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Effect of Growth Regulators on the Structure and Ontogeny of Cotyledonary Stomata of *Helianthus annuus*

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With 77 figures (1 table)

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Abstract

Effect of some growth regulators on the structure and ontogeny of stomata in the cotyledons of *Helianthus annuus* L. var. EC. 68414 is described. In control anomocytic stomata are noticed. In addition to this type, paracytic, cyclocytic and stoma with a single subsidiary cell are noticed in some of the treatments. Sometimes, an anomocytic stoma surrounded by three unequal epidermal cells simulates with anisocytic type. The ontogeny of all the types is perigenous. Aberrant types such as single guard cells, persistent stomatal cells, degeneration of guard cells, division of guard cells and cytoplasmic connections are noticed in various treatments. The varied behaviour of meristemoid and formation of stomata by amitotic division is a characteristic feature of Morphactin treatment. The effect of growth regulators on stomatal density, index and size is also discussed.

Zusammenfassung

Wirkung von Wachstumsregulatoren auf Struktur und Ontogenie der Stomata der Keimblätter von *Helianthus annuus*

In unbehandelten Kontrollpflanzen von *Helianthus annuus* L. var. EC. 68414 sind die Stomata der Keimblätter anomocytisch. Die durch Behandlung mit Rohrzucker (2000 ppm), Gibberellinsäure, Indolessigsäure, Kinetin, Trijodobenzoesäure, Colchicin, Cumarin, Maleinhydrazid, Sulfanilamid und Morphactin in verschiedenen Konzentrationen erzielten Veränderungen werden beschrieben. Ein abweichendes Verhalten der Meristemoide und Bildung der

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Stomata durch amitotische Teilung ist für die mit Maleinhydrazid behandelten Pflanzen charakteristisch. Die Wirkung der genannten Substanzen auf Dichte und Größe der Stomata sowie den Stomataindex wird diskutiert.

(Editor transl.)

Introduction

PANT & VERMA (1963), RAMAYYA & RAO (1968), RAWSON & CRAVEN (1975), BHATT & INAMDAR (1975) and HUSSON (1975) studied the structure and ontogeny of stomata in some *Compositae*. As far as the authors are aware no report exists on the effect of growth regulators on stomatal structure and development in the *Compositae*.

Material and Methods

The seeds of *Helianthus annuus* L. var. EC. 68414 were bought from the Institute of Agriculture, Anand. These seeds were cultured following the methods described by INAMDAR & GANGADHARA (1975) using the following substrates: Control (distilled water, DW), Sucrose (SUC) 2000 ppm; Gibberellic acid (GA), Indole-3-acetic acid (IAA), Kinetin (KIN), 2, 3, 5-Tri-iodobenzoic acid (TIBA), Colchicine (COL), Coumarin (COU), Maleic hydrazide (MH), Sulphanilamide (SUL) and Morphactin (MOR) in three concentrations viz.: 25,50, and 100 ppm.

Mean values of 10 observations are taken for stomatal index, frequency, size of guard and epidermal cells from epidermal peels of cotyledons stained with Delafield's haematoxylin and mounted in glycerin.

Observations

Dormant cotyledons: In dormant cotyledons the developmental stages are not observed (Fig. 1). Stomatal initiation was observed only after the emergence of the radicle.

Mature epidermis: The epidermal cells are polygonal, isodiametric variously elongated with either straight, arched or sinous anticlinal walls (Fig. 3, 7, 36, 70). Stomata are present all over the surface of the lower epidermis of cotyledons, and are arranged without any definite pattern of orientation in treated as well as untreated plants.

Mature stomata and their ontogeny: In a young epidermis, the protoderm cells are polygonal, isodiametric, uninucleate with uniform staining and mostly with straight walls. The meristemoids are cut off either in corners or on one side of the protoderm cells, and can be easily dis-

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Fig. 1—21. Epidermal peels showing either developping or mature stomata in the cotyledons (lower epidermis). Fig. 1: Cleared cotyledon; Fig. 2—8: Control; Fig. 9—15: Gibberellic acid, 25 ppm; Fig. 16, 17: id., 100 ppm; Fig. 18—21: Kinetin, 25 ppm. (1—12, 17: ×220; 13—16, 18—21: ×730)

