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GENETIC-PHYTOHORMONAL INTERACTIONS IN MALE FERTILITY AND MALE STERILITY PHENOTYPE EXPRESSION IN SUNFLOWER (*Helianthus annuus* L.)

Communication 1. COMPARATIVE INVESTIGATION OF AUXIN AND GIBBERELLIN QUANTITIES IN DIVERSE SUNFLOWER GENOTYPES

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SUMMARY

Amounts of indole-3-acetic acid (IAA) and gibberellic acid (GA_3) in vegetative and reproductive tissues of diverse sunflower genotypes have been investigated using gas-liquid chromatography. Quantification of endogenous GA_3 content in the homozygous line MB 514, characterized by cytoplasmic male sterility (*cms*), revealed a lower level of the hormone in contrast to the fertility restorer line RW 637 R*f*. The highest amount of IAA was found in the heterozygous F_1 hybrid obtained by crossing these lines, regardless of tissues and ontogenetic phases analyzed. Similar features were found in leaves, apices, inflorescences and disk flowers in most of the investigated variants.

Key words: **auxins, *cms*-R*f* system, gibberellins, *Helianthus annuus* L., male fertility, male sterility**

INTRODUCTION

The genetic *cms*-R*f* system (*cytoplasmic male sterility-pollen fertility restoration*) is a well-known and extensively studied phenomenon, due to its importance in heterosis breeding of commercial hybrid (Vranceanu and Stoenescu, 1971a, 1971b; Voscoboinik, 1977; Anascenko, 1977). Besides, this genetic system represents a useful model for study of nucleus-cytoplasm interaction mechanisms in male sterility-fertility expression. It was shown that *cms* in sunflower is associated with mitochondrial gene *orfH522* (Laver *et al.*, 1991; Horn *et al.*, 1994) that can be suppressed in F_1 hybrids based on *cms* by the action of nuclear-encoded fertility restorer genes, homozygous and heterozygous R*f* genes (Vranceanu and Stoenescu, 1971b, 1975; Anascenko and Duca, 1985a, 1985b).

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Also, male sterility can be induced by gibberellic acid (GA_3) treatment of plants (Anascenko, 1971) and the same class of phytohormones restores male fertility in sterile plants (Kasembe, 1967). These phenomena sustain the point of view that plant hormones regulate the nucleus and other cellular structures activity by inductive or suppressive cytoplasmic systems of gene expression (Collett *et al.*, 2000). It was supposed that the phenotype expression of hereditary male fertility/sterility traits is under phytohormone regulation.

Quantification of IAA and GA_3 endogenous levels in five sunflower genotypes during their ontogenesis was carried out to study effects of interactions between genetic (nuclear and mitochondrial) factors and phytohormones on *cms*–R*f* phenotype expression and how these interactions influence the physiological and biochemical basis of microsporogenesis.

Two isonuclear lines distinguished only by cytoplasm genes (MB 514 and MB 514 *cms* with mitochondrial *orf*H522), the line RW 637 R*f* with nuclear homozygous restoration nuclear gene R*f* and their F_1 hybrid with restored male fertility (R*f*) were chosen for analyses. In addition, we studied two functional states of the male gametophyte (male sterility/fertility) in the same nuclear context, using the phenocopy method, which could provide information on nuclear effects on mitochondrial genome expression related to the *cms*-R*f* genetic system.

MATERIAL AND METHODS

Plant materials

Sunflower plants were cultivated at the experiment field of Moldova State University applying conventional practices (Vranceanu, 1973; Vronskih, 1980) during four years. Sunflower (*Helianthus annuus* L.) seeds were kindly provided by SRC Magroselect (Soroca, Republic of Moldova).

