Treated
Gynophore

Fig. 24. Aerial fructification induced by the chemical and physical environment treatment of gynophores. Note: The air control had shrivelled by end of experiment.


OVARY DIAMETER
INCREASE (mm)
0
1
2
3
4
5
6
SOIL
DARK
AIR
DARK
AIR
NORMAL
TREATED
CONTROL

DISCUSSION

Exogenously applied growth regulators are capable of influencing the development of the peanut pod. This is in agreement with the results on peas (Eeuwens and Schwabe, 1975) and in many other fruits (see Wittwer and Bukovac, 1962; Crane, 1964; Weaver, 1973). The results demonstrate that under normal soil conditions, the fructification process is inhibited as long as the IM proximal to the ovules is active. Thus GA which increased the depth of fructification by prolonging IM activity effectively postponed ovary swelling. Zamski and Ziv (1976) reported the deleterious effects of possibly supraoptimal GA levels on the ovary in which the entire gynophore tip degenerated. Soil applied GA in this experiment did not show such effect. Ovary length which is indicative of the activity of the proembryos on surrounding tissues (and the "resumptive" IM between them), was reduced by GA treatment showing that embryo development is retarded possibly at the expense of IM activity. Regulators such as CEPA, morphactin and IAA which reduced depth of fructification promoted ovary length and radial growth. Their effects may be either on hastening embryo development, which as reported by Smith (1956) influences growth of the pericarp by causing radial expansion of pericarp cells. Gibberellic acid, IAA, BA and ethylene seem to regulate the onset of fructification -- GA as an inhibitor and others as promotors of this process. These results are consistent with those obtained on tuber formation in which ethylene (Catchpole and Hillman, 1969), CK (Palmer and Smith, 1969; Esashi and Leopold, 1968) promote tuber growth in potatoes and Begonia. Fructification shows similarity to tuberization except that the former is a result of growth in the reproductive phase. It is suggestive that IM activity relative to proembryo development determines the onset of fructification in soil and it has been shown (see Part I) that the latter regulates the former.

Jacobs, (1951a) suggested that IAA from the ovary which inhibited IM

activity was responsible for ovary swelling. Sreeramulu and Rao (1971) confirmed that IAA increased in the ovary as fructification occurred. The role of IAA and ethylene in regulatory processes has been reported (Burg and Burg, 1965). The effects of IAA and CEPA on ovary diameter were similar to the control. This may be explained by considering that IAA which increases at the onset of fructification may induce ethylene evolution as reported for other plants (see Abeles, 1973). Ethephon (CEPA) breaks down in the plant to release ethylene and subsequently elevates endogenous ethylene biosynthesis (Suzuki et. al. 1971; Leopold, 1972). When applied alone, CEPA may produce the same effects as auxin (see Levitt, 1974). As gynophores grow through soil, they encounter constant obstruction and ethylene would possibly be formed as reported for pea hypocotyls (Goeschl, et. al., 1967) and roots (Kays, et. al., 1975) subjected to physical obstruction and Jaffe (1976) suggested it may be involved in thigmomorphogenesis. The root-like nature of the gynophore has been reported (Jacobs, 1947) and it is apparent that IAA and ethylene regulate its growth as reported for pea roots (Chadwick and Burg, 1970) presumably in the manner summarized by Levitt (1974). Thus in moist soil, a gynophore may be regarded as auxin and ethylene rich. The fact that Ag^{+} ion treatment of gynophores retarded radial ovary swelling is further evidence that endogenous ethylene regulates the process. The adiageotropic growth, enhanced fructification, and reduced elongation observed in gynophores arising from subterranean cleistogamous flowers is indicative of ethylene effects as first noted in peas by Neljubov (see Abeles, 1973). The levels of endogenous ethylene which would depend on soil texture (hence on the degree of mechanical stimulation) may play a role in depth perception and adjustment in this organ. The observations on pod growth in sand and clay soil (Shibuya, 1935) and abnormal pod elongation in artificial media (Zamski and Ziv, 1976) would similarly be explained.

Growth retardants CCC and ancymidol had opposite effects to those of GA.

