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Effect of Low and Sublethal Doses of Irradiation on the Ribosome Content and on the Incorporation of [^{3}H]Uridine into the RNA of Growing Tubes of Pine Pollen

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Low doses of X rays and uv light delivered at low dose rates stimulated the tube growth of *Pinus silvestris* pollen, while sublethal doses supplied at moderate dose rates inhibited the tube growth significantly. The irradiation also altered the level of ribosome content. The polysome content measured after 72 hr of tube development was twice as high in samples irradiated with sublethal doses as in samples irradiated with low doses. The control samples possessed only light oligosomes, while in low-dose irradiated samples all polysomes were heavy polysomes, and in sublethally irradiated samples only 20% of polysomes were heavy polysomes. The irradiated pollen, incubated for more than 56 hr, incorporated more uridine than the control: The low-dose samples had twice as much labeled uridine in the rRNA as the sublethally irradiated samples.

INTRODUCTION

The stimulating effects of low doses of ionizing irradiation and uv light on pollen tube growth have been already reported (*1*, *2*). The mechanisms which cause the stimulatory effects are not yet known. Ehrenberg *et al.* (*3*) suggested that the oxidizing effect of irradiation shifts the equilibrium of NADP $\leftrightharpoons$ NADPH to the oxidized side and enhances indirectly RNA synthesis through the hexose monophosphate shunt. It has been found that the peroxide content and the level of NAD(P) were remarkably higher in irradiated pine pollen than in the control (*4*). Moreover, in radiation-stimulated samples the NAD(P) reached its maximum earlier than in samples having absorbed inhibiting amounts of radiation (*4*). If the hypothesis of Ehrenberg *et al.* (*3*) is to be valid for pine pollen, the irradiated sample has to have a higher RNA content than the unirradiated one.

In guinea pigs the number of polysomes increased during a period between 9 and 15 hr after massive whole-body irradiation (*5*). The incorporation of [^{14}C]orotic acid into the nuclear RNA fraction of the liver of the guinea pig also showed a 50 to 100% increase between 3 and 12 hr after 2000 rad of irradiation (*6*). The syntheses of rRNA and ribosomes in pear fruit cells were stimulated

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(*7*) by a γ-radiation dose of 250 krad, and the effect persisted for several days. On the other hand, the specific activity of DNA polymerase in *Tetrahymena* increased with increasing doses of uv light (*18*). The authors suggested that the stimulation by uv light acts through a repair mechanism. Massive X-ray doses (250–500 kR) significantly enhanced the accumulation of ^{32}P in the nucleic acid of peanut seeds (*9*). The amounts of [^{3}H]uridine and [*methyl*-^{14}C]methionine incorporated into rRNA and tRNA were significantly higher in irradiated sugarbeet roots (*10*). It has also been reported that sublethal doses of γ radiation lead to a rapid, dose-dependent decrease of polysome content of *Tetrahymena*, followed by an increase to normal and supranormal levels (*11*).

The changes of RNA synthesis and ribosome content in irradiated cells and organs were mostly observed when the applied doses caused damage. This is the opposite of the effect with low-dose irradiation, which stimulated pollen tube growth. The present investigation was initiated in order to determine (a) if low-dose irradiation or only sublethal irradiation change the incorporation of labeled uridine into the RNA and the content of polysomes, in pollen tubes, and (b) if there is conformity between the effects of uv-light and X-ray irradiations not only concerning pollen tube growth but also in regard to changes of the incorporation of labeled uridine into RNA and of the polysome content.

MATERIALS AND METHODS

Growth Procedure

Harvest of the strobili and storage of the pollen grains of the pine, *Pinus silvestris*, have been described elsewhere (*2*). Pollen grains (15 mg for the experiments of RNA isolation and 20 mg for the isolation of ribosomes) were incubated on a watch glass in 0.75 ml of fourfold distilled water. After irradiation, 0.25 ml of a mixture of antibiotics (125 μg of chloramphenicol, 125 μg of penicillin, and 250 μg of mycostatin) was added to the pollen samples to prevent infection.

In the experiments for the qualitative determination of RNA synthesis 3.7 $\times$ 10^5 Bq (10 μCi) of L-[*methyl*-^{14}C]methionine (50 μmCi/mmol) and 18.5 $\times$ 10^5 Bq (50 μCi) of [5-^{3}H]uridine (25 Ci/mmol) were added, whereas in experiments for the quantitative determination only [5-^{3}H]uridine (Amersham-Buchler, Braunschweig) of the same activity was applied.

During germination and tube growth the pollen grains were illuminated by fluorescence lamps (Osram colors No. 15 and 77-2) with an intensity of 1200 lux. The temperature was kept at 26°C. Each sample was controlled under the microscope for infection. The tubes were measured with an ocular micrometer.

