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SPATIAL AND TEMPORAL DISTRIBUTION OF AUXINS AND GIBBERELLINS IN SUNFLOWER (*Helianthus annuus* L.)

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SUMMARY

Occurrence and parallel variation of free indole 3 acetic acid (IAA) and gibberellins (GA_3) in different organs of *Helianthus annuus* L. have been investigated at various development stages by the gas chromatography method. The highest concentration of IAA was found in aboveground organs while the IAA concentration in roots was much lower. Genotype variation has also been determined. It has been established that the percentages of free IAA in roots, leaves, inflorescences and flowers were much higher in parent lines than in the F_1 hybrid. These data demonstrated a direct correlation between auxins and hybrid vigor.

The obtained results demonstrate the spatial (roots, leaves, inflorescences and flowers) and temporal distribution (during various ontogenetic phases) of auxins, which confirm their taking part in polarity formation and indicating dominant centers of activity in sunflower.

Key words: **generative organs *Helianthus annuus* L., hormone interaction, physiological gradients, IAA and GA_3 concentrations, vegetative organs**

INTRODUCTION

Phytohormones, important regulators of physiological processes in plants, induce differentiation of multicellular organisms (Thimann *et al.*, 1963; Chailahean and Hreanin, 1982), play a significant role in the establishment of hereditary information (Kuznetsov *et al.*, 1994; Macheev and Kuznetsov, 1996), determine the various types of regulatory mechanisms in plants (Kefeli and Ciailahean, 1975) and maintain functional integrity at the cellular, tissular and organismal levels of plant organization (Polevoi and Salamatova, 1991). It is known that phytohormones have

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an important role in the longitudinal polarization (Mochizuki *et al.*, 2001), helicoidal and radial axes formation (Sabatini *et al.*, 1999; Steinman *et al.*, 1999, Paquette and Benfey, 2001), these phenomena causing the functional differentiation of cellular, tissular and organismal specialization (Scher *et al.*, 2001; Berleth and Sachs, 2001).

Auxins and gibberellins are important "classical" plant growth hormones (Kende and Zeevaart, 1997). Earlier investigations provided information on auxin and gibberellin synthesis, degradation, physiological function and genetic determinism (Abel and Theologis, 1996; Fischer-Iglesias *et al.*, 2001; Picciarelli *et al.*, 2001). More recently, possible relationship was discussed between AIA and GA (Ross and Oneil, 2001) and it was shown that auxins promote gibberellin biosynthesis (Ross *et al.*, 2002).

To define more accurately the temporal and spatial distribution of free IAA and GA_3 and their relationship during ontogenetic development, levels of these phytohormones were determined in vegetative and generative plant organs.

Due to the fact that sunflower is characterized by bilateral axial structure, and because flowers in the inflorescence are situated regularly according to a logarithmic spiral that simultaneously reflects the different microsporogenetic phases, the main goal of the present investigation was to make a comparative analysis of the phytohormone content, to determine their ontogenetic evolution, their role in polarity formation and determination of centers of activity.

MATERIALS AND METHODS

Plant Material. The experiments were realized using different genotypes of sunflower *Helianthus annuus* L. (2n=34), which represents *cms-Rf* genetic system, including the lines MB514, MB514 *cms* and RW637 *Rf*, produced in association with "Magroselect", and the F_1 hybrid MB 514 *cms* × RW637 *Rf* developed in our laboratory. Sunflower was cultivated according to conventional technologies (Vrânceanu, 1975; Berengena, 1978; Vronskih, 1980).

Samples were collected at different vegetative phases (cotyledons, first leaves, bud formation, active growth, flowering). Sampling was harmonized with growth and development of the generative organs and the process of microsporogenesis (Neagu, 1960; Kuperman, 1984). We analyzed cotyledon leaves, shoot apexes (0.5 cm), leaves from the apical growth zone with or without receptacle and receptacles without leaves. The experiments reported here were performed in the field and repeated for three successive years.

Extraction and Purification. The quantitative study of phytohormones was performed by gas chromatography method (Duca *et al.*, 1997), which had been derived from the method described by Cavell *et al.* (1967).

