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RESEARCH PAPERS

Effect of 2,4-D on Cell Proliferation and Elongation in the Roots of *Arabidopsis thaliana*

A. N. Filin and V. B. Ivanov

Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, ul. Botanicheskaya 35, Moscow, 127276 Russia
e-mail: ivanov_vb@mail.ru

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Abstract—We investigated the effect of 2,4-D (2,4-dichlorophenoxyacetic acid) at concentrations of 1.5, 15, 30, and 60 nM on the growth of the main root of 3–7-d-old plants of *Arabidopsis thaliana* L. On the basis of measurements of the rate of root growth, lenght of fully elongated cells, and the number of cells in the meristem and elongation zone, we calculated the rates of cell proliferation and their transition to elongation, duration of cell cycle, and life span of cells in the meristem. At a concentration of 1.5 nM, 2,4-D did not affect these characteristics. At concentrations above 1.5 nM, 2,4-D noticeably retarded root growth, which was accounted for by a reduction in the length of cells that completed elongation, deceleration of cell proliferation and their transition to elongation, and prolongation of cell cycle and life span of the cells in the meristem. Thus, auxin decelerated root growth not only as a result of suppression of cell elongation but also at the higher concentrations via retardation of cell divisions in the meristem and their transition to elongation.

Keywords: Arabidopsis thaliana, root physiology, proliferation, cell cycle, transition to elongation, phytohormones, 2,4-D

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INTRODUCTION

Phytohormones, including indole-3-acetic acid (IAA), play an important role in regulation of plant growth and morphogenesis. The effect of IAA on root growth is described in extensive literature too numerous to deal with in this paper. It is known that, in contrast to above-ground organs, the growth of roots is only slightly stimulated by auxins at very low concentrations [1–3] with an appreciable stimulation of root branching. It is generally accepted that IAA plays a leading role in the regulation of root morphogenesis and maintenance of the pool of stem cells, which was shown by various methods [4–6]. The role of IAA in the regulation of cell proliferation in the main meristem and their transition to elongation is much less investigated. Unlike coleoptiles and hypocotyls that are very often used to look into the effect of auxins [3], the process of cell elongation takes much less time in the roots, and maintenance of root growth depends on transition of fully elongated cells. The mechanism of regulation of cell transition to elongation in the roots remains essentially unknown, and the role of auxins in this process is indefinite. Moreover, it is important that the rate of cell transition to elongation in the roots depends on the intensity of divisions [7, 8]. Therefore, in order to more clearly understand the mechanism of changes in the rate of root growth under the effect of auxins, one should find out how auxins affect individual components of root growth.

The growing part of the root consists of the meristem and elongation zone. The rate of root growth depends on the rate of cell proliferation in the meristem, the rate of their transition to elongation, and lenght of fully elongated cells. If the root grows at a constant rate, the rate of cell transition to elongation is equal to the rate of cell production in the meristem. The rate of cell proliferation in the meristem (V_m) depends on the duration of cell cycle (T) and the number of cells in the meristem (N_m). For an individual file of cells, N_m depends on the number of division cycles after cell production as a result of division of the first cell at the border of quiescent center before it leaves the meristem (p). The time a cell spends within the meristem we call life span of the cell in meristem (T_m) [7]. In the meristem above the quiescent center, T is essentially constant [7], therefore $T_m = pT$. In order to estimate the effect of an agent on root growth, it is necessary to make a thorough cellular analysis that will show the effect of this agent on the rate of cell proliferation, duration of cell cycle, life span of the cells within meristem, and the rate of their transition to elongation [8].

Under exogenous treatment with auxins (including 2,4-D), various components of root growth change differently. Burström was one of the first to show it [9, 10]. In particular, he showed [11] that α-NAA at a concentration of 3×10^{-7} M suppresses the growth of wheat roots by approximately 35% owing to a reduc-

tion in final length of elongated cells, and the number of produced cells remains unchanged. In the roots of arabidopsis, Beemster and Baskin [12] investigated the mechanism of 2,4-D action at a cellular level. They showed that, under the effect of 30 nM 2,4-D, deceleration of root growth by approximately 50% occurred owing to a prolongation of the cell cycle (by 15%) and a slight reduction in the final length of elongated cells with life span of the cells in the meristem rising. Other concentrations of 2,4-D were not tested.

The aim of this work was to study the effect of 2,4-D in a wider range of concentrations on individual components of root growth, in particular, on the duration of cell cycle, the rate of cell proliferation and their transition to elongation, and on life span of the cells in the meristem and final length of elongated cells in *Arabidopsis thaliana*.