Irradiation of Pollen Samples

The irradiation was carried out after exactly 3 min of water uptake by the dehydrated pollen grains. The source of ionizing radiation was an X-ray tube, with a 1-mm beryllium window equivalent to 0.075 mm of aluminum, operated at 30 kV and 5 mA. The uv irradiation was performed with a medium-pressure mercury arc lamp (Osram HQA 125-W with glass bulb broken off) and a uv

interference filter (14-16-8, 265-nm Baird Atomic). With the X-ray tube the stimulating dose of 23 Gy at 0.48 Gy/sec and the inhibiting dose of 2000 Gy at 23 Gy/sec were applied. The uv irradiation was 7×10^7 J/m^2 at 0.134×10^3 W/m^2 for stimulating effects and 2.9×10^9 J/m^2 at 1.34 W/m^2 for inhibitory effects.

Isolation and Separation of Ribosomes

A modification of the method by Linskens *et al.* (*12*) was employed for the extraction of polysomes and monosomes. Pollen grains were suspended in ice-cold buffer B (pH 7.8, 10 m*M* Tris–HCl, 10 m*M* $MgCl_2$, 10 m*M* KCl, and 300 m*M* sucrose). The pollen was immediately homogenized in a Potter S homogenizer (Braun AG, Melsungen, Germany) for 2 min. Almost all the pollen grains showed breakage. The wall fragments were sedimented by centrifuging at 4000 rpm for 5 min in the Laborfuge (Heraeus-Christ GmbH, Osterode, Germany). All operations were carried out at 0 to 4°C. Deoxycholate (1%, w/v) was added to the cytoplasmic supernatant. The extract (0.4 ml) was layered on top of a 16.8-ml linear sucrose gradient (10–30%) made in buffer A (pH 7.8, 10 m*M* Tris–HCl, 10 m*M* $MgCl_2$, and 10 m*M* KCl). The centrifugation was carried out in a Spinco SW-27.1 rotor for 4 hr at 22,000 rpm at 2°C. After centrifugation the tube was punctured at the bottom, fractions were collected, and the absorption (optical density) of each was measured at 260 nm in a Zeiss PMQ II spectrophotometer. The amounts of monosomes and polysomes were calculated from planimeter measurements of the appropriate areas under the spectrophotometric absorption curve (*11*).

Isolation and Separation of RNA

Thirty milligrams of pollen were homogenized in a Potter S homogenizer at 0°C. RNA was extracted twice at 0°C with phenol-saturated buffer containing 0.1% 8-hydroxy quinoline and with 100 m*M* Tris–HCl containing 1% sodium dodecyl sulfate at pH 7.6 (*13*). From the buffer phase the nucleic acids were precipitated with 0.1 vol of 10% NaCl and 2.5 vol of ethanol at −20°C overnight. The total amounts of nucleic acids were determined from the absorption at 260 nm.

The separation of RNA was carried out with polyacrylamide gel electrophoresis described by Loening (*14*). For the qualitative determination a tandem gel of 3 and 7.5% polyacrylamide (*15*) was used, whereas for the quantitative determination a 2.6% polyacrylamide gel was used. The gels had been prepared in vertically positioned flat plates in an apparatus constructed by Desaga (Heidelberg, Germany). Two glass plates (8.5 × 10 cm), one of them with 3-mm rims at the longer sides, were placed together and put into a specially constructed box, which could be cooled by water during the electrophoresis. After filling the space between the plates with gel, six holes of 3 × 10 mm cross section and 15 mm depth were pressed vertically into the gel with the help of Teflon pocket formers. The dissolved RNA (in E-buffer containing 0.4 *M* Tris, 0.3 *M* NaH_2PO_4, 0.01 *M*

TABLE I

The Effect of Irradiation on the Contents of Monosomes and Polysomes during Pollen Germination and Tube Growth[a]