Phytohormones were extracted from the vegetative tissue by cold homogenization with 80% acetone at the temperature of -10 to 0°C for 24 hours. The obtained extract was purified by filtration, evaporation and pigment bleaching with toluene. Phytohormones were separated from the aqueous residue which was acidulated to the pH 2 with 0.1 N HCl by toluene extraction. The obtained mixture was again acidulated with HCl and phytohormones were extracted with ethyl acetate. Samples were dried in vacuum at 40°C until sediment formation which was further on dissolved in 0.1 ml of ethyl acetate. The addition of 5% sodium bicarbonate allowed the passing of phytohormones into water in the form of sodium salts. The obtained mixture was acidulated with HCl and phytohormones were again extracted with ethyl acetate. The extract was evaporated in vacuum at 40°C until the formation of a sediment which was dissolved in 0.1 ml N,O-bis(trimethylsilyl)-acetamide with addition of 0.05 ml of trimethylchlorosilan (1%). The purified phytohomone extract was used for chromatographic analysis in the form of trimethylsilylic ethers of the phytohormones (1 μl). 3-indoleacetic acid (IAA) and gibberellic acid (GA_3) were used as pure standards. Phytohormone content was expressed in milligrams per gram of fresh substance (mg/g f.s.).

We used a gas chromatograph FRACTOVAP 4200 equipped with a flame ionization detector, line programs for temperature MOD 410, integrator MEGA SERIES SP 4270, rustproof column (2m × 4mm) with 5% SE-30 DMCS Cromoton W, 60/80 mesh (0.15-0.2 mm). Gas carrier was N_2 - 25 ml/min. Air flow was maintained at 300 ml/min, hydrogen flow was 25 ml/min. The injector port temperature was +210°C, the detector temperature was +210°C. Phytohormones were determined in the following temperature regime: after the injection, the temperature was maintained at 60°C for 4 min, and after that the temperature was increased at the rate of 12°C/min until the temperature of 240°C was achieved. This temperature was maintained until the end of chromatography run.

The statistic processing of the experimental data from the three independent experiments with three replicates was done according to standard methods, using Microsoft®Excel 2000 program for Microsoft®Windows´98. Average values were used for graphic presentation of results, with the significance of differences ($P<0.05$) calculated by the t test (Dospehov, 1985).

RESULTS

The data obtained in this investigation and analyzed for their spatial and temporal relations with the plant ontogenesis are important for elucidation of integration mechanisms involved in the processes of growth and development.

IAA and GA_3 concentrations in the shoot and radicular apexes. Taking into account the fact that radicular and foliar apexes represent dominant centers, which due to the high metabolic activity determine the vector orientation of the different indexes, we conducted quantitative investigations of auxins and gibberellins in these tissues.

The analyses of the obtained data show the unequal quantitative distribution of gibberellins and auxins in leaves and roots. The F_1 hybrid and its parent lines were characterized by higher quantities of phytohormones in the aboveground organs than in the radicular system. The gibberellin content in leaves was about ten times higher then that in roots, but the auxin content was about twice as large (Figure 1).

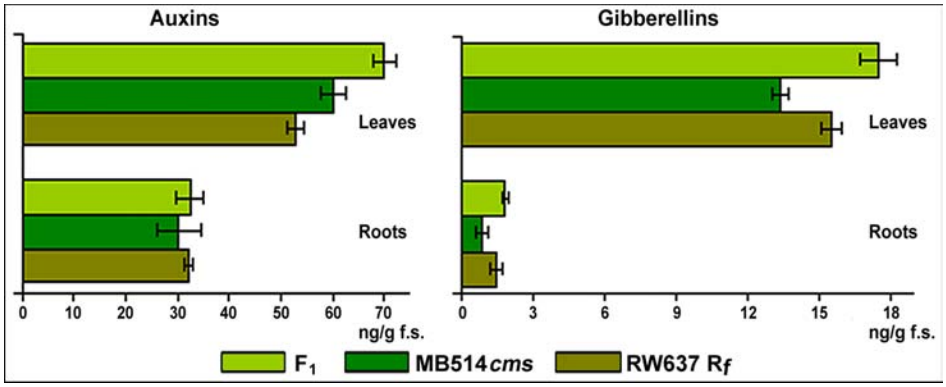

Figure 1: Phytohormone content in sunflower leaves and roots, first true leaves phase

At this stage, phytohormone content was associated with the genotype. The IAA content in the first true leaves had maximal values in the F_1 hybrid (69.99 ng/g f. s.) and minimal values in the line RW 637 *Rf* (52.78 ng/g f.s.). At the root level, the difference between the respective values was insignificant, 32.43 and 32.33 ng/g f.s.