This is consistent to their known mode of action (Cathey, 1964; Lang, 1970; Shive and Sisler, 1975; Montague, 1975). Ancymidol inhibits GA action (Leopold, 1971; Montague, 1975) while it is well documented that CCC inhibits its biosynthesis. Their effects on fructification could thus be explained since GA inhibits this process. Tri-iodobenzoic acid (TIBA), an auxin transport inhibitor (Winter, 1968), promoted radial ovary growth, a result which cannot be reconciled with its effect of lowering free auxin (Andus and Thresh, 1956). It may, however, interact synergistically with auxin at low concentrations as suggested (Thimann and Bonner, 1948; Aberg, 1953) or it could imply that fructification process is at least not controlled by a master hormone, contrary to the suggestion of Jacobs (1951a).

Reed (1924) indicated that cell divisions in the pericarp account for radial ovary growth which, as reported by Smith (1956b), coincides with rapid divisions in the endosperm and proembryo. The effectiveness of BA to inhibit GA-promoted growth (Part I) and its reported effects on promoting cell division is coherent with its ability to enhance fructification. Morphactin, an inhibitor of auxin transport, and intact gynophore elongation could have stimulated ovary growth by creating a high auxin level in the ovary (since it reduces the capacity of the plant to transport auxin (Krelle and Libbert, 1968b) or it could have interacted with other endogenous hormones (see Schneider, 1970) in a yet undisclosed mechanism to enhance fructification.

The development of peanut pod components show similarity to the report by Schenk (1961) on field grown Spanish bunch variety. There exists growth correlation between the pericarp and the seed. The results show that pericarp development precedes that of the seed. Young pods are strong sinks and monopolize photosynthates (Khan and Akosu, 1969; Patee et al., 1976) and it is demonstrated that initially the pericarp and later the seeds exerted mobilizing power, however, the developing seeds accumulated most of the dry weight

indicating more partitioning into them in agreement with results of Duncan et al., (1977). Cytokinin (BA) increased both dry and fresh weights and on a whole fruit basis, it increased water content. Auxin has been reported to increase water uptake by plant tissues (Bonner et. al., 1956). Recognizing that young pods have supraoptimal auxin, BA a strong mobilizing agent (Mothes, 1964) could possibly act cooperatively with auxin to enhance water intake by the pericarp. Benzyladenine (BA) was capable of increasing distal seed development (Fig. 21) to the final size of the proximal seed. This result confirms previous suggestion (see Brennan, 1961) that competition for assimilates accounted for the disparity between the proximal and distal seed sizes. The incidence of poorly filled pods was drastically reduced by BA treatment indicating that assimilate availability to the ovules is a major constraint to their full development. BA treatment at "pegging" may be a practical method of producing uniform seeds.

Since the studies of Shibuya (1935) and recently Zamski and Ziv (1976) light has been shown to inhibit fructification. The results (Fig. 22) indicate that light inhibition of this process is dependent on the duration of permitted subterranean growth prior to exposure. Pericarp growth is preferentially checked to that of the seeds. The observation that early exposure of pods caused their excessive lignification suggest that light inhibits growth by promoting lignin formation, however, it is also suggestive that greening of the pods and cotyledons would prevent their further development possibly as shown by Blaaw-Jensen (1954) in other plants that chlorophyllide can be photoconverted into a growth inhibitor. Taylor (1976) reported that light exposure reduced cell number in cotyledons of geocarpic Trifolium although the actual mechanism is unknown. Shibuya (1935) suggested that fructification is phytochrome controlled so that perhaps a number of key yet unknown photo-regulated processes leading to fructification may thus be influenced (see Mohr, 1969). However, light has been reported to suppress ethylene in peas (Goeschl et. al., 1968) which has been related to fructification in

this study. The removal of the mechanical stimulus necessary for this process (Yasuda, 1943; Zamski and Ziv, 1976) would retard further pod growth and this would explain the gradual ineffectiveness of late exposures of pods on pericarp and seed growth.

The induction of aerial fructification by B^+, Ca^{++}, CEPA and BA treatment (Fig. 24) indicates their key roles on this process. Both B^+ and Ca^{++} are less mobile in the phloem (Biddulph et. al., 1959) and in a moist environment, the exogenous supply in the 'pegging' zone becomes the only means of their being available (Wiersum, 1951). The roles of B^+ and Ca^{++} in fructification have been elaborated (see Reid and Cox, 1973). A moist and dark atmosphere was conducive to ovary swellings, however, the treatment of light exposed ovaries enabled limited fructification indicating that light may inhibit this process possibly by affecting the production or action of these hormones. It is also demonstrated that the hormonal treatment could partially substitute for mechanical stimulation although no further ovary enlargement was observed after the termination of treatment suggesting that continuous physical stimulus is necessary. Further study relating concurrent changes of endogenous hormones with the fructification process is necessary.