Time of germination (hr)	*Control*		*Low dose/low dose rate*				*High dose/high dose rate*			
			uv light		*X rays*		*uv light*		*X rays*	
	Monosomes	*Polysomes*	*Monosomes*	*Polysomes*	*Monosomes*	*Polysomes*	*Monosomes*	*Polysomes*	*Monosomes*	*Polysomes*
0 (d)	1.5 ± 0.3	0.7 ± 0.1								
0 (w)	3.9 ± 0.2	3.2 ± 0.7	4.2 ± 0.2	3.2 ± 0.7	2.5 ± 0.2	3.6 ± 0.6	4.1 ± 0.1	3.7 ± 0.3	2.6 ± 0.1	2.0 ± 0.5
2	2.9 ± 0.2	3.1 ± 0.7	2.1 ± 0.2	2.6 ± 0.7	2.7 ± 0.3	3.2 ± 0.6	3.0 ± 0.3	2.5 ± 0.6	1.8 ± 0.2	2.2 ± 0.6
16	2.9 ± 0.3	3.7 ± 0.6	1.1 ± 0.2	1.5 ± 0.5	1.9 ± 0.1	4.5 ± 0.3	1.6 ± 0.1	3.8 ± 0.3	1.7 ± 0.2	2.2 ± 0.5
24	2.0 ± 0.3	2.9 ± 0.6	1.0 ± 0.3	1.3 ± 0.6	1.4 ± 0.2	3.0 ± 0.5	1.1 ± 0.2	2.5 ± 0.8	1.7 ± 0.4	2.1 ± 0.5
32	1.5 ± 0.3	2.6 ± 0.4	1.6 ± 0.3	3.2 ± 1.1	1.8 ± 0.2	2.2 ± 0.8	2.0 ± 0.3	2.1 ± 0.1	1.1 ± 0.4	1.1 ± 0.2
40	1.1 ± 0.1	2.2 ± 0.5	1.6 ± 0.2	1.5 ± 0.8	2.2 ± 0.6	1.3 ± 0.6	2.1 ± 0.1	3.2 ± 0.5	1.1 ± 0.1	2.6 ± 0.7
48	1.2 ± 0.2	2.0 ± 0.8	1.3 ± 0.3	1.3 ± 0.6	1.7 ± 0.3	1.6 ± 0.6	1.5 ± 0.3	1.4 ± 0.6	1.3 ± 0.2	2.2 ± 0.5
64	1.8 ± 0.2	1.5 ± 0.7	1.4 ± 0.1	1.5 ± 0.2	1.7 ± 0.1	1.9 ± 0.6	2.2 ± 0.2	1.8 ± 0.7	1.0 ± 0.1	1.3 ± 0.2
72	2.2 ± 0.5	1.8 ± 0.6	1.4 ± 0.3	0.7 ± 0.4	1.6 ± 0.3	0.8 ± 0.6	1.7 ± 0.3	2.5 ± 0.5	1.0 ± 0.1	3.4 ± 0.4

[a] d, dry pollen; w, wet pollen.

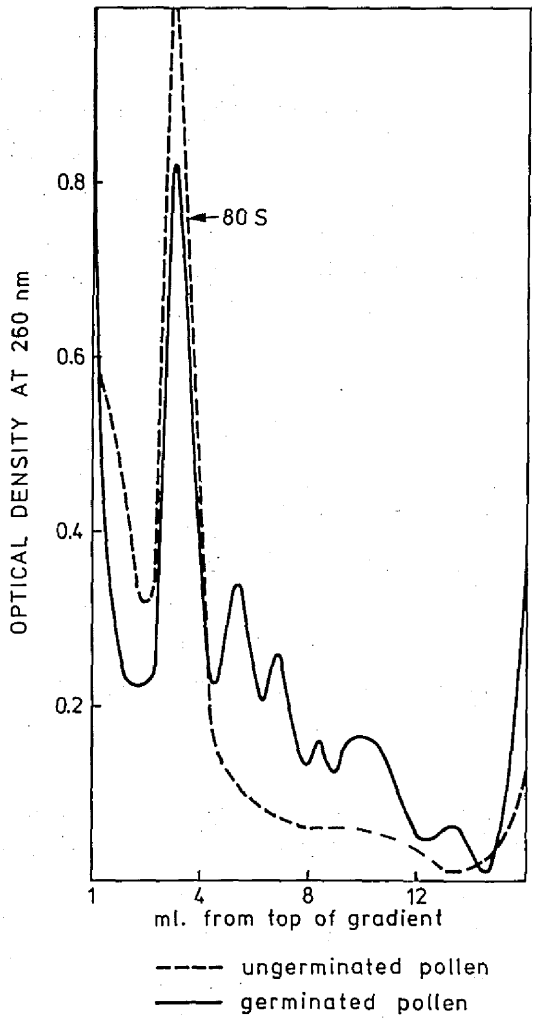


FIG. 1. The ribosome profiles of the pollen, obtained after centrifugation.

EDTA, and 10% sucrose at pH 7.8) was taken up by a special microsyringe and was layered under the electrode buffer at the bottom of the holes.

Electrophoresis was carried out at 4°C in 10-fold diluted E-buffer (without sucrose) containing 0.2% SDS, with a current of 80 mA at 160 V for 3 hr (qualitative determination) or 44 mA at 100 V for 6 hr (quantitative determination). After electrophoresis the gel slabs containing the separated RNA were cut out and scanned at 260 nm using a Joyce Loebl scanner. The gel was cut into 1-mm slices with a Mickle gel slicer. Each slice was put into a minivial with 0.25 ml of tissue solublizer (TS 1) and digested at 65°C for 3.5 hr. After cooling, 3 ml of Minisolve were added to each sample, and the radioactivity was measured in a Packard Tri-Carb liquid scintillation spectrometer. All chemicals used for the determination of the radioactivity were supplied from Zinsser (Frankfurt, Germany).