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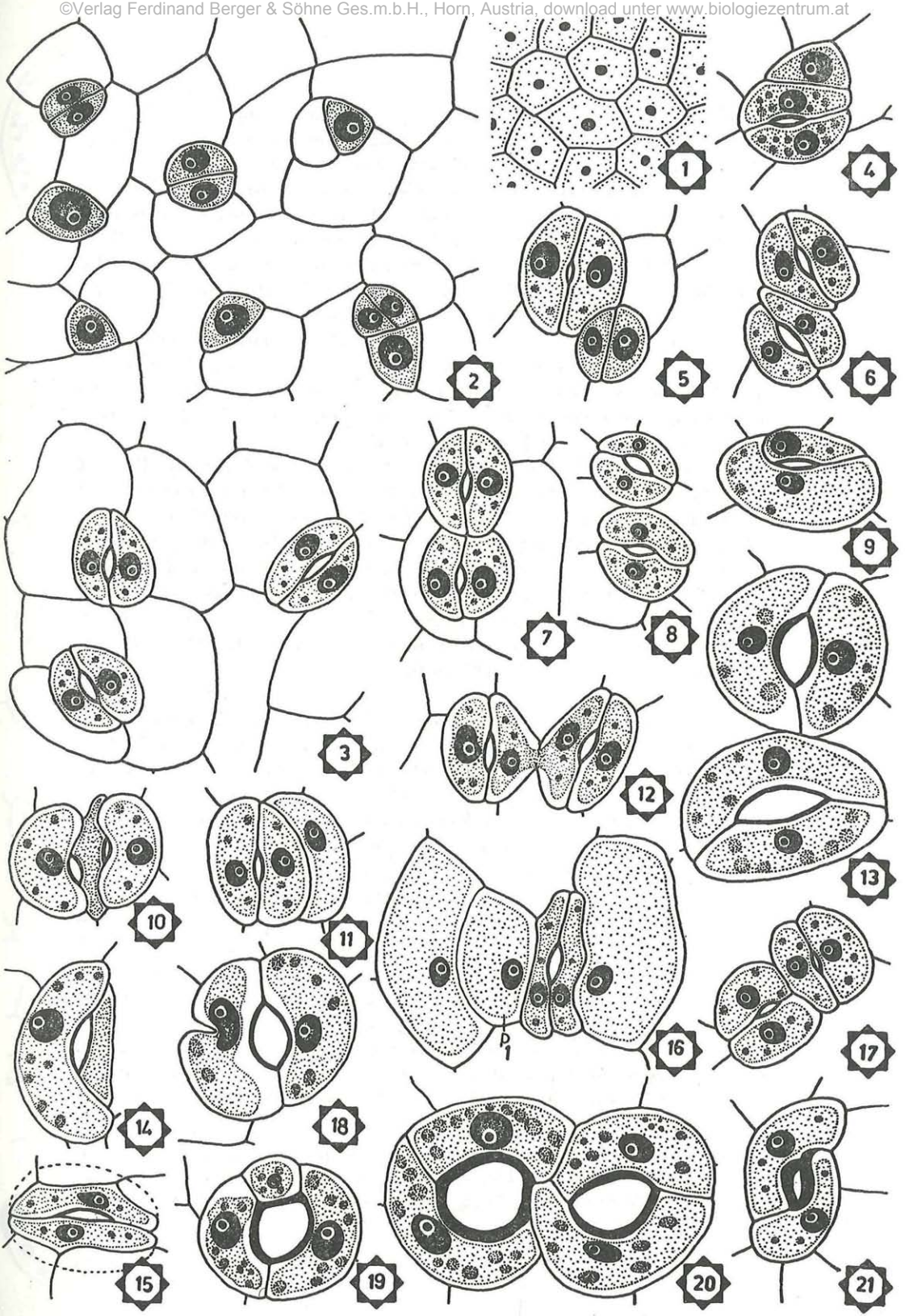

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tinguished by their smaller size, shape, prominent nucleus and dense staining properties. Meristemoids occur either solitary or in pairs (Fig. 2). The ontogeny of different types of stomata is as follows:

(a) Anomocytic: A meristemoid enlarges, becomes rounded and divides by a straight wall to form a pair of guard cells between which an intervening lenticular pore develops (Fig. 2). Mature stoma is surrounded by 3—6 ordinary epidermal cells. Sometimes, an anomocytic stoma surrounded by three ordinary epidermal cells simulate with an anisocytic type, the smaller cell being the one which cuts off the meristemoid (Fig. 3).

