Effect of GA_3 , IAA and their mixtures on the formation and development of cell systems in the vegetative and generative thallus of *Chara vulgaris* L.

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Abstract

In concentrations ranging from 10^{-7} to 10^{-5} M IAA strongly stimulates the growth of the main axis and pleuridia internodal cells, while it does not affect the number of lateral branches and generative organs. In the higher concentrations it reduces the number of spermatozoids in the antheridium. In the same concentration range, GA_3 inhibits the growth of the main axis and pleuridia internodal cells, does not affect the number of lateral branches, increases the number of antheridia and increases the number of forming spermatozoids.

Incubation in mixture of both regulators has shown that: a) IAA eliminates the inhibitory effect of GA_3 on the growth of internodal cells of the main axis and its stimulatory action is slightly weakened by GA_3 , b) IAA in a concentration of 10^{-5} M along with a low concentration of GA_3 (10^{-7}) increases the number of main axis lateral branches.

The conclusion is drawn that the growth of the vegetative part of the thallus is more intense when auxin predominates, but generative development requires a high level of gibberellin.

Key words: GA_3 , IAA, morphogenesis, *Chara vulgaris* L.

INTRODUCTION

Studies of the influence of some growth substances on algae were initiated by Yin in 1937 (Conrad and Saltman 1962) on the role of IAA on cell size in *Chlorella vulgaris*. Jahnke and Libbert (1964) demonstrated the presence of IAA in the thallus of *Chara* sp. Different extraction procedures and detection methods were used to show that IAA was present in the thallus of *Caulerpa paspaloides* (Jacobs et al. 1985). Gibberellin-like substances were found in thalli of *Chara* sp. (Murakami 1966) and in many other groups of algae (Radeley 1961, Mowat 1963, Jennings and McComb 1967, Gupta and Argawal 1973). This fact promoted investigations on their role in life processes in algae.

The culture of *Chara vulgaris* in an artificial medium became a particularly convenient model for studies on the influence of hormones on plant development. The thallus of *Chara vulgaris* grows by successive mitotic division of the apical cell. Two cells are formed after every division: a new-apical and subapical cell (Pickett-Heaps 1967a). The subapical cell divides once more and forms two sister-cells: the upper cell — which organizes the haploidal node, and the basal cell — which forms the internode (Ducruix 1968). The internodal cell nucleus becomes polyploid (Shen 1967a) and after amitotic fragmentation, the internodes are made up of multinuclear cells (Shen 1967b). The nodes initiate the development of lateral pleuridia which consist of nodes and internodes. The cells of the pleuridial nodes undergo mitotic divisions and form the generative organs: antheridia and oogonia.

Earlier complex investigations have shown that GA_3 accelerates the development of generative organs i.e. the oogonia and antheridia. GA_3 was also found to increase the number of spermatozoids produced in the antheridia (Godlewski and Kwiatkowska 1980). Inhibition of the elongation of internodes in the main axis and pleuridia of the thallus was observed simultaneously. Decreasing the level of endogenous gibberellins by AMO-1618 stimulated the elongation of the thallus (Kwiatkowska and Godlewski 1980).

Autoradiographic and cytochemical investigations of successive cell cycles of antheridial filaments preceding formation of spermatozoids have shown that GA_3 accelerates the course of all phases of interphase (Godlewski 1977). However, a high level of auxin is necessary for initiation of mitosis (Godlewski 1980). IAA (10^{-5} M) shortened the duration of G2 phase and mitosis, while PCIB (10^{-5} M) caused their prolongation and a fall in mitotic activity. Simultaneously IAA reduced the number of spermatozoids produced in the antheridium resulting from a decrease in the number of divisions in the first stage of spermatogenesis (Godlewski 1980). The effect of IAA on this process is opposite to that caused by exogenous GA_3 (Godlewski and Kwiatkowska 1980) and similar to the effect of AMO-1618 (Kwiatkowska and Godlewski 1988).

The aim of the present investigation was: 1) to compare the individual influence of IAA and GA_3 on the development of the vegetative part of the thallus and generative organs formed on it; 2) to investigate the way in which IAA and GA_3 used simultaneously modify the development of the *Chara* thallus. Interactions between these hormones in the regulation of developmental processes were noticed in many publications (F.e. Nair et al. 1979, Maheshwari et al. 1980, Adams and Ross 1983, Law and Hamilton 1984, and ref. Cleland 1969).