RESULTS

Forty-three percent less ribosomes were isolated from ungerminated pollen grains (dry pollen) than from pollen which were incubated in water for a few minutes (germination time, 0 hr) (Table I). Averaging 27 measurements, the ungerminated dry pollen contained 39% polysomes (Fig. 1). After a few minutes

of water uptake the monosome content of unirradiated pollen increased to an amount which was about three times higher than that of dry pollen. Up to 40 hr of incubation a continuous decrease of the monosome content could be observed, followed by a significant increase with longer incubation times (Table I). The monosome content of the ungerminated wet pollen (time of germination, 0 hr) was significantly lower in X-ray-irradiated samples than in the control and in uv-irradiated samples. During the incubation the monosome content in irradiated samples decreased in different ways. Except for the high-dose X-irradiation sample, the lowest content of monosomes was found at 24 hr of incubation, followed by a slight increase.

The polysome content of the unirradiated, ungerminated wet pollen was about four times higher than that of the unirradiated, dry pollen. Until 24 hr of incubation no significant change could be observed. In samples with longer incubation times a slight, continuous decrease could be detected. Except for the high-dose X-irradiated samples at 0 hr the polysome content of the irradiated pollen was as high as that of the control measured at 0 hr of incubation. The decrease of the polysome content in irradiated samples was not as smooth as in the unirradiated pollen. In the low-dose uv-irradiated pollen a second maximum was observed at 32 hr, while in low-dose X-irradiated pollen the highest amount of polysomes was found at 16 hr. At 72 hr of incubation only a relatively small fraction of polysomes could be detected. In the high-dose irradiated samples the decomposition of polysomes was less than in low-dose irradiated samples, and at 72 hr relatively high amounts of polysomes could be observed. This is generally true for both kinds of radiation.

The ratio between the tube length and the content of polysomes (Fig. 2) indicates that between 32 and 64 hr of development the stimulated pollen had less polysomes per unit tube length than the control and the high-dose-irradiated samples. After 72 hr only light oligosomes were found in the control samples, while in low-dose-irradiated samples all polysomes were heavy polysomes, and in high-dose-irradiated samples only 20% of polysomes were heavy ones.

The RNA was isolated after 16, 32, and 72 hr of incorporation. Figure 3 shows that only a very small amount of low-molecular-weight RNA was detected in the 7.5% gel section of the tandem-gel used for qualitative determination of RNA. No [*methyl*-^{14}C]methionine incorporation could be detected in the 7.5% section of the gel. This indicates that no tRNA synthesis occurs in the tube (*16*). The peaks of the high-molecular-weight RNA showed a splitting a 16 hr (radioactivity) and at 32 hr (optical density) which was probably due to the technique of separation used.

When the RNA separation was carried out on the 2.6% polyacrylamide gel, no splitting of the RNA peaks could be detected. A comparison with the RNA of *Petroselinum sativum* (*17*) showed that the positions of the two main RNA components of pine pollen correspond to the positions of 25- and 18-S RNA (Fig. 4).

Pollen irradiated with high doses of X rays and uv light developed shorter tubes than the controls; these effects were only significant when the incubation was longer than 32 hr (Table II). To measure the effect of external irradiation