MATERIALS AND METHODS

Plant material and growing conditions. We studied the effect of 2,4-D on root growth in *Arabidopsis thaliana* L. of wild type (ecotype Columbia 0).

The seeds were surface-sterilized in 5% solution of sodium hypochlorite and then washed in three portions of sterile distilled water by 5 min in each portion. Surface-sterilized seeds were planted in petri dishes on the medium containing a quarter-strength MS, 1% sucrose, 0.8% agar, and 0.5 g/L 2-(N-morpholino)ethanesulfonic acid (MES), pH 5.8, supplemented with 1.5, 15, 30, and 60 nM 2,4-D. In the control type of treatment, 2,4-D was not added. Stratification was conducted at 4°C in the dark for 2 days in petri dishes. After stratification, the seedlings were grown in petri dishes vertically accommodated in a controlled-climate chamber at light period of 16 h, illuminance of 10 klx, and temperature regime of 22/18°C (day/night).

Fixation of material and microscopy procedures. Prior to root fixation, petri dishes with the seedlings were scanned using an Epson Perfection V300 Photo light scanner (Epson, Indonesia) at a resolution of 600 dpi for subsequent determination of root length. The roots were fixed in 4% formalin in phosphate buffer (pH 7.2) for 4 h at room temperature. Subsequently, the seedlings were transferred to 30% glycerol in 2% dimethyl sulfoxide and incubated for 30 min at room temperature. Before the examination under microscope, the seedlings were transferred to a so-called clarifying solution.

The clarifying solution consisted of 61 g of KI and 198 mg of $Na_2S_2O_3$ in 100 mL of 2% dimethyl sulfoxide. Thirty-five milliliters of this solution was mixed with 65 mL of 100% glycerol. The seedlings were incubated in the clarifying solution for at least 1.5 h; then, temporary preparations in 50% glycerol were mounted on glass slides.

The experiments were conducted in duplicate (1.5 nM 2,4-D type of treatment) or quadruplicate (control material, 15, 30, and 60 nM 2,4-D types of treatment), each replicate comprising 15 plants per type of treatment. Quantitative characteristics of root growth obtained as a result of measurements and calculations were treated using MS Excel 2007 software and presented as means and their standard deviations.

Length of roots and size of meristem. Preparations were examined under an Imager D1 microscope (Carl Zeiss, Germany) equipped with Nomarski optics (Carl Zeiss). The length of main roots was measured using an IMAGE J program. The length of the main root was measured from the quiescent center to the end of the root collar. The cells in the meristem and elongation zone of the main root were counted using a Carl Zeiss AxioVision program. Final length of elongated cells was measured on the micrographs by means of Carl Zeiss AxioVision software (application Length). All the measurements were taken along one longitudinal file of cortex.

Calculation of characteristics of root cell growth. The duration of the cell cycle (T, h) was calculated according to a formula proposed by Ivanov [7, 8]:

$$T = (\ln 2 N_m l)/V, \quad (1)$$

where N_m is the number of meristematic cells in a file, l is final length of elongated cells (μm), and V is rate of root growth (μm/h). Applicability of this formula to calculation of average duration of cell cycle in root meristems was shown in a number of works [12, 13].

Life span of the cells in the meristem (T_m, h) [7, 8] was calculated as follows:

$$T_m = pT, \quad (2)$$

where T is duration of cell cycle (h) and p is number of division cycles from the moment when the cell separates from the first cell at the border of the quiescent center to the time it leaves meristem. p may be calculated according to a formula [7, 8]:

$$p = \ln(N_m - 1)/\ln 2. \quad (3)$$

The number of cells that completed elongation (N) was calculated according to the formula [7, 8]

$$N = \Delta L/l, \quad (4)$$

where ΔL is increment in root length (μm) and l is final length of elongated cells (μm).

The number of cells in the meristem may be directly counted on a micrograph in a cortex file from quiescent center to the beginning of elongation zone or calculated if we know p [7, 8]:

$$N_m = 2^{p+1} - 1, \quad (5)$$

where p is the number of division cycles.