In the hybrid, the highest gibberellin contents in leaves and roots were 17.48 ng/g f.s. and 1.82 ng/g f.s., respectively. The male sterile line MB514 *cms* had reduced contents of this hormone in leaves and roots, 13.35 ng/g f.s. and 0.82 ng/g f.s., respectively (Figure 1).

IAA and GA_3 concentrations in leaves during ontogenesis. To assess the temporal dynamics of the analyzed indexes, we studied the quantitative dynamics of phytohormones in the growing apex, from the first pair of leaves till bud formation. Afterwards, phytohormones were monitored separately in leaves and inflorescences, till the flowering (blossoming) phase.

Regardless of plant genotype, in all investigated variants and all samples, maximal values of auxin content were found at the cotyledon phase. In the next stage, reduction of the IAA content was registered (Table 1).

Table 1: IAA content in leaves during ontogenesis in the F_1 hybrid and the inbred lines (ng/g of f.s.)

Biological material	Phase of growth and development				
	Cotyledons	First leaves	Bud formation	Active growth	Flowering
F_1 [1]	95.80 ± 2.05	69.99 ± 1.52$^{*2;3}$	62.90 ± 1.86	68.43 ± 1.71^{*3}	51.21± 1.58$^{*2;3}$
MB 514 *cms* [2]	91.44 ± 3.23	60.30 ± 2.44$^{*1;3}$	58.53 ± 2.19	59.13 ± 1.40^{*3}	48.02 ± 1.49$^{*1;3}$
RW 537 *Rf* [3]	87.64 ± 2.48	52.78 ± 2.32$^{*1;2}$	53.43 ± 1.09	52.12 ± 1.49$^{*1;2}$	71.35 ± 1.92$^{*1;2}$

*Significant at $P < 0.05$

The quantitative dynamics of gibberellins, unlike that of auxins, showed a growing increase of the GA_3 content, starting from cotyledons, where lowest quantities were found (10.11-11.1 ng/g f.s.), and ending with the flowering phase characterized by maximum values (18.01- 20.73 ng/g f.s.) in leaves of all investigated genotypes (Table 2).

Table 2: GA_3 content in leaves during ontogenesis in the F_1 hybrid and the inbred lines (ng/g of f.s.)

Biological material	The phase of growth and development				
	Cotyledons	First leaves	Bud formation	Active growth	Flowering
F_1 [1]	$10.11 \pm 0.94^{*3}$	$13.62 \pm 0.42^{*3}$	$14.33 \pm 0.28^{*2;3}$	$15.89 \pm 0.55^{*2;3}$	$20.73 \pm 0.58^{*2;3}$
MB 514 ASC[2]	9.40 ± 0.27	$10.17 \pm 0.32^{*3}$	$9.51 \pm 0.31^{*1;3}$	$12.72 \pm 0.51^{*1;3}$	$16.70 \pm 0.44^{*1;3}$
RW 537 *Rf* [3]	$11.10 \pm 0.40^{*1}$	$16.30 \pm 0.78^{*1;2}$	$17.41 \pm 0.47^{*1;2}$	$18.90 \pm 0.57^{*1;2}$	$18.01 \pm 0.62^{*1;2}$

*Significant at $P < 0.05$

Further analyses demonstrated that in all investigated phases, with exception of the flowering phase, highest concentrations of gibberellins were found in the male fertile genotypes, especially in RW 637 *Rf*. It is supposed that gibberellins can be transported intensively from the apical part to the inflorescence.

Phytohormone concentration in inflorescences. The analyses conducted separately on leaves from the stem apex (materials were presented before) and on inflorescences during last three phases provided information about the processes which take place in the foliar apex in the process of floral induction and after that in the process of formation of the new structural organs-inflorescence and flowers.