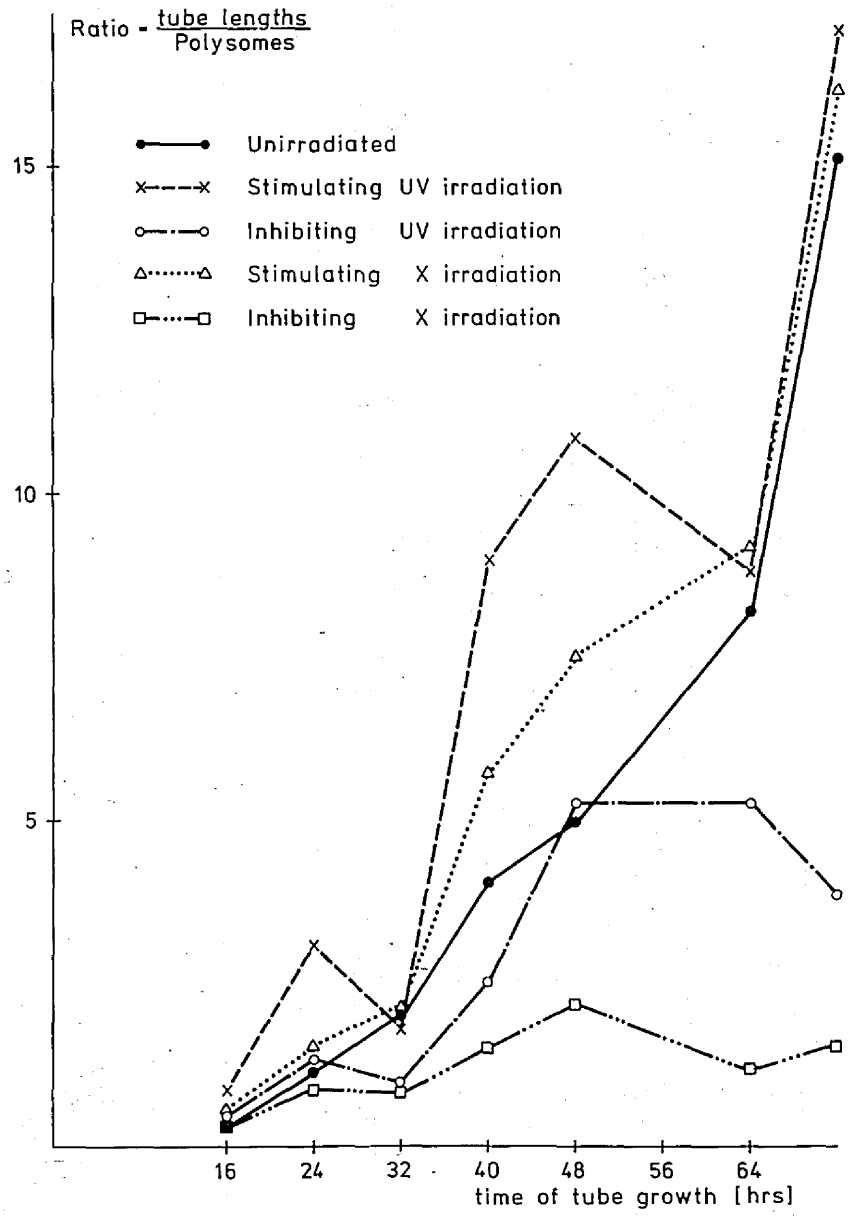
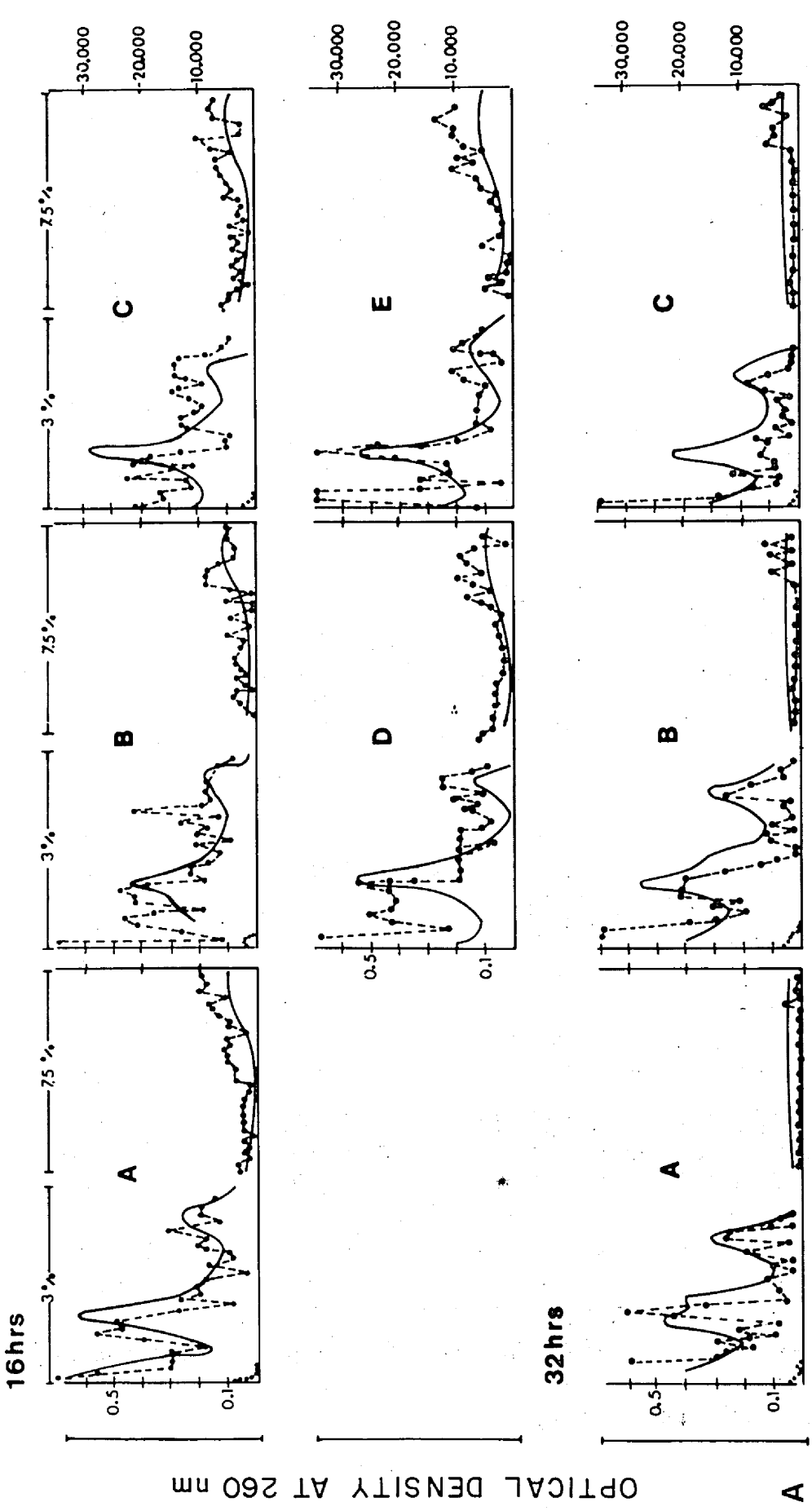