(b) Stoma with a single subsidiary cell: The stomatal development is similar to that of anomocytic type, but a single perigene subsidiary cell is cut off from the adjacent epidermal cell or the cell which cuts off the meristemoid differentiates into a single subsidiary cell (Fig. 11.) Mature stoma is flanked by a single perigene subsidiary cell.

(c) Paracytic: The development of stomata is similar to that of anomocytic one. Here, two subsidiary cells are cut off parallel to the guard cells from adjacent epidermal cells (Fig. 55). Sometimes, one of the subsidiary cells is cut off from the adjacent epidermal cell parallel to the guard cells while an adjacent epidermal cell differentiates as a second subsidiary cell (Fig. 16). Mature stoma is flanked by two parallel perigene subsidiaries.

(d) Cyclocytic: Here, the ontogeny of stoma conforms to that of an anomocytic one, but a narrow ring of perigene subsidiary cells are cut off from adjacent epidermal cells (Fig. 49).

Treatments:

1) Control (Distilled water, DW) (Figs. 2—8): Stomatal types: Anomocytic (Figs. 3, 4). Sometimes, an anomocytic stoma surrounded by three ordinary epidermal cells simulates with an anisocytic type (Fig. 3). Aberrant types: Contiguous stomata which develop from adjacent meristemoids (Figs. 2, 4, 5). Contiguous stomata are either superimposed or obliquely oriented or at right angles to each other (Figs. 6—8) depending upon the orientation of division in the adjacent meristemoids.

2) Gibberellic acid (GA) 25 ppm (Figs. 9—15), 50 ppm and 100 ppm (Figs. 16, 17): Stomatal types: Anomocytic, paracytic (Fig. 16) and with a single subsidiary cell (Fig. 11). The guard cells are angular in GA 100 ppm. Aberrant types: Degeneration of guard cells (Figs. 14, 15), unequal guard cells (Fig. 9) and contiguous stomata (Figs. 13, 17). Sometimes, the two central guard cells of juxtaposed stomata are crushed and degenerate which may be due to the pressure of the enlarging outer guard cells (Fig. 10). During the course of degeneration of guard cells, first the nucleus degenerates followed by the vacuolation and degeneration of cytoplasm.

Fig. 22—43 (continued). Fig. 22—32: Kinetin, 25 ppm; Fig. 33—35: id., 50 ppm; Fig. 36: Sucrose, 2000 ppm; Fig. 37: Coumarine, 25 ppm; Fig. 38: id., 50 ppm; Fig. 39—43: Colchicine 25, ppm (22—35, 37—43: ×730; 36: ×220)

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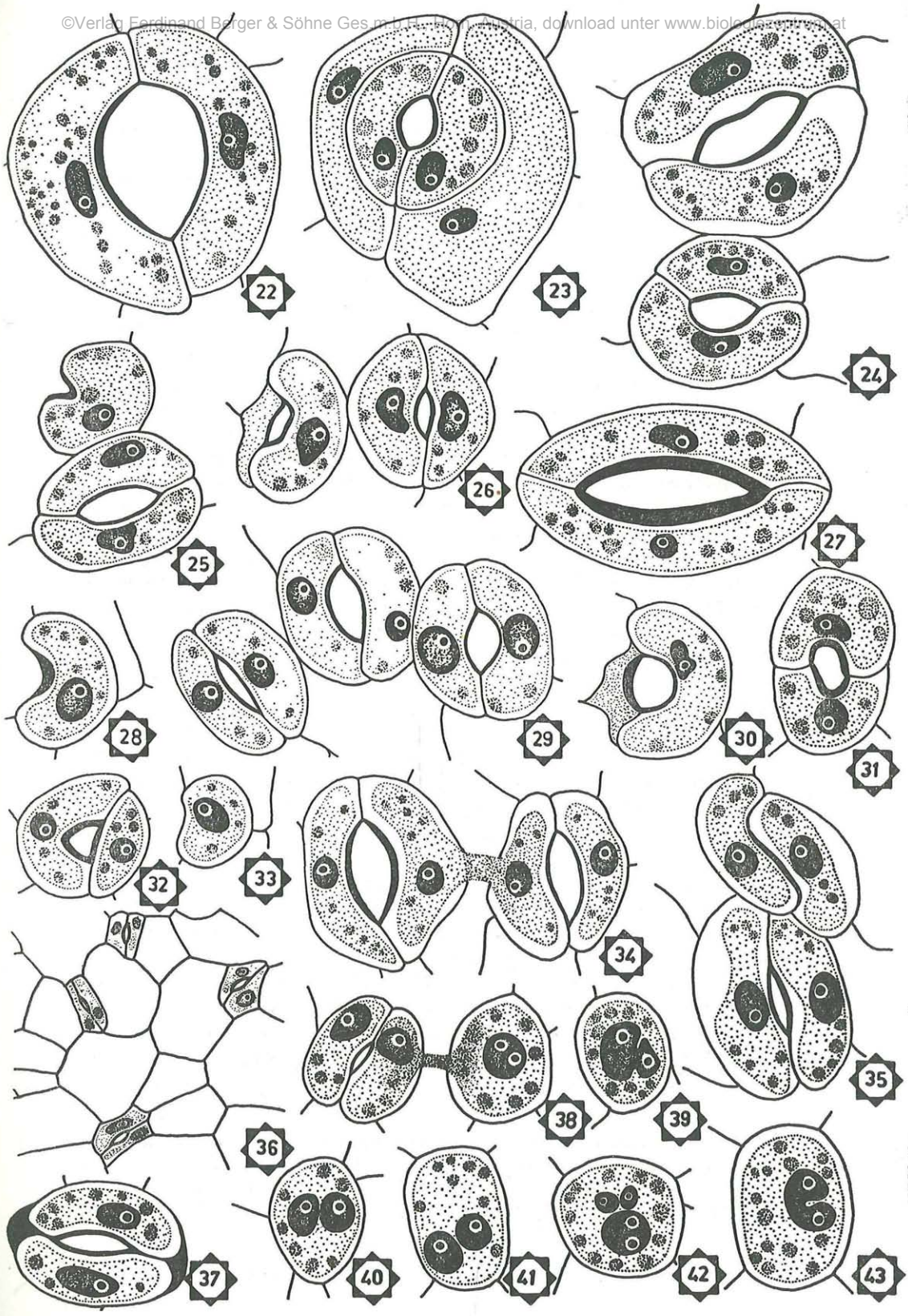