The rate of production of new cells in a file (V_m, cells/h) was calculated according to the formula

$$V_{m(1\text{-}2)} = N_{(1\text{-}2)} + (N_{m2} - N_{m1}) + (N_{e2} - N_{e1}), \quad (6)$$

where $N_{(1\text{-}2)}$ is the number of cells in a file, which completed elongation between the first and second days; N_{m1} is the number of meristematic cells in a file on the first day; N_{m2} is the number of meristematic cells in a

Table 1. Measured characteristics of root growth in Arabidopsis plants grown in the presence and absence of 2,4-D

Type of treatment	Length of the main root, mm						Final length of elongated cells, μm		
	3rd day		5th day		7th day		3rd day	5th day	7th day
	abs.	%	abs.	%	abs.	%			
Control material	7.0 ± 0.6	100	12.1 ± 0.9	100	18.8 ± 2.1	100	101 ± 12	117 ± 17	146 ± 9
1.5 nM 2,4-D	6.6 ± 0.1	94	11.0 ± 1.0	91	16.7 ± 0.9	89	97 ± 10	106 ± 9	133 ± 20
15 nM 2,4-D	2.1 ± 0.3	30	4.1 ± 0.3	34	5.8 ± 0.4	31	65 ± 7	61 ± 10	28 ± 4
30 nM 2,4-D	0.9 ± 0.1	13	1.9 ± 0.2	16	2.9 ± 0.3	15	33 ± 4	31 ± 9	27 ± 5
60 nM 2,4-D	0.7 ± 0.1	10	1.3 ± 0.1	11	2.2 ± 0.1	12	21 ± 2	25 ± 3	22 ± 1

For each type of treatment, the means and their standard deviations are shown. The length of roots is given in absolute values (abs.) and as a percentage of control level. For 1.5 nM, the data obtained for 30 roots are shown; for all the other types of treatment, those for 60 roots are shown.

file in 2 days; N_{e2} is the number of cells in a file in elongation zone in 2 days; and N_{e1} is the number of cells in a file in elongation zone on the first day.

The rate of meristematic cell transition to elongation (V_{me}, cells/h) in a file was calculated according to the formula

$$V_{me(1\text{-}2)} = V_{m(1\text{-}2)} - (N_{m2} - N_{m1}), \quad (7)$$

where $V_{me(1\text{-}2)}$ is the rate of cell production between the measurements (cells/h); N_{m1} is the number of meristematic cells on the first day; N_{m2} is the number of meristematic cells in two days.

Average duration of elongation growth (t_e, h) was calculated according to the formula

$$t_e = \Delta N_e / V_n, \quad (8)$$

where ΔN_e is average number of elongating cells in the period between observations and V_n is average rate of increase in the number of cells that completed elongation between observations equal to $N/\Delta t$. In our experiments, Δt was equal to 48 h.

RESULTS AND DISCUSSION

The rate of growth of control roots increased between the 3rd and 7th days from germination. 1.5 nM 2,4-D did not affect the growth of arabidopsis roots. At 2,4-D concentration of 15 nM and above, we observed a considerable decrease in the growth rate of the main root (Table 1) and active formation of lateral and adventitious roots that were much longer and thicker than the main root (data not shown).

Effect of 2,4-D on the Length of Fully Elongated Cells

At high concentrations, 2,4-D considerably decreased the length of fully elongated cells (Table 1); it is interesting that the higher 2,4-D concentration in the medium was, the less the length of cells became. For instance, in the presence of 60 nM 2,4-D, the cells that completed elongation were five and more times shorter than in control roots. Knowing the increment in the length of the main root during a certain time interval and final length of the cells that completed elongation, we calculated the total number of cells in the root that completed elongation according to formula (4). At 2,4-D concentrations above 15 nM, total number of fully elongated cells, meristematic cells and elongating cells in the root was somewhat lower than in control material (Tables 2, 3).

Effect of 2,4-D on the Duration of Cell Cycle (T)

Calculation of T according to the formula (Tables 4 and 5) showed that, at a concentration above 1.5 nM, 2,4-D slightly prolonged the mitotic cycle, which corroborates the results earlier obtained by Beemster and Baskin who studied the effect of this compound at a concentration of 30 nM [12].