FIG. 2. The ratio between the tube length and the content of polysomes (in arbitrary units) during the tube development.

on the incorporation of labeled uridine into the 25- and 18-S RNA, the counts of both RNA peaks were combined. The unirradiated control incorporated the most labeled uridine at 40 to 48 hr of incubation. The irradiated samples showed the highest activity at 64 hr. Up to 32 hr the irradiated pollen incubated more labeled uridine than the control. Between 32 and 48 hr there were no significant differences between the activity of the control and that of the stimulated pollen. Incubation for more than 56 hr showed that the irradiated pollen incorporated more uridine than the control. The stimulated samples had twice as much labeled uridine in the *r*RNA than the high-dose-irradiated samples. Essentially the same results were obtained in a second experiment.

DISCUSSION

The mature pollen grain is a dehydrated and metabolically inactive structure (*13*, *18*). The first stage in pollen grain germination is imbibition of water, which



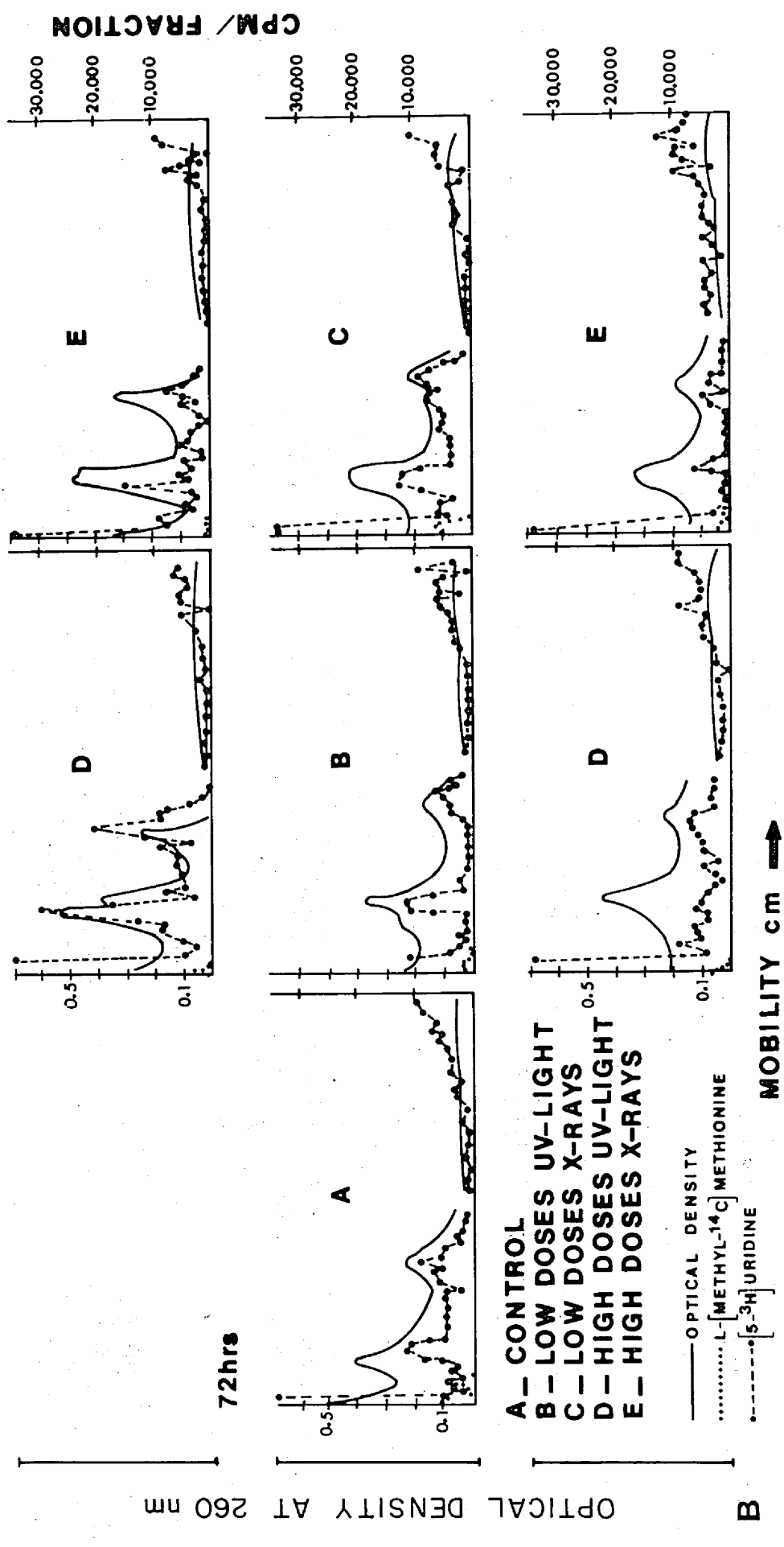