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3) Indole-3-acetic acid (IAA) 25 ppm, 50 ppm and 100 ppm: Stomatal types: Anomocytic and with a single subsidiary cell. Aberrant types: contiguous stomata which are either superimposed or juxtaposed or at right angles to each other and degeneration of guard cells.

4) Kinetin (KIN) 25 ppm (Figs. 18—32), 50 ppm (Figs. 33—35) and 100 ppm: Stomatal types: Anomocytic and paracytic. Sometimes, a meristemoid is cut off in between the protoderm cells on one of the sides. The meristemoid directly develops into a stoma which looks-like paracytic as it is surrounded by two epidermal cells (appearing like subsidiaries) lateral and parallel to the guard cells (Fig. 23). Here, the surrounding cells at maturity look-like mesogene subsidiary cells but in fact are perigene in origin. Aberrant types: 2—3 contiguous stomata which are either juxtaposed (Figs. 24, 26) or superimposed (Figs. 20, 35) or obliquely oriented, division of one of the guard cells of a stoma (Fig. 19), notching of guard cells (Fig. 18), obliquely oriented guard cells (Fig. 21), unequal guard cells (Fig. 32), single guard cells (Figs. 28, 33), a single guard cell contiguous with a normal stoma (Fig. 25), cytoplasmic connections between guard cells of nearby stomata (Fig. 34) and degeneration of guard cells (Fig. 26, 30). Another important feature noticed in KIN treatment is the frequent occurrence of giant stomata with abnormally big pore and elongated guard cells (Figs. 22, 27). The shape of the pore is also variable. It may be oval or lenticular. Sometimes, the pore is at right angles to the guard cells (Fig. 31).

Single guard cells develop directly from the meristemoids. Here, the meristemoid does not divide, but enlarges, becomes reniform and notched on one side. A differential thickening appears at the region of the notch, chloroplasts appear and differentiates into a single guard cell (Fig. 28, 33).

5) Sucrose (SUC) 2000 ppm (Fig. 36): Stomatal types: Anomocytic and with a single subsidiary cell. The guard cells are angular in outline. Aberrant types: Contiguous stomata which are either juxtaposed or superimposed. Abnormalities are rather rare.

6) 2, 3, 5-Tri-iodobenzoic acid (TIBA) 25 ppm, 50 ppm, and 100 ppm: Stomatal types: Anomocytic. Aberrant types: Rather infrequent. Single guard cells, contiguous stomata and cytoplasmic connections between nearby stomata are rarely met with.