During bud formation and active growth phase, the auxin content in inflorescences is maintained at a relatively constant quantitative level, with maximal values in the heterozygous form (78.47-80.22 ng/g f.s.) and minimal values in the line RW 637 *Rf* (55.93-62.13 ng/g f.s.).

In the flowering phase, the IAA content in inflorescences, unlike that in leaves (Table 1), increases in all genotypes, with the maximal value in the F_1 hybrid, 89.23 ng/g f.s. In the line RW 637 *Rf*, the IAA increases considerably at flowering (54.1%) in comparison with the level found in the bud formation phase (Figure 2).

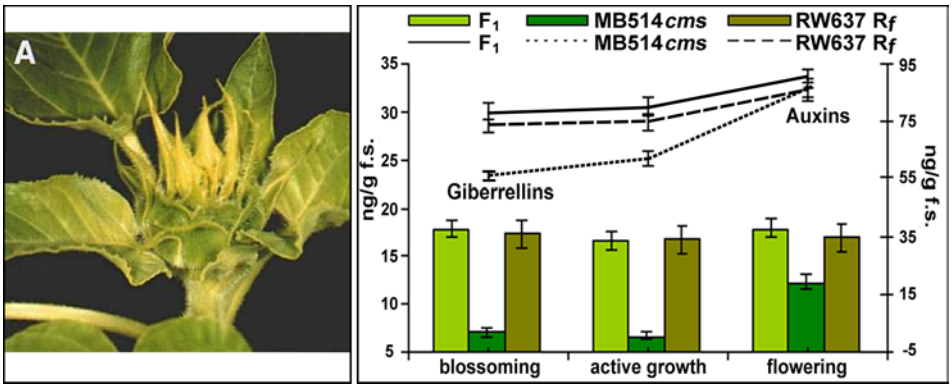

Figure 2: IAA and GA_3 contents in inflorescences of sunflower hybrid and inbred lines

The quantitative dynamics of GA_3 showed that the line MB 514 *cms* had lower concentrations of GA_3 than the male fertile forms in the first two phases. The gibberellin content in that line kept growing during the flowering phase. The concentration of gibberellins was higher in the heterozygous plants than in RW 637 *Rf*, but only during the flowering phase and only by 6.41% (Figure 2).

Phytohormone concentration in flowers. The flowers of one inflorescence bloom gradually during a period of 10-12 days. Successive phases of microsporogenesis, archesporogenesis, sporogenesis and carpogenesis were investigated in the same inflorescence.

The IAA content gradually decreases in the tubular flowers as they matured. Maximal quantities of this phytohormone were found in the archesporogenesis phase (Figure 3).

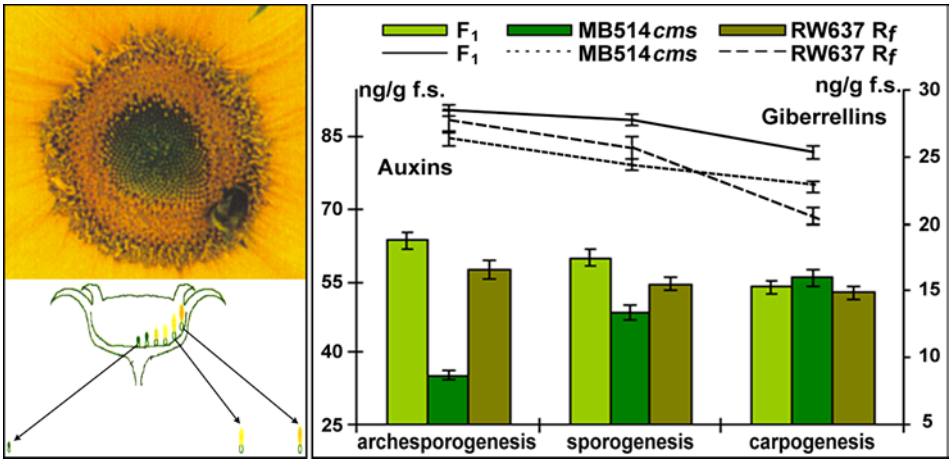

Figure 3: Phytohormone contents in flowers at three phases of gametogenesis

The gibberellin content decreases gradually from archesporogenesis to carpogenesis, which demonstrated that gibberellin level was lower in mature tissues. The highest content of phytohormones in the tubular flowers, during all three investigated development phases, was found in the F_1 hybrid and the male fertile parent line, with maximal values occurring in the archesporogenesis phase.