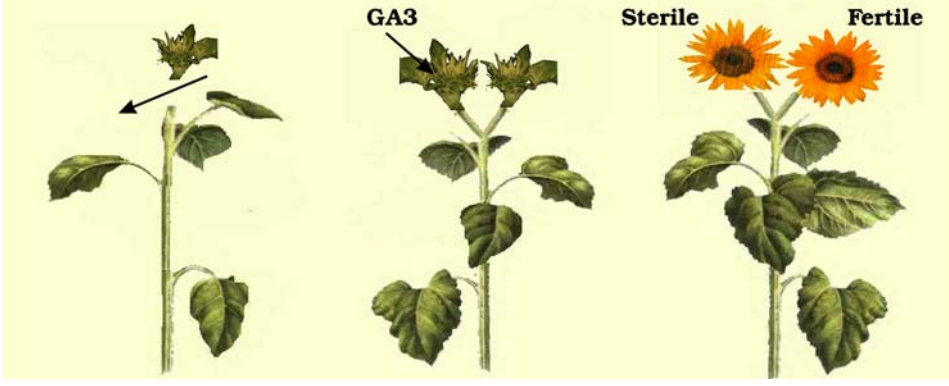

Figure 1: Schematic representation of producing phenocopies of sunflower plants

Apex decapitation at two-leaf stage is a good way to obtain phenocopies, which are known as convenient models for functional activity study of the gene. As a result of apical dominance exclusion, two lateral branches have developed. One of them was treated with exogenous gibberellic acid (GA+). Thus, we obtained two inflores-

cences on the same sunflower plant, one fertile and another with induced male sterility (Figure 1).

EXPERIMENTAL CONDITIONS

Treatment with exogenous gibberellic acid. GA_3 (Sigma) solution was prepared by dissolving GA_3 in a small amount of ethanol (96%), and further diluting it with distilled water to a final concentration of 0.005%. Plant spraying with GA_3 solution was carried out at the flower bud stage. At this stage, prior to disk flower opening, male meiosis occurs in their anthers (Anascenko, 1971). Non-GA_3 treated plants (control) were sprayed with distilled water. For assaying non-GA_3 treated plants (control) and GA_3 treated plants were assayed 24 hours after the treatment.

Phytohormone extraction. Plant materials were collected at various vegetative stages that were correlated with development and microsporogenesis stages. Phytohormone assays were performed on cotyledons, apices with 2-3 true leaves, inflorescences without bracts and disk flowers without parenchyma tissues of peduncles. Heads were sliced radially, to analyze the anthers at different development stages on the single inflorescence.

Fresh plant material (about 10 g) was harvested in the morning. The samples were homogenized and fixed in cold (-20°C) 80% acetone (1:30 ratio) and extracted at 3-5°C during 24 h. After a series of organic extractions and purifications the extracts were dried in vacuum at 40°C. The residue was dissolved in 0.1 ml N,O-bis(trimethylsilyl)-acetamide with addition of 0.05 ml of trimethylchlorosilane (1%) and then subjected to chromatography.

Chromatographic analysis. Quantitative analysis of phytohormones was performed using the gas-liquid chromatographic method and indole-3-acetic acid and gibberellic acid (Sigma) as internal standards, as described previously by Cavell *et al*. (1967) and modified by Duca *et al*. (1997).

A gas chromatograph FRACTOVAP 4200, equipped with flame ionization detector, line programs for temperature MOD 410, integrator MEGA SERIES SP 4270, and rustproof column (2 m × 4 mm) with 5% SE-30 DMCS Cromoton W, 60/80 mesh (0.15-0.2 mm), was used for analysis with N_2 - 25 ml/min as gas carrier. The air flow was maintained at 300 ml/min, the hydrogen flow at 25 ml/min. The injector temperature was +210°C, the detector temperature also +210°C.

Temperature regime. The phytohormones were determined using the following temperature regime: after the injection, the temperature was maintained at 60°C for 4 min, and then increased to 220°C at the rate of 12°C/min. This temperature was maintained until the end of the chromatography run. The phytohormone content was expressed in ng per gram of fresh weight (ng/g fwt).

Data are presented as means ±SE (standard errors) of three separate experiments (n=6 for each experiment). Student's *t* test ($P<0.05$ and $P<0.09$) was used to determine the statistical significance of differences between the genotypes.

RESULTS AND DISSCUSION

Plant hormones metabolism and keeping the hormonal balance in appropriate temporal and spatial patterns affect the intensity, localization, structure and quality of all morphogenetic processes. The pathways of GA biosynthesis and catabolism and their physiological role have been investigated for many years by a variety of approaches, including the application of active GAs, chemical inhibitors of GA biosynthesis, and the analysis of mutants of plants such as maize, pea, and *Arabidopsis* (Kende and Zeevaart, 1997).