7) Colchicine (COL) 25 ppm, (Figs. 39—45) 50 ppm (Fig. 46) and 100 ppm: The meristemoids rarely differentiate into anomocytic stomata. Aberrant types: Here, the nucleus of the meristemoid divides mitotically but not followed by the wall formation. Hence, 2—5 nuclei are observed in a single meristemoid which is destined to differentiate as a persistent

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Fig. 44—73 (continued). Fig. 44, 45: Colchicine, 25 ppm; Fig. 46: id., 50 ppm; Fig. 47—51: Maleic hydracide, 25 ppm; Fig. 52—55: id., 50 ppm; Fig. 56—58: id., 100 ppm; Fig. 69: Morphactin, 100 ppm; Fig. 70: Sulphanilamide, 25 ppm; Fig. 71, 72: id., 50 ppm; Fig. 73: id., 100 ppm (44—50, 52—73: ×730; 51: ×220)

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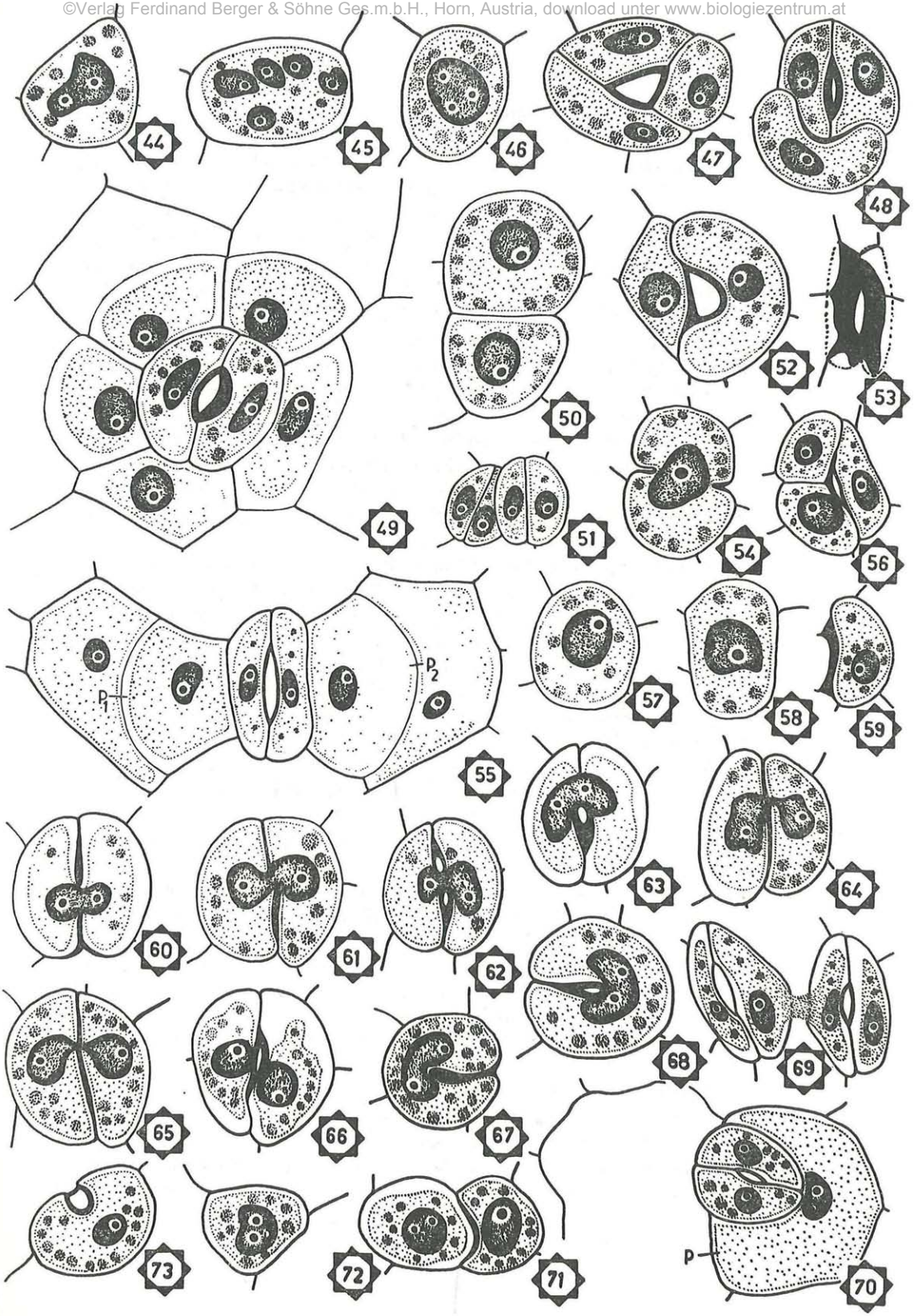