MATERIAL AND METHODS

The apical parts of *Chara vulgaris* L. thalli used in the experiments were cultivated in Forsberg's medium (1965) in Nessler's tubes under artificial illumination with a natural photoperiod (L:D = 14:10) for 21 days. Five-nodal

parts of thalli were placed in Forsberg's medium containing IAA in the following concentrations: 10^{-5} , 10^{-6} , 10^{-7} M; GA₃ in concentrations: 10^{-5} , 10^{-6} , 10^{-7} M and mixtures of these regulators in the following variants: IAA 10^{-5} + GA₃ 10^{-5} M, IAA 10^{-5} + GA₃ 10^{-7} M and IAA 10^{-7} + GA₃ 10^{-7} M.

The appearance of new nodes, lateral branches and rhizoids on the main axis, the opening of antheridia with liberation of spermatozoids and maturation of oogonia with transformation into brownish oospores were observed during the experiment.

The length of the main axis, internodes and pleuridia were measured using photographs of the plants at the start and at the end of the experiment.

After 21 days the plants were fixed in an ethanol-acetic acid mixture (3:1, v/v). Isolated antheridia were stained with acetic carmine and squashed on slides for estimation of the number of filaments and number spermatids in the filaments and the antheridium.

The results were analysed statistically. Standard error (SE) and significance of differences using Student's test at $p = 0.05$ were calculated.

RESULTS

THE LENGTH OF AXIAL INTERNODES

The length of internodes was measured as the difference between the length at the start and at the end of the experiment, taken from photographs (Fig. 1). The internodes were numbered from the oldest (I) to the youngest (VIII). Internode V

Fig. 1. Apical fragment of *Chara vulgaris* thallus. A — at the start of the experiment, B — after 21 days of cultivation

had already been formed before the administration of hormones and was in the course of development during the experiment. Internodes VI, VII and VIII were formed and developed during the experiment. The maximum effect on elongation was observed on internodes V, VI and VII.

Internodes treated with IAA were longer than control cells, but this was statistically significant only in V and VI at a concentration of 10^{-7} M (Table 1).

Table 1

Increases in the length of axial internodes after treatment with IAA, GA_3 and their mixtures

Experimental variant	No of internodes		
	V	VI	VII
Control	10.3 ± 1.0	12.1 ± 1.0	9.5 ± 0.9
IAA 10^{-5} M	11.6 ± 1.0	13.5 ± 1.2	12.1 ± 2.0
10^{-6} M	12.8 ± 1.3	11.8 ± 0.9	9.5 ± 1.3
10^{-7} M	13.4 ± 1.2	14.1 ± 1.0	11.6 ± 1.4
GA_3 10^{-5} M	8.4 ± 0.6	9.2 ± 0.6	5.9 ± 0.7
10^{-6} M	6.6 ± 0.5	5.4 ± 0.3	2.2 ± 0.3
10^{-7} M	8.7 ± 0.5	9.6 ± 0.5	7.3 ± 0.9
IAA 10^{-5} + GA_3 10^{-5} M	11.8 ± 1.4	15.4 ± 1.0	12.7 ± 1.4
IAA 10^{-5} + GA_3 10^{-7}	11.1 ± 1.2	11.8 ± 1.4	10.2 ± 1.5
IAA 10^{-7} + GA_3 10^{-7} M	11.1 ± 1.4	12.5 ± 1.5	10.9 ± 1.7

GA_3 in all concentrations caused statistically significant shortening of the internode length with the maximum effect being observed at a concentration of 10^{-6} M.

All of the IAA and GA_3 mixtures used in the experiments increased the length of internodal cells.

THE LENGTH OF PLEURIDIA

The length of pleuridia from nodes V, VI, VII and VIII, which were formed and developed under experimental conditions was measured from the photographs taken on the last day of the experiment (Table 2). All of the concentrations of used IAA caused the length of pleuridia to increase. This effect was statistically significant for all of the nodes. The plants treated with GA_3 had shorter pleuridia than the control plants. This was statistically significant for nodes V, VI and VII.