IAA and GA_3 are essential hormones that act synergetically on diverse developmental processes in plants (Ross and O'Neil, 2001). Moreover, auxins stimulate gibberellin biosynthesis (Symoons and Reid, 2002). Based on this information, quantitative analysis of hormonal balance variation has been performed on some sunflower genotypes including F_1 hybrids and their parent lines, during different ontogenetic stages. Our results showed the quantitative variation of IAA and GA_3 levels depended on plant tissues, development stages (Duca and Port, 2002) and environmental factors (Duca, 2003).

The most interesting data obtained relate to hormone amounts in different sunflower genotypes that compose the *cms*-R*f* genetic system. The F_1 hybrid was found to contain the highest IAA amount versus RW 637 R*f*, the male fertility restorer line, which had a lower hormone level. These features were found for apices, leaves and inflorescences (Table 1). Hormone levels in roots showed no significant quantitative variations between the studied genotypes.

Table 1: IAA amounts in different sunflower genotypes, ng/g fwt

Genotype	Plant number: *fertile* / *sterile*	Phenotype / Genotype	Ontogenetic phase			
			First pair of true leaves		Flower bud stage	
			Roots	Apex	Leaves	Inflorescence
F_1	76 / 0	fertile / S R*f*	32.79 ± 0.12	70.98 ± 0.31	62.99 ± 0.64	81.64±0.29
MB 514 *cms*	2 / 58	sterile / S rfrf	30.47 ± 0.24	57.03 ± 0.05	60.15 ± 1.17	77.40±0.83
RW 637 R*f*	78 / 0	fertile / F RfRf	31.71 ± 013	50.41 ± 0.25	54.99 ± 4.70	61.05±1.86
LSD	0.95		0.093	0.432	0.265	0.367
	0.99		0.140	0.654	0.401	0.556

S – male sterile cytoplasm containing mitochondrial *orfH522*; F-male fertile cytoplasm

It is known that IAA induces DNA replication (Barlow, 1976). High IAA level in F_1, associated with increased mitotic activity (Capatina, 2004) and with other morphological and physiological indices (Savca *et al.*, 2002), suggests that correlation exists between IAA amount and heterosis. It is also possible that the low IAA amount in the homozygous line RW 637 R*f* is the cause of the reduced height of these plants (Savca *et al.*, 2002).

It is important to emphasize that the gibberellin level in all studied tissues and genotypes of sunflower was six-fold less than the IAA level, as has been shown for maize (Polevoi, 1992). Highest GA_3 concentrations were found in the male fertile genotypes, the F_1 hybrid and the line RW 637 R*f*, which was distinguished by the increased biosynthesis during ontogenesis (Table 2). The intensity of phytohormone accumulation was significantly higher for the line RW 637 R*f* than for the F_1 hybrid and the line MB 514 *cms* (Duca, 1998).

The gibberellin level had maximal values in roots and leaves of heterozygous plants and in the apices and inflorescences of homozygous plants, but these differences were not statistically significant either at 0.95 or 0.99 probability levels.

Table 2: Gibberellin content in different sunflower genotypes, ng/g fwt

Genotype	Plant number: *fertile* / *sterile*	Phenotype / Genotype	Ontogenetic phase			
			First pair of true leaves		Flower bud stage	
			Roots	Apex	Leaves	Inflorescence
F_1	76 / 0	fertile / S R*f*	2.04 ± 0.05	16.94 ± 0.03	18.07 ± 0.21	14.3 ± 0.24
MB 514 *cms*	2 / 58	sterile / S rfrf	0.36 ± 0.03	11.82 ± 0.87	7.21 ± 0.63	9.50 ± 0.42
RW 637 R*f*	78 / 0	fertile / F RfRf	0.97 ± 0.04	17.40 ± 0.20	17.30 ± 1.03	17.40 ± 0.52
LSD	0.95		1.868	0.493	1.050	0.709
	0.99		2.828	0.747	1.590	1.074

S – male sterile cytoplasm containing mitochondrial *orfH522*; F-male fertile cytoplasm

Isogenic lines and phenocopies of sunflower are a good experimental genetic system for investigation of phytohormone interactions and their role in gene expression. Thus, the IAA level during the ontogenesis of the three sunflower lines, MB 514, MB 514 *cms* and MB 514 treated with exogenous GA_3, showed a lower value in the male sterile homozygous line than in its male fertile analogue, characterized by normal bisexual flowers with fertile pollen (Table 3).