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stomatal cell (Figs. 39—46). Sometimes, a single very large nucleus with 2—3 nuclei are noticed. The meristemoids differentiate as persistent stomatal cells. During differentiation, the meristemoids enlarge with their nuclei, chloroplasts appear and a uniform thickening does develop around the meristemoids which then differentiate as persistent stomatal cells. The shape of the persistent stomatal cells is either spherical or oval or triangular or rectangular with 1—5 nuclei and each nucleus with 1—3 nucleoli (Figs. 39—46). The shape of the nucleus is also variable (Figs. 39—46). It may be spherical, horse-shoe shaped, amoeboid or oval.

8) Coumarin (COU) 25 ppm (Fig. 37), 50 ppm (Fig. 38) and 100 ppm: Stomatal types: Anomocytic and with a single subsidiary cell. Sometimes an anomocytic stoma surrounded by three unequal epidermal cells simulates with an anisocytic type. Very rarely a stoma with cuticular thickening at the polar regions is observed in COU 25 ppm (Fig. 37). Aberrant types: Contiguous stomata which are either juxtaposed or obliquely oriented or at right angles to each other, persistent stomatal cells and cytoplasmic connections between the guard cells of a stoma and a persistent stomatal cell and between guard cells of nearby stomata.

9) Maleic hydrazide (MH) 25 ppm (Figs. 47—51), 50 ppm (Figs. 52—55, 75) and 100 ppm (Figs. 56—68, 74, 76, 77): Stomatal types: Anomocytic and paracytic (Fig. 55). Very rarely cyclocytic stomata are observed in MH 25 ppm (Fig. 49). Aberrant types: Division of guard cell (Figs. 47, 56), one and a half contiguous stomata (Fig. 48), persistent stomatal cells which are either solitary or in pairs (Figs. 50, 57, 58), degeneration of guard cells of a stoma (Figs. 53, 59), unequal guard cells (Fig. 52) and contiguous stomata (Fig. 51).

Varied behaviour of the meristemoid and development of stomata by amitotic division is an important feature noticed in MH treated plants. The following varied behaviour is noticed: (i) Formation of guard cells by amitotic division: The meristemoid increases with its nucleus. The nucleus initially spherical becomes crescentic and later becomes horse-shoe shaped followed by the centripetally advancing furrows from periphery on one or both sides of the meristemoid (Figs. 54, 67, 74, 75). In the former case the furrow may end blindly in the centre of the cell lumen and may not have a pore at the distal free end (Figs. 67, 68), while in the latter case, the furrows extend from both sides and meet in the centre dividing the nucleus as well as the meristemoid into two guard cells. A pore may or may not be formed (Figs. 54, 60—66, 76, 77), (ii) Persistent stomatal cell: Meristemoid directly differentiates into a persistent stomatal cell (Fig. 50, 57).

10) Sulphanilamide (SUL) 25 ppm (Fig. 70), 50 ppm (Figs. 71, 72) and 100 ppm (Fig. 73): Stomatal types: Anomocytic. However, a stoma with a single subsidiary cell looking like polocytic (Fig. 70) is noticed in SUL 25 ppm. An anomocytic stoma surrounded by three unequal epidermal cells simulates with that of an anisocytic type. Abberrant types: Single guard cells (Fig. 73),