SUMMARY

The regulation of peanut gynophore elongation and the fructification process were studied using Spanish bunch variety grown under constant temperature (26.5°C), photoperiod (12 hr) and relative humidity (ca 90%) in a growth chamber. The experimental material consisted of tagged flowers or gynophores continuously made available by replanting.

A technique utilizing the floral morphology was devised to study effects of exogenous growth substances applied independently or in combinations on the induction of IM activity (gynophore initiation) in the absence of fertilization and syngamy. Growth substances are able to evoke IM activity thus substituting for the syngamic stimulus. The effect of GA was dose-dependent suggesting that it may be a critical factor in gynophore initiation, however, a mixture of GA, IAA and BA was more effective than individual or combined effects of BA and IAA. Morphactin showed stimulatory effect on IM activity. When applied to fertilized flowers, CEPA and Ag^+ ions inhibited IM activity, the latter by postponing hypantha abscission. In the absence of exogenous auxin, gynophores initiated without fertilization failed to show geotropic curvatures denoting the role of auxin in mediating normal geotropism. Growth substance initiated gynophores were incapable of fructification and their limited elongation was suggestive of the necessity of proembryonic secondary stimuli for these processes.

Gibberellic acid promoted while other tested growth substances i.e. IAA, BA, CEPA, TIBA, CCC and morphactin inhibited intact gynophore elongation. Ovule removal stagnated elongation partially overcome by GA confirming the role of the proembryos for sustained IM activity. Auxin or BA inhibited GA-promoted intact gynophore elongation depending on gynophore age auxin being more inhibitory on the younger gynophores being least responsive irrespective of concentration. When applied to flowers at anthesis, morphactin transiently inhibited geotropic curvature development but copiously altered gynophore trajectory.

The size and activity of the IM zone decreases towards the ovule base with progressive gynophore lengthening. Gibberellic acid affects elongation by increasing length of IM cells whose elongation is basipetally polarized. The inverse relationship between fructification depth and gynophore length is attributed to the decreasing size and activity together with internal differentiation of the IM zone with age.

A definition of peanut 'fruit-set' is suggested as being at time of IM induction (i.e. gynophore initiation phase of fruit development) and the gynophore as a physiologically unique young fruit.

The observation that ovule removal delayed but did not prevent curvature development of excised gynophores suggested the perceptive and responsive nature of the IM to geotropic stimulus. Morphactin enhanced elongation of excised gynophores for all concentrations with optima at 0.1 and 10 ppm and effectively altered geotropic curvature even at 0.1 to 1 ppm. Higher morphactin concentrations rendered gynophores ageotropic. There was an inverse relationship between the anti-geotropic effect and growth stimulation. Morphactin, however, failed to stimulate growth in the presence of auxin which partially reversed its effects on geotropism. Auxin inhibited excised gynophore elongation for all concentrations but progressively reduced the degree of curvature. The effect of morphactin and auxin on elongation are further evidence on gynophore physiological similarity to roots and the regulation of geotropic curvature by auxin. Tri-iodobenzoic acid (TIBA) and BA inhibited elongation and curvature with increasing concentration, TIBA more drastically than BA. While GA stimulated growth without appreciable effects on curvature, it partially reversed concentration dependent ancymidol-induced inhibition of these parameters.

The fructification process, characterized as simultaneous cessation of gynophore elongation and ovule enlargement is enhanced by growth inhibitors,

morphactin, IAA and CEPA while GA postponed it by perpetuating IM activity with resultant greater fructification depths. The inhibitory effects of Ag^{+} ions, an anti-ethylene agent on fructification suggest the involvement of ethylene in regulating this process. Depth perception by gynophores is attributed to endogenous hormones acting on the IM.

Pericarp growth which is mainly by water retention by the tissue precedes that of the seed but the latter accumulates most of the dry weight in the course of growth. Benzyladenine (BA) enhances fruit growth by increasing water content and kernel dry matter. Distal seed growth was greatly improved by BA treatment by increasing its sink strength which resulted in the reduction of pops and single seededness.

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