FIG. 3. A scanning pattern of RNA, which was separated on a tandem polyacrylamide gel. The tandem gel consisted of an upper part (3% polyacrylamide) and a lower part (7.5% polyacrylamide). The pollen were irradiated with low doses of uv light and X rays supplied at low dose rates, and with high doses of uv light and X rays supplied at high dose rates. The pollen grains germinated in the presence of 50 μCi of [5-^{3}H]uridine and 10μCi of L-[*methyl*-^{14}C] methionine for 16, 32, and 72 hr. After separation of the RNA on polyacrylamide gel the amount of incorporated label and the optical density of the gel section were measured.

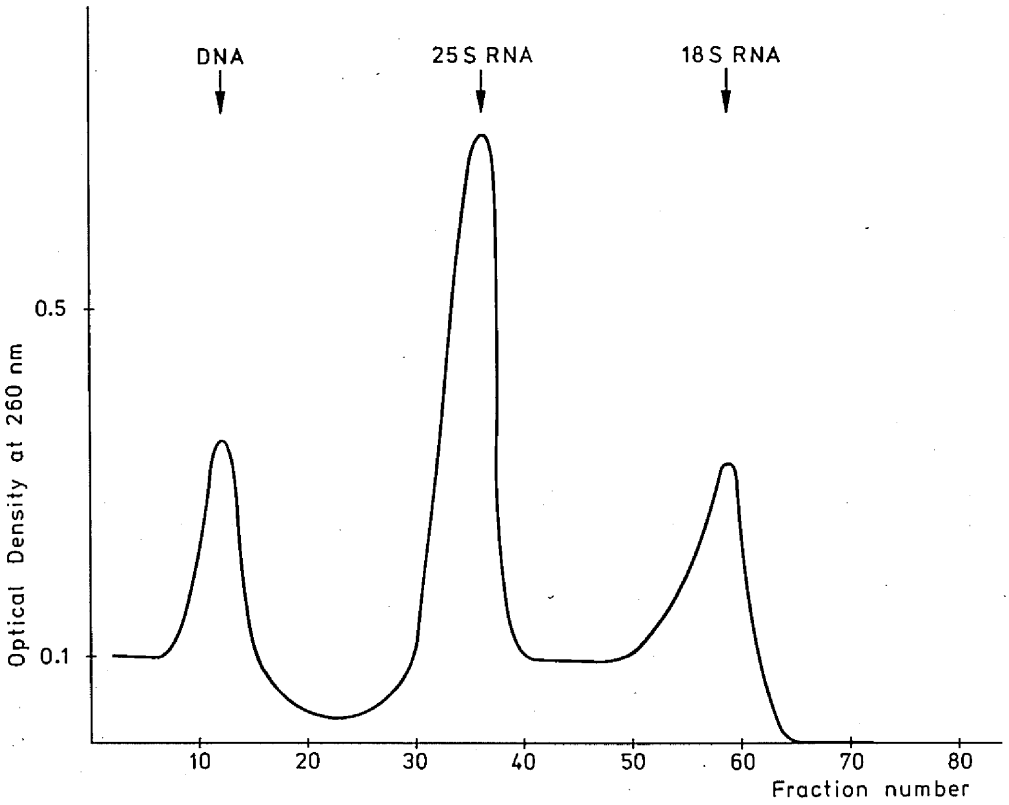


FIG. 4. Typical scanning pattern of high-molecular-weight RNA separated on 2.6% polyacrylamide gel.

is a very rapid process and which is completed within a few seconds. Germination ends with the growing of a pollen tube. It has been shown earlier that the pollen germination is accompanied by the initiation of protein synthesis (*12*, *13*, *18*, *19*). The inactive pollen grain is equipped with a ribosomal system which becomes active immediately after hydration. The control of the protein-synthesizing

TABLE II

The Effect of Irradiation on the Tube Length of 100 Grains and on the Incorporation of [5-^{3}H]Uridine into the rRNA