Table 3: Auxin content of three isogenic sunflower lines, ng/g fwt

Genotype	Plant number	Phenotype / Genotype	Ontogenetic phase					
			Bud development		Active growth		Blossoming	
			Apex	Inflorescence	Apex	Inflorescence	Apex	Inflorescence
MB 514	60	fertile / F rfrf	60.57±1.14	75.80±1.23	61.50±0.92	76.90±2.26	49.53±2.49	85.40±0.28
MB 514 *cms*	58	sterile / S rfrf	58.53±2.08	73.20±2.22	59.13±1.16	74.10±1.02	48.00±2.08	85.00 ±1.41
MB 514 +GA_3	10	sterile / F rfrf	60.77±0.94	75.57±0.77	85.57±1.28	88.47±3.21	45.50±0.59	83.80±0.71
LSD	0.95		0.120	0.064	0.526	0.241	0.138	0.037
	0.99		0.182	0.097	0.797	0.365	0.210	0.057

S – male sterile cytoplasm containing mitochondrial *orfH522*; F – male fertile cytoplasm

As a result of exogenous hormonal treatment, the microsporogenesis was blocked. This phenomenon is associated with significant increases of IAA amount during flower bud stage and active growth stages.

Also, it was found that the nucleic acids level, especially of RNA (Duca and Savca, 1998), and protein biosynthesis were increased (Duca *et al.*, 1998). However, at the flower stage, the auxin content and the above mentioned parameters decreased below the corresponding values in the *cms* lines (Table 3). At this reproductive stage, the *cms* plants and those treated with gibberellins displayed abnormally developed anthers and lack of pollen.

Our results showed that maximal GA_3 contents were in the apex and inflorescence tissues of the line MB 514 and also in plants exogenously treated with GA_3. The lowest GA_3 levels were was found in the cytoplasmic male sterile analogue – the line MB 514 *cms* (Table 4).

Table 4: Gibberellin content in three sunflower isogenic lines, ng/g fwt

Genotype	Plant number	Phenotype / Genotype	Ontogenetic phase					
			Bud development		Active growth		Blossoming	
			Apex	Inflorescence	Apex	Inflorescence	Apex	Inflorescence
MB 514	60	fertile F rfrf	17.90±0.14	18.50±0.33	18.13±0.47	16.26±0.32	24.50±0.14	18.37±1.18
MB514 *cms*	58	sterile S rfrf	9.50±0.42	7.20±0.57	12.7±0.19	6.70±0.47	16.70±0.45	1.33±0.43
MB 514 +GA_3	10	sterile F rfrf	17.90±0.09	18.50±0.33	20.43±0.58	16.80±0.19	18.40±0.19	13.40±0.52
LSD		0.95	0.786	1.082	0.570	1.051	0.506	0.573
		0.99	1.190	1.693	0.863	1.591	0.766	0.868

S – male sterile cytoplasm containing mitochondrial *orfH522*; F – male fertile cytoplasm

During the flower stage, the gibberellin quantity in the GA_3-treated line MB 514 decreased by approximately 30% in comparison with the *cms* analogue and by 20% compared with the untreated line MB 514. MB 514 *cms* plants had low concentrations of this hormone unlike the male fertile plants in all studied ontogenetic phases. Gibberellin content increase in the fertile line MB 514 occurred during ontogenetic stages, reaching high levels at the flower stage (24.5 ng/g fwt). Exogenous gibberellin application changed its endogenous concentration. Maximal values of endogenous IAA and GA_3 contents were determined at the flower bud stage, 24 hours post treatment and also during the active growth stage.

Data from the isogenic lines study provided more complete information related to auxin-gibberellin regulation of differentiation and generative processes in sunflower. Comparative analysis of endogenous auxin and gibberellin levels at different stages of microsporogenesis (Figures 2 and 3) revealed that the phytohormone con-

centration in disk flowers decreased from the center of the inflorescence towards the periphery in all genotypes studied.