Effect of 2,4-D on the Rate of Cell Proliferation and Transition to Elongation

Tables 4 and 5 show that 2,4-D somehow retarded cell proliferation and decelerated their transition to elongation. This caused a reduction in the number of cells in the meristem (Table 3), because the rate of their transition to elongation decreased to a slighter degree that the rate of proliferation. Having calculated the number of meristematic, elongating, and elongated cells according to formula (7), we found the rate of transition to elongation (V_{me}) (Tables 4 and 5), i.e., the number of meristematic cells that proceeded to elongation per time unit. The value of V_{me} may depend on the share of cells that start elongating during this time or on the number of cells produced as a result of divisions while they still stay in the zone of meristem. The experiment showed that a prolonged exposure to 2,4-D reduced the rate of transition to elongation. As this process depends on the number of cells that start elongating, it is also necessary to find out how long the

Table 2. Effect of 2,4-D on average duration of elongation (h)

Type of treatment	ΔN_e		$N/\Delta t$		t_e	
	3–5 days	5–7 days	3–5 days	5–7 days	3–5 days	5–7 days
Control	10.5	14.0	1.0	1.1	10.5	12.7
1.5 nM 2,4-D	12.5	15.0	0.9	1.0	13.9	15.0
15 nM 2,4-D	9.5	12.0	0.7	0.8	13.6	15.0
30 nM 2,4-D	9.0	11.5	0.6	0.7	15.0	16.4
60 nM 2,4-D	10.5	13.5	0.6	0.6	17.5	22.5

ΔN_e—average number of cells in the elongation zone; N—average number of fully elongated cells; Δt—average time between observations, in our experiment equal to 48 h; t_e—average duration of elongation.

Table 3. Number of cells in the roots of arabidopsis plants grown in the presence and absence of 2,4-D

Type of treatment	Number of cells							
	in the meristem (N_m)			in the elongation zone (N_e)			fully elongated (N)	
	3rd day	5th day	7th day	3rd day	5th day	7th day	3–5 days	5–7 days
Control	21 ± 1	24 ± 1	25 ± 1	9 ± 1	12 ± 1	16 ± 2	47 ± 9	51 ± 16
1.5 nM 2,4-D	21 ± 1	22 ± 1	26 ± 1	11 ± 1	14 ± 1	16 ± 1	44 ± 16	49 ± 14
15 nM 2,4-D	18 ± 1	21 ± 1	24 ± 1	8 ± 1	11 ± 1	13 ± 1	32 ± 7	38 ± 9
30 nM 2,4-D	18 ± 1	21 ± 1	22 ± 1	8 ± 1	10 ± 1	13 ± 1	30 ± 8	34 ± 10
60 nM 2,4-D	16 ± 1	19 ± 2	22 ± 1	9 ± 1	12 ± 2	15 ± 2	27 ± 5	31 ± 8

For each type of treatment, the means and their standard deviations (±) are shown. For 1.5 nM, the data obtained for 30 roots are shown; for all the other types of treatment, those for 60 roots are shown.

Table 4. Calculated characteristics of root growth in arabidopsis plants grown in the presence and absence of 2,4-D (3–5 days)

Type of treatment	T_m, h	T, h	V_m, cells/h	V_{me}, cells/h	p, number of cycles	Rate of root growth (V), mm/h
Control	57.2 ± 2.0	16.7 ± 3.5	53 ± 6	50 ± 9	3.4 ± 0.1	106 ± 22
1.5 nM 2,4-D	59.2 ± 4.0	17.7 ± 5.3	48 ± 15	47 ± 3	3.3 ± 0.2	92 ± 27
15 nM 2,4-D	67.4 ± 1.6	21.0 ± 5.1	39 ± 7	45 ± 7	3.2 ± 0.2	42 ± 8
30 nM 2,4-D	73.3 ± 3.2	22.8 ± 6.0	37 ± 7	33 ± 1	3.2 ± 0.1	20 ± 4
60 nM 2,4-D	68.0 ± 2.1	22.0 ± 3.8	34 ± 7	31 ± 1	3.0 ± 0.1	13 ± 2

Duration of cell cycle (T), life span of the cells in meristem (T_m), number of division cycles (p), the rate of cell proliferation (V_m), and the rate of meristematic cell transition to elongation (V_{me}) were calculated as described in Materials and Methods. For each type of treatment, the means and their standard deviations (±) are shown. For 1.5 nM, the data obtained for 30 roots are shown; for all the other types of treatment, those for 60 roots are shown.

cells remain in the zone of meristem and how quickly they divide, since these parameters are interconnected.