DISCUSSION

The investigation of the contents of auxins and gibberellins in different organs and in different ontogenetic phases provided evidence on their distribution gradients and correlations with the diverse functional activities. The results clearly demonstrate that there existed gradients in IAA and GA_3 concentrations from the root system towards the apex or from the top of the plant to its base, as previously indicated by Beveridge *et al.* (1994).

Unequal auxin and gibberellin contents were registered in stem and root apexes (Figure 1), regardless of the investigated genotype, which indicates that the longitudinal axial polarization is determined by the synthesis of these phytohormones in the foliar meristems and by their basipetal transport (Steinman *et al.*, 1999). The wider spectrum of the gibberellin values as compared with the auxin quantitative values (Figure 1) probably could be explained by the different physiological role of the investigated phytohormones in the apical meristematic centers during this stage of growth and development, due to the fact that auxins are involved in cell division processes (Kruglova *et al.*, 1999) and gibberellins in sex determination processes (Chailahean and Hreanin, 1982).

Significant differences were registered by the comparative analysis of IAA content in different plant organs. The data presented in Table 1 and Figure 1 demonstrated that the auxin concentration at the beginning of growing season is maximal in cotyledons and the apex. During ontogenesis, the IAA content decreased in foliar apexes and it gradually increased in inflorescences. Highest concentrations were found in flowers.

In this way, starting from the phase of bud forming, the translocation of auxins from leaves to the reproductive organs intensifies and the acropetal gradient is formed (Figures 2 and 4). The obtained results bear evidence of the auxins role in the succession of dominant centers in the sunflower ontogenesis, stated in the literature, demonstrating that the organs containing more IAA utilize the assimilated substances more intensively and are characterized by higher functional activity (Berleth and Sachs, 2001; Sterling and Hall, 1997).

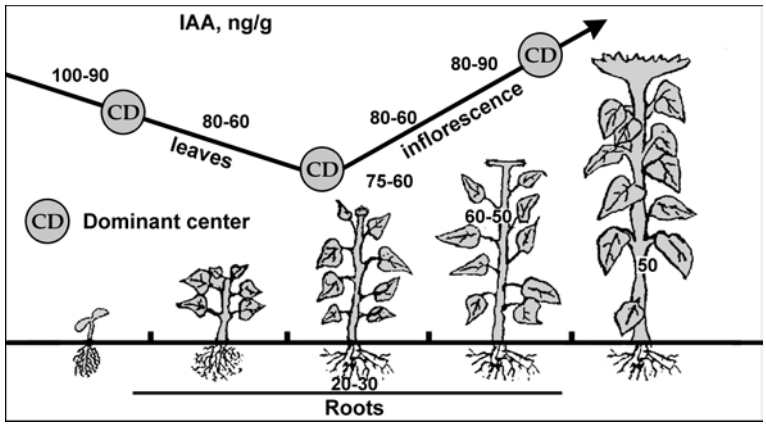

Figure 4: The succession of dominant centers in the course of sunflower ontogenesis

These results confirm the variable character of the physiological gradients correlated with the succession of the dominant centers, which are essential factors for maintaining the temporal integrity of the plant organism.

The investigation of auxin and gibberellin contents in roots, leaves and inflorescences indicated the presence of a spatial concentration gradient that was ascend-

ent oriented. The gradient of GA_3 concentration was more significantly pronounced in the male fertile genotypes, the difference between aboveground and underground organs being about five-six times in favor of the former, with maximal values reached in inflorescences. In the *cms* lines, unlike the heterozygous form and the male fertile lines, highest GA_3 concentrations were determined in leaves.

The ontogenetic evolution of auxins during growth and development of the investigated genotypes, demonstrated by the significant increase in inflorescences and by gradual reduction in leaves, reflects the intensification of their translocation in the direction of reproductive organs.