All of the mixtures of IAA and GA_3 used in the experiment caused a marked increase in the length of pleuridia as compared with controls, but their length did

Table 2

The length of pleuridia after treatment with IAA, GA₃ and their mixtures

Experimental variants	No of node			
	V	VI	VII	VIII
Control	5.6±0.8	5.0±0.2	6.0±0.6	5.7±0.6
IAA 10 ⁻⁵ M	8.9±1.3	10.6±1.2	11.8±1.1	10.3±1.4
10 ⁻⁶ M	7.5±0.8	10.3±0.6	10.3±0.7	8.6±0.7
10 ⁻⁷ M	8.2±1.1	9.7±1.1	12.8±0.7	11.0±0.7
GA ₃ 10 ⁻⁵ M	4.3±0.3	4.0±0.3	4.7±0.4	4.9±0.5
10 ⁻⁶ M	4.2±0.2	4.7±0.2	5.0±0.2	5.3±0.4
10 ⁻⁷ M	4.5±0.2	4.3±0.3	4.8±0.3	4.9±0.4
IAA 10 ⁻⁵ + GA ₃ 10 ⁻⁵ M	7.3±0.5	8.8±1.1	10.5±1.1	9.6±1.0
IAA 10 ⁻⁵ + GA ₃ 10 ⁻⁷ M	8.2±0.7	9.2±1.0	11.1±0.9	9.3±1.2
IAA 10 ⁻⁷ + GA ₃ 10 ⁻⁷ M	8.4±1.1	9.9±0.7	11.3±1.2	9.4±1.4

not exceed that after treatment with IAA. The maximum statistically significant effect was observed in the variant where both hormones were in equal concentrations of 10⁻⁷ M.

THE NUMBER OF LATERAL BRANCHES

The buds which initiate the development of lateral branches and rhizoids are formed at a certain distance from the thallus apex at the base of the pleuridia. This distance is the longer the higher is the elongation rate of the main axis. The number of lateral branches is higher when the breakdown of apical domination is more effective.

Neither IAA nor GA₃ changed the number of lateral branches to a statistically significant extent if applied separately. A similar effect was observed for mixtures in which both hormones were in equal concentrations i.e. 10⁻⁵ M or 10⁻⁷ M. (Fig. 2). A statistically significant increase in the number of lateral branches, from 2.5 in the control to 4, was found only in one experimental variant: IAA 10⁻⁵ + GA₃ 10⁻⁷ M (Fig. 2).

THE NUMBER OF ANTHERIDIA AND OOGONIA

In *Chara* the development of antheridia and oogonia is initiated at early stages of formation of pleuridia in apical parts of the thallus (Pickett-Heaps 1967b). In the control plants, the number of antheridia and oogonia was similar and their mutual ratio oscillated around 1.0.

Fig. 2. The number of lateral branches of the main axis formed after treatment with IAA, GA₃ and their mixtures

IAA did not change the number of antheridia (Fig. 3b) or oogonia (Fig. 3a) in any of the experimental concentrations. The investigations with GA₃ showed that the optimum concentration of this hormone for production of antheridia was 10⁻⁶ M (a statistically significant increase) (Fig. 3b). A similar effect (but not as strong and statistically insignificant) was observed for oogonia (Fig. 3a). In concentrations of 10⁻⁶ and 10⁻⁵ M the antheridia-oogonia ratio was higher than in the control.

Fig. 3. The number of oogonia (a) and antheridia (b) after action of IAA, GA₃ and their mixtures

The greatest increase in the number of generative organs formed on *Chara* thalli after treatment with IAA and GA_3 mixtures was found in the variant with GA_3 in concentrations of 10^{-7} M and IAA 10^{-5} M. This effect was noticed both for antheridia and oogonia, so their mutual ratio remained at the same level (Fig. 3a and b).

THE PRODUCTIVITY OF AN ANTHERIDIUM

The biological productivity of an antheridium is defined by the number of spermatozoids developing within an antheridium. This parameter depends on two processes: 1) the mitotic activity of capitular cells and 2) the number of cellular divisions within the filaments. The first process determines the number of antheridial filaments, the second one — the number of cells in one filament which are transformed into spermatozoids.

The highest concentration (10^{-5} M) of IAA caused a significant reduction of the number of spermatozoids inside the antheridium. The other variants did not modify this parameter. The opposite effect was observed for GA_3 , i.e. the highest productivity of the antheridia was found at the concentrations of 10^{-6} and 10^{-7} M (Fig. 4).

Fig. 4. The number of spermatozoids in antheridia after treatment with IAA, GA_3 and their mixtures

All of the mixtures of IAA and GA_3 used in this experiment caused a statistically significant increase in the number of spermatozoids per antheridium from about 6200 in the control to 7000-7400 depending on the variant. The strongest influence was noticed for IAA 10^{-5} + GA_3 10^{-5} M (Fig. 4).