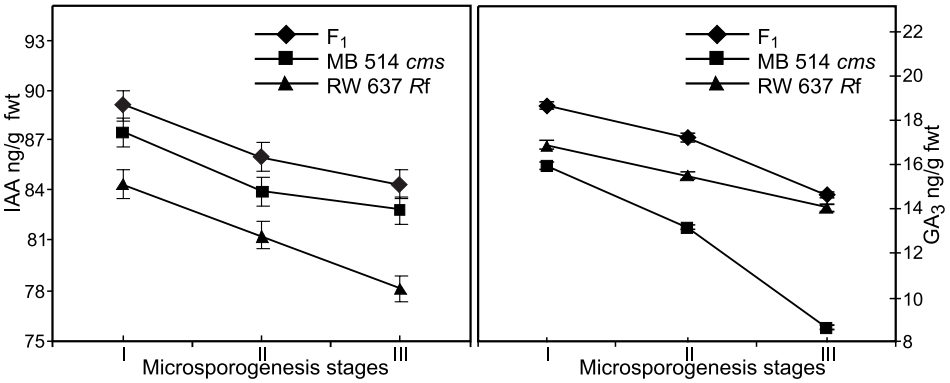

Figure 2: Phytohormone levels in flowers at various stages of microsporogenesis: I – arhesporogenesis; II – sporogenesis; III - carpogenesis.

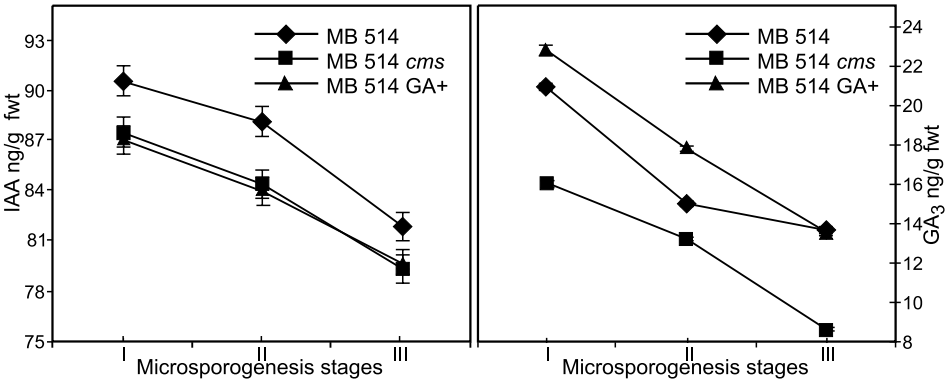

Figure 3: Different phytohormone levels in flowers of three isogenic sunflower lines during the following stages of microsporogenesis: I– archesporogenesis; II – sporogenesis; III - carpogenesis

Our data support previous findings related to higher contents of both hormones in hybrid plants and the lowest IAA level in the male fertility restore lines, but the lowest GA_3 level in the *cms* plants.

The exogenous GA treatment decreased the IAA concentration in disk flowers. The obtained results showed no significant difference between plants with induced male sterility and *cms* plants. However, the endogenous gibberellin content in the treated genotype was higher then those detected in the other two isogenic lines.

Beside the complex functional role of the studied parameters, the research on IAA and GA_3 contents in different sunflower genotypes during ontogenesis revealed several features regarding growth regulators levels and genetics of the *cms*-R*f* system.

A high level of GA_3 was present in the line RW 637 R*f* in comparison with the other genotypes, but the level kept decreasing in that line as well as in the F_1 hybrid. The line MB 514 *cms* contained the lowest level of gibberellins that kept increasing during all the analyzed phases, even in disk flowers. The fertile line MB 514 (as well as the other male fertile genotypes) had higher auxin and gibberellin contents than its male sterile analogue during all studied phases.

Genotypic peculiarities related to auxin content were considerably lower in magnitude and less specific then those revealed for gibberellin content, apparently indicating a less significant functional role of the former in the phenotypic expression of the *cms*-R*f* system. However, it could be supposed that high gibberellin content is associated with restored male fertility and low auxin content with pollen sterility.