This investigation permitted to stabilize the sustainable growth of the GA_3 content parallel with the ontogenetic phase in the F_1 hybrid and its inbred lines. The dynamics of the investigated parameter was similar in the initial phases of the study, with exception of the flowering phase, in which a significant increase of gibberellins occurred in leaves and inflorescences of the line MB 514 *cms* and a decrease occurred in leaves of the line RW 637 *Rf*. This pattern was different from the values found in the heterozygous form, in which the gibberellin content in inflorescences was higher in all phases than in the parent lines.

While synergism was manifested between auxins and gibberellins in inflorescences and tubular flowers (except in the line 514 *cms*), antagonism between the two phytohormones took place during leaf ontogenesis, with gibberellin concentration increasing and auxin concentration decreasing.

The increase of auxins and the decrease of gibberellins during the flowering phase, established in leaves of the line RW 637 *Rf*, could be attributed to the redistribution of these phytohormones in leaves and inflorescences, while the average concentrations reflect the true synergism of these two phytohormones.

The previous results indicate that the dynamics of phytohormones in plants at different stages of microsporogenesis as well as during the different ontogenetic phases is complex and it mainly depends on the genotype**.** The evaluation of the investigated parameters in flowers demonstrated the similarity of function in the microsporogenesis phase, although the gibberellins unlike the auxins showed high genotypic specificity. The large differences in auxin content observed in the carpogenesis phase indicate that auxin accumulation in seeds depends on the genotype.

CONCLUSIONS

The investigation of auxin and gibberellin contents in sunflower roots, leaves and inflorescences demonstrated the presence of a spatial concentration gradient that was ascendant oriented.

The gradient of GA_3 concentration was more significantly pronounced in the male fertile genotypes. The difference between aboveground and underground

organs was about five-six times in favor of the former, with maximal values in inflorescences.

The concentration of auxins in cotyledons, leaves, inflorescences and flowers correlated with the dominant centers of activity. The concentration of the investigated phytohormones in the different organs reveals a gradual acropetal distribution of auxins.

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DISTRIBUCIÓN ESPACIAL Y TEMPORAL DE AUXINA Y GIBERELINA EN GIRASOL (*Helianthus annuus* L.)

RESUMEN

La aparición y la variación simultánea del ácido indol-3-acético libre (IAA) y giberelina (GA_3) en los diferentes órganos de la especie *Helianthus annuus* L. fueron investigadas en diferentes fases de desarrollo de la planta por el método de cromatografía gaseosa. La concentración más alta de IAA fue detectada en los órganos aéreos, mientras que la concentración de IAA en la raíz, fue mucho más baja. También fue determinada la variación genotípica. Fue determinado que los porcentajes de la IAA libre en la raíz, las hojas, inflorescencias y flores, eran mucho más altos en las líneas parentales que en los híbridos F_1. Estos datos indican la vinculación directa entre auxina y la potencia híbrida.

Los resultados obtenidos demostraron la existencia de la distribución espacial (raíz, hojas, inflorescencias y flores) y temporal (diferentes fases ontogenéticas) de auxina, lo que confirma que auxinas participan en formación de polaridad e indica los centros de actividad dominantes en girasol.

DISTRIBUTION SPATIALE ET TEMPORELLE DES AUXINES ET DES GIBBÉRELLINES DANS LE TOURNESOL (*Helianthus annuus* L.)

RÉSUMÉ

L'apparition et la variation synchrone d'acide indol acétique libre 3 (IAA) et de gibbérellines (GA_3) dans différents organes de *Helianthus annuus* L. ont été étudiées à différents stages du développement de la plante par la méthode de chromatographie en phase gazeuse. La plus grande concentration de IAA a été constatée dans les organes aériens tandis que la concentration de IAA dans les racines était beaucoup plus faible. La variation de génotype a aussi été déterminée. On a constaté que les pourcentages d'acide acétique indol libre dans les racines, les feuilles, les inflorescences et les fleurs était beaucoup plus élevés dans les lignées parentales que dans l'hybride F_1. Ces données indiquent une corrélation directe entre les auxines et la vigueur hybride.

Les résultats obtenus démontrent l'existence de distributions d'auxines spatiales (racines, feuilles, inflorescences et fleurs) et d'auxines temporelles (au cours de différentes phases ontogénétiques), ce qui confirme qu'elles prennent part à la formation de la polarité et indiquent des centres d'activité dominants dans le tournesol.