Time of incorporation (hr)	*Control*		*Low dose/low dose rate*				*High dose/high dose rate*			
			uv light		*X rays*		*uv light*		*X rays*	
	Tube length (μm)	*cpm (× 10³)*	*Tube length (μm)*	*cpm (× 10³)*	*Tube length (μm)*	*cpm (× 10³)*	*Tube length (μm)*	*cpm (× 10³)*	*Tube length (μm)*	*cpm (× 10³)*
2.5	0	1.1	0	3.0	0	4.2	0	5.3	0	1.5
5	0	4.9	0	6.6	0	5.9	0	4.0	0	3.6
16	366	5.7	959	6.1	527	11.6	376	11.5	204	5.0
24	328	10.4	374	—	537	20.4	271	22.3	280	14.9
32	806	12.6	1594	19.9	1265	19.3	711	—	395	14.1
40	2440	34.7	3623	26.1	3230	—	1248	19.7	1173	14.5
48	3835	34.6	4173	39.5	3805	32.7	2422	17.9	1274	18.9
56	2888	31.3	3942	—	4656	38.5	2163	24.3	1273	18.2
64	3789	23.3	5288	53.8	4432	47.7	3258	30.2	2118	29.2
72	4361	16.1	6090	28.0	8058	29.5	3572	19.3	1887	22.0

system includes the formation of polysomes and the presence of mRNA probably in a masked form (*12*). The fact that the samples incubated for 0 hr (to be more precise, these samples were incubated during the irradiation and the control samples were incubated for a few minutes) had a higher ribosome content than the ungerminated dry pollen, suggests that either the demasking process of the mRNA or the formation of the ribosomes is completed during the first minutes of incubation. It indicates also that in pine pollen no precompleted polysome system is available, but there is probably a system of polysomes rapidly building up during the first minutes of activation.

The content of polysomes, which was found in ungerminated pollen, is in agreement with the results of Mascarenhas and Bell (*18*), who found 38% of polysomes in *Tradescantia paludosa*, but it is in disagreement with the results of Linskens *et al.* (*12*), who did not find any polysomes in ungerminated *Petunia hybrida*. The possibility that the polysomes in ungerminated pollen grains are formed during the process of homogenization cannot be excluded.

A certain recovery of polysomes from the irradiation damage (*11*) could only be found in samples which were irradiated with high doses. This effect is certainly not caused by low-dose irradiation. Mascarenhas and Bell (*18*) found that in ungerminated pollen the polysomes are very large and they sediment in the pellet during sucrose density gradient centrifugation, while in the germinating pollen grain the polysomes are of smaller size. In pine pollen certain alterations could be observed by applying radiation. In the control pollen the polysomes were found to be relatively small oligomers, while in low-dose-irradiated pollen nearly all of the polysomes were heavy, and in high-dose-irradiated pollen about 80% of the polysomes were small oligomers. Kunico *et al.* (*11*) found that, following irradiation, the relative loss of heavy polysomes was greater than that of small oligomers. Experiments so far have not distinguished between the possibility that mRNA, which is not involved in polysomes in the ungerminated pollen grain, becomes newly associated with ribosomes and the possibility that mRNA, being already part of polysomal aggregate, becomes more fully saturated with ribosomes during the period of incubation. Which of these processes was influenced by irradiation is also not known.

It has already been found that pine pollen grown in suspension cultures pass through at least three phases of growth (*20*, *21*). In *Pinus silvestris* the first phase is between 12 and 32 hr, the second is between 32 and 48 hr, and the third phase is between 56 and 72 hr of tube development (*21*). The RNA required for the early growth phase (first phase) seems to be already present in the mature pollen grain. For the later phases (second and third phases) the synthesis of new RNA is required (*19*, *22*). It is well known that mostly the third phase can be stimulated by low doses of radiation (*21*). By the addition of radioactive substances the second phase can also be stimulated. In Table II it is seen that the irradiated samples were able to incorporate more labeled uridine into the tRNA than the control pollen—not only in a later, but also in the first growth phase. But how can the exogenously supplied uridine be incorporated into the RNA when in the first phase of tube growth no new RNA synthesis occurs? Nygaard (*20*) has studied the pathways of the nucleic acid synthesis of pine pollen. Exogenously

supplied ^{14}C-labeled nucleosides contribute significantly to the synthesis of nucleosides by auxiliary pathways. This indicates that pine pollen is able to re-utilize purine and pyrimidine nucleosides, derived from the degradation of reservoirs of nucleic acids. He could also demonstrate that nucleosides can be incorporated into the RNA by *de novo* pathways and via re-utilization pathways from breakdown products of nucleic acids.

The results presented in Table II indicate that the irradiation either stimulates the turnover of the nucleotide pool in the first phase, or it accelerates the process of breakdown of nucleic acids. In the second growth phase there is no difference in the incorporation of uridine into the RNA of irradiated and unirradiated pollen. In the third phase the tube growth stimulation is correlated with a probably enhanced RNA synthesis. This can occur, as Ehrenberg *et al.* (*3*) has suggested. Moreover, the enhanced uridine incorporation into the RNA may correspond with enhanced RNA synthesis following irradiation, as observed in other organisms (*5–10*).

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