Effect of 2,4-D on Life Span of the Cells in the Meristem

Duration of cell cycle (T) is constant throughout the whole meristem [7]; therefore, the number of division cycles after cell separation from the first cell at the border of quiescent center to the time it leaves meristem (p) and the number of meristematic cells in a file (N_m) are connected by a simple relationship. Having determined the number of meristematic cells in the file, one can calculate p occurring from the time when a new cell separates from the first cell at the border of quiescent center to the moment it leaves meristem according to formula (3). Thus, a basal cell that emerged after division of the first cell at the border of quiescent center leaves meristem having undergone p divisions. It takes a time interval that we call the life span of the cell in the meristem (T_m), which may be calculated according to formula (2). Results of calculations are shown in Tables 4 and 5. Our data show

Table 5. Calculated characteristics of root growth in arabidopsis plants grown in the presence and absence of 2,4-D (5–7 days)

Type of treatment	T_m, h	T, h	V_m, cells/h	V_{me}, cells/h	p, number of cycles	Rate of root growth (V), mm/h
Control	61.5 ± 3.4	17.2 ± 1.1	55 ± 9	54 ± 10	3.6 ± 0.1	140 ± 45
1.5 nM 2,4-D	64.8 ± 5.2	18.2 ± 1.5	55 ± 14	51 ± 3	3.5 ± 0.2	119 ± 31
15 nM 2,4-D	80.3 ± 2.2	23.3 ± 6.0	43 ± 9	40 ± 9	3.4 ± 0.1	35 ± 9
30 nM 2,4-D	78.8 ± 4.0	23.4 ± 8.1	38 ± 10	37 ± 2	3.3 ± 0.2	21 ± 5
60 nM 2,4-D	74.0 ± 4.1	22.0 ± 7.0	36 ± 8	33 ± 1	3.3 ± 0.2	16 ± 4

Duration of cell cycle (T), life span of the cells in meristem (T_m), number of division cycles (p), the rate of cell proliferation (V_m), and the rate of meristematic cell transition to elongation (V_{me}) were calculated as described in Materials and Methods. For each type of treatment, the means and their standard deviations (±) are shown. For 1.5 nM, the data obtained for 30 roots are shown; for all the other types of treatment, those for 60 roots are shown.

that, under the effect of 2,4-D (at a concentration of 15 nM and above), the cells spent more time in the meristematic zone.

Effect of 2,4-D on the Duration of Elongation

According to formula (8), we calculated average duration of elongation between 3–5 and 5–7 days after the beginning of the experiment (Table 2). At concentrations below 60 nM, 2,4-D slightly extended the duration of elongation. At 2,4-D concentration of 60 nM, duration of elongation increased by 80%. It is interesting however, that an increase in the duration of elongation hardly influenced the root length increment. The point is that if even all the cells in the elongation zone elongated, the increment in root length would increase by the value equal to $N_e \times 1/2l$. This value accounted for only 10–15% of root increment over 48 h. Thus, the greatest contribution to deceleration of root growth could be made by elongation of the cells that stopped elongating having reached a moderate length and not by changes in the duration of elongation growth. More thorough analysis of the mechanism of 2,4-D action on elongation of the cells did not fall within the purpose of this work.

Cellular analysis of the effect of 2,4-D at different concentrations showed that a prolonged exposure of plants on the medium with its concentration above 1.5 nM retarded cell transition to elongation and inhibited elongation of root cells. As a result, the growth rate decreased and, in the final account, total length of main root reduced. At concentrations above 1.5 nM, 2,4-D also induced a slight retardation of cell proliferation in the meristem. Simultaneously, the growth of lateral and adventitious roots was activated, which we observed in our experiments (data not shown).

Thus, investigation of the effect of 2,4-D on growth processes in the root we conducted in a wide range of concentrations (from 1.5 to 60 nM) showed that it differently affected individual growth processes. The most significant was the reduction in the final length of elongated cells, which caused a suppression of the main root growth. To a lesser extent, the rate of cell division was inhibited owing to an increase in the duration of cell cycle. However, in this case, the life span of the cells within meristem somewhat increased, which partly compensated for prolongation of the cycle because the cells spent more time in the meristematic zone. For the above-noted reasons, the number of cells in the meristem in the presence of 2,4-D did not differ much from that in the roots of plants growing on hormone-free medium.

Under the effect of used concentrations of 2,4-D, all the processes of cell growth and division acting as components of root growth were modified. We did not manage to detect a selective action of 2,4-D on a certain growth process. This was probably accounted for by rather high concentrations of 2,4-D we used. Unlike the effect on coleoptiles and hypocotyls, auxins only slightly stimulate the growth of root at low concentrations [1–3]. At higher concentrations, other points of application of natural and synthetic auxins (including 2,4-D) may arise with numerous growth components being affected and growth suppressed. Physiological mechanisms underlying these changes are not known so far, and their investigation is urgent for elucidation of the mechanisms of auxin action on the growth of roots and other plant organs.

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