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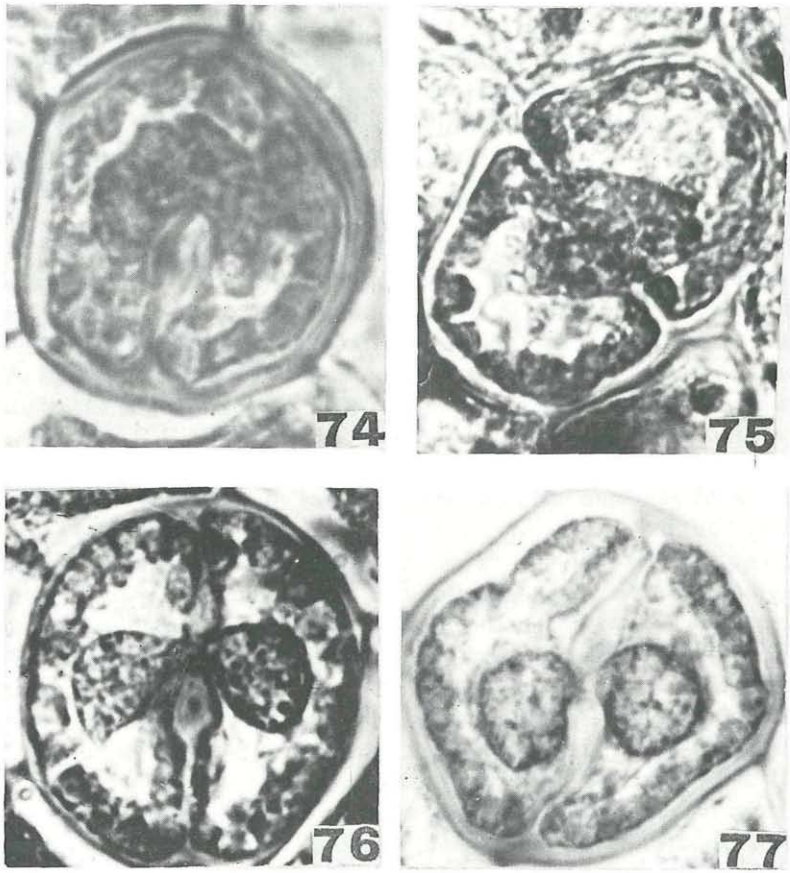

Fig. 74—77. Formation of guard cells by amitotic division. Fig. 75: After treatment with Maleic hydrazide, 50 ppm; Fig. 74, 76 and 77: id., 100 ppm (74—77: ×2200)

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persistent stomatal cells which are either solitary (Fig. 72) or contiguous with a single guard cell (Fig. 71), stoma with obliquely oriented guard cells, contiguous stomata, cytoplasmic connections between guard cells of nearby stomata.

11) Morphactin (MOR) 25 ppm, 50 ppm and 100 ppm (Fig. 69): Stomatal types: Anomocytic. Aberrant types: Cytoplasmic connections between guard cells of adjacent stomata (Fig. 69), contiguous stomata which are either juxtaposed or superimposed or at right angles to each other.

Discussion

A survey of literature reveals that attempts have been made by different research workers to investigate the effect of environment, temperature, growth regulators, wounding etc. on the stomatal structure and ontogeny (*see* INAMDAR & GANGADHARA 1975, GANGADHARA & INAMDAR 1975, INAMDAR *et al.* 1976). But no attempt practically have been made to study the effect of growth regulators on the members of the *Compositae* especially on *Helianthus annuus*. During the course of present study the stomatal types observed are anomocytic, with a single subsidiary cell, paracytic and cyclocytic in various treatments, the ontogeny of which is always perigenous. In addition to normal types, abnormalities such as contiguous stomata, division of guard cells, single guard cells, cytoplasmic connections, degeneration of guard cells, persistent stomatal cells and giant stomata are noticed in different concentrations of various treatments. Giant stomata with abnormally big pores are commonly met with in KIN treatments. GERTZ (1919) induced division of guard cells in the hypocotyl of *Cucurbita pepo* and cotyledons of *Luffa cylindrica*. THEILMAN (1925) failed to induce guard cell division in culture. DEHNEL (1960) also failed to induce division of guard cells by wounding. While TUCKER (1974, 1975) has discussed at lenght the division of guard cells during wound repair in some magnoliaceous plants. INAMDAR *et al.* (1976) noticed the division of guard cell nuclei in the cotyledons of *Luffa aegyptica* treated with colchicine. During the course of present investigation, the varied behaviour of stomatal meristemoid and formation of stomata by amitotic division of meristemoid by centripetally extending walls is observed which is an unusual phenomenon. In COL treatment the formation of stomata is inhibited as the meristemoids develop into persistent stomatal cells. GANGADHARA *et al.* (in press) after reviewing the literature have concluded that the action of COL is more or less consistent in all the plants studied.