DURATION OF SPERMATOGENESIS

Spermatogenesis is considered to last from the appearance of initial cells of the antheridial filaments up to the formation and liberation of mature spermatozooids and disintegration of the antheridium. In all of the experimental concentrations, IAA caused significant prolongation of the duration of spermatogenesis (Fig. 5). After treatment with GA_3 , statistically significant reduction of the time of spermatogenesis was observed for all concentrations of this hormone.

Fig. 5. The duration of spermatogenesis after treatment with IAA, GA_3 and their mixtures

All of the mixtures of IAA and GA_3 used in the experiment showed similar effects as IAA, i.e. prolongation of spermatogenesis. The results obtained for all of the experimental variants were statistically significant, but the strongest effect was observed for IAA 10^{-5} + GA_3 10^{-7} M.

DISCUSSION

As shown by results of numerous investigations, interactions between auxins and gibberellins can be very different: synergistic, additive, subadditive or antagonistic (ref. Brian 1966, Kazama and Katsumi 1974, Jacobs 1986). The mechanisms of these processes are not well-known yet. GA_3 may increase the auxin level as a result of stimulation of IAA synthesis or reduction of IAA-oxidase activity (ref. Cleland 1969, Lantican and Muir 1969, Law and Hamilton 1984, 1989). It was found that gibberellins can also influence the basipetal transport of auxins (Maheshwari et al. 1980). In many cases, gibberellins affect elongation only in the presence of auxins. The addition of antiauxins inhibits their stimulatory effect (Cleland 1969).

Gibberellins act in another way, unrelated to auxins, on many morphogenetic processes such as activation of the subapical meristem, flowering of short-day

plants, sex determination (ref. Cleland 1969). This action may be based on the expression of specific genes. The alga *Caulerpa prolifera* reacts to GA_3 added to the culture medium in a way that contrasts with its response to IAA. GA_3 stimulates rhizome elongation and the rate of rhizoid initiation, but IAA has no effect on rhizoid regeneration and decreases their elongation (Jacobs and Davies 1983, Jacobs 1986).

The results of the present experiments demonstrating the effect of IAA and GA_3 on many morphogenetic processes in *Chara vulgaris* seem to show that on the level of the organism, the effects of these hormones are complementary to each other. Harmonious development of the plant as a whole and of its generative organs was observed only when the appropriate quantitative ratio of these hormones was used.

IAA caused an increase in the length of multinuclear internodes of pleuridia (Fig. 6a), but GA_3 's action on the development of the vegetative thallus was opposite to that of IAA (Figs 6a, b). In this case, the effect of GA_3 cannot be attributed to an increased auxin level. In contrast to the generatively mature thallus, the immature thallus, growing from oospores reacts to increased GA_3 levels by stimulation of the elongation of internodes and pleuridia (Imahori and Iwasa 1965) and *Nitella* (Stirling et al. 1974). The hypothesis was set forth that the inhibitory effect of exogenous gibberellin on the elongation of vegetative cells is the result of a supraoptimal levels of endogenous gibberellins in the generatively mature thallus (Kwiatkowska and Godlewski 1980).

Fig. 6. A comparison of the effects of IAA (10^{-5} M), GA_3 (10^{-7} M) and a mixture of IAA 10^{-5} M + GA_3 10^{-7} M on the length of pleuridia (a), the length of internodes (b) and number of spermatozooids in antheridia (c)

The effect of AMO-1618 — an inhibitor of endogenous gibberellin synthesis (Lang 1970) — which caused an increase in the length of internodes and pleuridia supports the above hypothesis. The same growth-stimulating effect on pleuridia and some of the main axis internodes was observed after simultaneous addition of GA_3 and IAA, the length of pleuridia and internodes was, as a rule, the same as in the presence of only IAA (Figs 6a, b). The increase in the IAA level caused by addition of exogenous auxine seems to decrease the capacity of GA_3 to reduce the elongation of multinuclear vegetative cells of *Chara*. We assume that the addition of gibberellin inhibits the growth of these cells as the result of disturbing the quantitative ratio between these two hormones.