Evidence of the requirements for GAs in male reproductive development of flowering plants has resulted from genetic and physiologic studies of GA biosynthesis mutants. Typically, in addition to the dwarf stature, the GA-deficient mutants exhibit various defects in reproductive development (Kende and Zeevaart, 1997; Fadeeva *et al*., 1980). Of the many plant growth regulators used as gametocides (Suster, 1962; Zdrilco and Poleacov, 1966; Frank *et al*., 1978) only gibberellins induce male sterility (Anascenko, 1971). This suggests that microsporogenesis development proceeds normally when the level of GA is normal. The low level of this hormone in the line MB 514 *cms* and the high level in the line RW 637 R*f* (and in the other male fertile lines) seem to support the proposed hypothesis. Also, these conclusions are sustained by reports showing that tomato sl_2 gene mutants (nuclear male sterility) contain high IAA and abscisic acid contents but a low gibberellin content (Santokh and Sowhneu, 1993).

Thus it can be concluded that the quantitative differences in the auxin and gibberellin levels in various sunflower genotypes reveal that self-regulation of the *cms*-R*f* system in sunflower is mediated by endogenous phytohormones whose concentration depends on the genotype, ontogenetic phase and organ studied.

CONCLUSIONS

Quantification of endogenous IAA and GA_3 levels during ontogenesis of five sunflower genotypes, completed by the study of two functional states of male gametophyte in the same nuclear context, revealed certain aspects of the interactions between genetic factors and phytohormones contributing to the male sterility-male fertility phenotype expression:

- the homozygous line MB 514 *cms* had a lower level of endogenous GA that the fertility restorer line RW 637 R*f*;
- highest amounts of IAA, regardless of tissues and ontogenetic phases analyzed, were found in the heterozygous F_1 hybrid obtained by crossing the above lines;
- similar features of hormonal concentration were found in leaves, apices, inflorescences and disk flowers in most of the investigated variants.

Genotypic peculiarities related to auxin content were considerably lower in magnitude and less specific then those revealed for gibberellin content, apparently indicating a less significant functional role of the former in the phenotypic expression of the *cms*-R*f* system. It appears that high gibberellin content is associated with restored male fertility and low auxin content with pollen sterility.

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INTERACCIONES GENÉTICO-FITOHORMONALES EN LA EXPRESIÓN FENOTÍPICA DE LA ANDROFERTILIDAD Y ANDROESTERILIDAD EN GIRASOL (*Helianthus annuus* L.)

Parte I: Investigación comparativa de la cantidad de auxinas y giberelinas en diversos genotipos de girasol

RESUMEN

Se investigaron las cantidades de ácido 3-indol-acético (IAA) y ácido giberélico (GA_3) en tejidos vegetativos y reproductivos de diversos genotipos de girasol usando cromatografía líquido gaseosa. La cuantificación del contenido de GA_3 endógeno de la línea homocigota MB514, caracterizada por androesterilidad citoplasmática (*cms)*, reveló un nivel menor que la línea restauradora de la fertilidad RW637R*f*, que contiene una mayor cantidad de hormonas. El mayor contenido de IAA se encontró en el híbrido heterocigota F_1 obtenido a partir del cruzamiento de estas líneas, independientemente de los tejidos y fases ontogénicas analizadas. Se encontraron resultados similares en hojas, ápices, inflorescencia y flores del disco en la mayoría de las variantes investigadas.

INTERACTIONS GÉNÉTIQUES PHYTOHORMONALES DANS L'EXPRESSION PHÉNOTYPIQUE D'UN MALE FERTILE ET MALE STERILE DU TOURNESOL (*Helianthus annuus* L.)

Partie I: Recherche comparative de la quantité d'auxines et de gibberellins dans divers genotypes de tournesol

RÉSUMÉ

Les quantités d'acide acétique 3-indole (IAA) et d'acide gibbelerellic ont été étudiées dans les tissus végétatifs et reproductifs de divers génotypes de tournesol, au moyen de la chromatographie en phase liquide. La quantification du contenu endogène GA_3 de la lignée homozygote MB514, caractérisée par la stérilité male cytoplasmique (*cms*), a révélé un niveau plus bas contrairement à la lignée restauratrice de fertilité RW637R*f* qui contient une plus grande quantité d'hormones. La plus grande quantité de IAA a été trouvé dans l'hybride hétérozygote F_1, obtenu par croisement de ces lignées, indépendamment des tissus et des phases d'ontogénèse analysés. Des résultats similaires ont été trouvés dans les feuilles, apex, inflorescences et disques foliaires dans la plupart des variantes examinées.