BÜNNING & SAGROMSKY (1948) found that when the leaves of *Impatiens sultanii* are treated with 1/100 N solution of Potassium hydroxide, there was an increase in the stomatal frequency but when treated with 5—15 N solution of hypophoric acid and Indole acetic acid, the stomatal formation was arrested. TAL & IMBER (1971) pointed out that the stomatal density did not increase in the leaves of tomato treated with 2,4-Dichlorophenoxya-

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cetic acid. INAMDAR & GANGADHARA (1975). GANGADHARA & INAMDAR (1975) reported that the various concentrations of growth regulators affect the stomatal frequency and index. Present study also supports the latters' view (*see* Table I).

Table 1

Frequency (F) of stomata and epidermal cells, stomatal index (I) per mm², and size of guard cells and of epidermal cells (L = length, B = breadth, in μm)

Treatments		Stomata		Guard Cells		Epidermal Cells		
		F	I	L	B	F	L	B
1 Control (DW)		192	21	21	8	722	34	18
2a Gibberellic acid	25 ppm	196	28	24	8	480	35	20
2b Gibberellic acid	50 ppm	203	34	27	10	378	35	20
2c Gibberellic acid	100 ppm	280	35	29	11	304	36	23
3a IAA	25 ppm	304	33	22	10	694	32	21
3b IAA	50 ppm	328	30	20	10	742	33	22
3c IAA	100 ppm	336	28	23	11	880	34	22
4a Kinetin	25 ppm	227	28	30	11	560	35	18
4b Kinetin	50 ppm	196	32	31	12	400	31	17
4c Kinetin	100 ppm	256	38	34	12	416	36	19
5a Sucrose	2000 ppm	400	31	24	8	880	38	28
6a TIBA	25 ppm	160	16	25	9	848	32	20
6b TIBA	50 ppm	160	22	25	8	576	33	21
6c TIBA	100 ppm	187	20	24	10	786	33	21
7a Colchicine	25 ppm	53	12	29	13	400	34	23
7b Colchicine	50 ppm	—	—	34	20	—	38	20
7c Colchicine	100 ppm	—	—	34	22	—	38	18
8a Coumarin	25 ppm	141	26	26	11	416	43	23
8b Coumarin	50 ppm	240	37	28	11	395	52	25
8c Coumarin	100 ppm	304	30	25	13	704	39	23
9a Maleic hydrazide	25 ppm	208	22	27	10	755	40	24
9b Maleic hydrazide	50 ppm	112	19	32	12	480	43	26
9c Maleic hydrazide	100 ppm	112	19	24	11	464	39	24
10a Sulphanilamide	25 ppm	288	21	24	8	1040	30	23
10b Sulphanilamide	50 ppm	224	30	24	9	528	35	22
10c Sulphanilamide	100 ppm	192	26	21	8	544	36	20
11a Morphactin	25 ppm	192	28	30	11	496	41	25
11b Morphactin	50 ppm	304	31	23	9	688	30	18
11c Morphactin	100 ppm	352	32	26	8	768	36	22

According to BÜNNING (1952) depending upon the extrinsic factors impirnging upon the developing system, the guard cell differentiation occurs late in ontogeny. He (BÜNNING 1956) also pointed out that the spatial differential differentiation of stomata is controlled by the inhibitory zone around the meristemoid or developing stomata. While WOLPERT (1969) states that the differentiation may be controlled by the gradient concentra-

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tion of inhibitors and the rate of their diffusion. KAUFMANN *et al.* (1969) postulated that a lateral gradient of auxin and gibberellin could control cell expansion in long epidermal cells during intercalary growth. The early experiments of GERTZ (1919) und MICHE (1901) support the vie of BÜNNING (1952, 1956). But, it is very difficult to explain the 'inhibitory zone' concept of BÜNNING (1952, 1956) where 2—3 or sometimes more contiguous stomata develop from adjacent meristemoids. However, it can be explained when the two stomata differentiate at different times. INAMDAR & PATEL (1976) pointed out that both extrinsic and intrinsic factors might be involved in the abnormal stomatal development. The view of INAMDAR & PATEL (1976) can be supported by the experimental studies of MICHE (1901), GERTZ (1919), GUYOT (1964, 1970), GUYOT *et al.* (1968), PALIWAL *et al.* (1974), INAMDAR & GANGADHARA (1975), GANGADHARA & INAMDAR (1975) and INAMDAR *e. al.* (1976). It is possible that the extrinsic factors affect the intrinsic ones which might result in stomatal aberrations. A specific physiological balance being disturbed by the exogenous treatment of growth regulators which ultimately disturb the developmental pattern resulting in aberrant developments. This is due to the fact that the meristemoids respond variously to different growth regulators and in different concentrations.

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