The other type of vegetative cells in the *Chara* thallus is the apical cells of the main axis lateral resting buds. They are mononuclear and capable of mitotic divisions (Ducruex 1974). The measure of apical cells' mitotic activity is the number of nodes and internodes which appear as a result of these divisions. IAA and GA_3 or mixtures of both hormones do not significantly affect these divisions. But the mitotic activity of the apical cells of resting buds is accelerated after treatment with higher concentrations of GA_3 which leads to formation of more numerous lateral branches (see Kwiatkowska and Godlewski 1980). In contrast, IAA at a concentration of 10^{-7} M which slightly, statistically insignificantly, increases apical domination, causes a decrease in the number of lateral branches. After treatment with a mixture of IAA and GA_3 , the number of lateral branches is high, which confirms the stimulatory effect of GA_3 on this process.

The number of *Chara* antheridia does not change after GA_3 treatment, but following IAA they become less numerous. Oogonia are more numerous after treatment with IAA at the concentration of 10^{-5} M but their number is not affected by GA_3 . Simultaneous action of IAA and GA_3 caused a harmonious increase in the number of both antheridia and oogonia. Stimulation was most intense with a mixture in which IAA was at a concentration of 10^{-5} M and GA_3 10^{-7} M. The same mixture effectively increased the productivity of antheridia (Fig. 6c). This productivity is reduced by IAA and increases after addition of GA_3 . The number of spermatozoids in the antheridium is modified mainly by changes in the number of mitotic cycles in antheridial filaments (Kwiatkowska and Godlewski 1988).

The presented studies prove the requirement specificity of the different types of cells in the *Chara* thallus for the level of regulators and their mutual quantitative relations. In general, IAA or GA_3 selectively stimulate some processes and do not affect or inhibit others. Frequently, the effect of IAA is opposite to that of GA_3 . The majority of developmental processes in all parts of the *Chara* thallus is stimulated by hormones when the levels of both regulators are increased.

These observations seem to confirm the earlier views of Skoog and Miller (1957) that control of processes connected with growth and develop-

ment results not only from the action of a particular hormone but from the interaction and definite balance between different kinds of plant growth substances.

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Wpływ GA₃, IAA i ich mieszaniny na rozwój wegetatywnej części plechy i organów generatywnych Chara vulgaris L.

Streszczenie

IAA stosowany w zakresie stężeń od 10^{-7} do 10^{-5} M wyraźnie stymuluje wzrost komórek międzywęźli nibylodygi i pleuridiów, nie wpływa na liczbę odgałęzień bocznych plechy i liczbę organów rozmnażania, wydłuża czas spermatogenezy, a w większych stężeniach redukuje liczbę spermatozoidów tworzonych w anteridiach. GA₃ w stosowanych stężeniach 10^{-7} - 10^{-5} M hamuje wzrost komórek międzywęźli, nibylodygi i pleuridiów, nie wpływa na liczbę odgałęzień bocznych plechy, zwiększa liczbę anteridiów i przyspiesza ich rozwój oraz zwiększa liczbę tworzonych spermatozoidów. Inkubacje w mieszaninach obu regulatorów wzrostu wykazały, że: a) IAA znosi hamujący wpływ Ga₃ na wzrost komórek międzywęźli nibylodygi, a jego stymulujące działanie jest nieco osłabiane przez GA₃; b) stosowany w stężeniu 10^{-5} M, przy niskim stężeniu GA₃ (10^{-7} M), zwiększa liczbę odgałęzień bocznych plechy; c) IAA w obecności GA₃ powoduje przedłużenie czasu

spermatogenezy nie modyfikując korzystnego wpływu GA₃ na liczbę anterydiów i liczbę tworzonych spermatozoidów oraz wzmacnia wpływ GA₃ na liczbę powstających oogoniów.

W poprzednich badaniach prowadzonych na *Chara vulgaris* inkubacja w antygiberelinie (AMO-1618) powodowała stymulację wzrostu plechy i zmniejszenie liczby plemników tworzonych przez anterydia. Obniżenie poziomu gibereliny powoduje więc analogiczny efekt do uzyskanego obecnie po stosowaniu IAA. Wyniki tych badań potwierdzają wniosek, że wzrost wegetatywnej części plechy jest bujniejszy przy przewadze auksyny, natomiast rozwój generatywny wymaga wysokiego poziomu gibereliny. Wskazują też na istotne znaczenie nie tylko zawartości, ale i odpowiednich ilościowych proporcji między zawartością auksyny i gibereliny na różnych etapach morfogenezy plechy *Chara vulgaris*.