THE EFFECT OF COSMIC RADIATION ON PLANT ACTIVITY

By

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A. A. Shakhov

The great successes of Soviet science and technology in the study of the cosmos and near-earth space have placed extremely important and interesting tasks in front of the biologists.

A living organism, for example a plant, placed in the cabin of a spaceship or of an interplanetary station for regeneration of the air and for producing food, is under conditions sharply differing from those found at the earth's surface. One of the most important factors of such extreme conditions characteristic of the cosmos is the radiation regime, since the region of the solar spectrum beyond the earth's atmosphere is considerably broader. Therefore, for example, the investigation of the photosynthesis of plants under a closed ecological environment in a cosmonaut's cabin acquires especial importance (Sisakyan, Gazenko, Genin, 1961).

In addition to the specific problems associated with the activity of organisms under cosmic radiation conditions, a study of the effect on plants of various regions of the spectrum (in particular the ultraviolet and infrared regions) is of wider interest since it is part of the new problem--the photoenergy of plants. Biological photoenergetics can be an important link in understanding a plant as an intimate intermediary between the sun and life on earth. In his time Timiryazev (1956) called the process of the assimilation of solar light by chlorophyll the "cosmic function" of the plant: the chloroplast, "This negligible, black lumplet of matter is the true link joining the majestic explosion of energy in our central heavenly body with all the diverse manifestations of life on the planet we inhabit" (p. 199).

The problems of the photoenergetics of plants has been actively worked out in recent years in the B. A. Keller Laboratory of Evolutionary and Ecological Physiology of the Institute of Plant Physiology, USSR Academy of Sciences, under transpolar conditions, wherein especial attention was devoted to infrared radiation. At the present time we have begun a study of the effect on plants of the short-wave (ultraviolet) region of the spectrum. It is natural that in the light of the problems of space biology such investigations can be carried out most effectively when the conditions are to a certain extent close to the radiation conditions of the cosmos. From this point of view, of considerable importance are the highlands of Eastern Pamir, which are at an altitude of 4000 to 5000 m where, owing to the exceptional dryness and transparency of the air, the solar radiation is distinguished by a great intensity and specific spectral distribution. These features make Pamir a unique natural laboratory, as it were, especially intended for investigations of this nature.

The spectral distribution of the solar radiation reaching the earth's surface substantially depends on the thickness and properties of the air mass absorbing and scattering the radiation passing through it. The effect of the atmospheric layer is most strongly rendered on the ultraviolet region of the spectrum, since the absorption is greatest for these rays. The spectral distribution of radiation in the UV-region is decisively influenced by the ozone content in the air which absorbs all radiation with a wavelength of about 290 mμ. In addition to the ozone, the intensity of ultraviolet in the region from about 290 to about 400 mμ is also weakened by the air, water vapor, dust, and smoke which are usually present in the lower layers of the atmosphere. The effect of these factors results in the intensity of the UV-radiation being strongly dependent on the thickness of the air mass over the observation point, i.e., on the height above sea level and the position of the sun above the horizon.

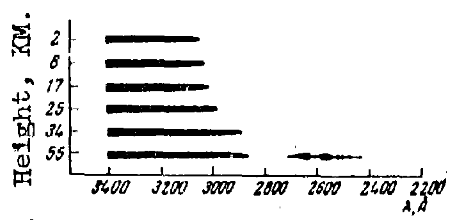

Fig. 1. Spectrograms obtained during flight of rocket (Kondrat'yev, 1954).

Figure 1 shows the short-wave regions of the spectrum of solar radiation obtained at different heights by means of rocket-borne instruments. As we see with respect to the radiation conditions, typical "cosmic conditions" characterizing the manifestation of hard radiation with a wavelength to 240 mμ already begin from heights of about 55 km.

Figure 2 shows the supposed distribution of energy in the X-ray and UV-spectra of the sun at the boundary of the earth's atmosphere (Yager, 1957). It follows from the curve that in the short-wave region the solar spectrum extends to the region of soft X-rays.

The total energy of the short-wave radiation of the sun (ultraviolet and X-ray) is not great--it is tens of thousands of times less than the energy of visible light. However, short-wave radiation by virtue of its extremely high activity ionizes air molecules, and the part of the radiation reaching the earth has a diverse biological action.

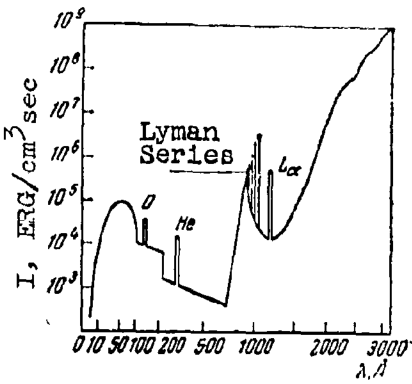

Fig. 2. Supposed energy distribution in the ultraviolet and X-ray spectrum of the sun.

According to Malyshev (1957), the intensity of direct solar radiation increases by 6% and of the ultra-violet radiation by 15% with a one kilometer ascent in the Caucasus. Stanko and others (1958) established that in the mountains of the Zailiyskiy Altay, the direct solar radiation at an altitude of 2980 m increased at noon by 20%, UV-radiation by 55%, IR-radiation by 24% in comparison with radiation at an altitude of 780 m. Referring to the data in the literature, Stanko noted that many high-mountain plants have a relative resistance to short UV-rays. Petrishin and Landau (1953) consider that high in the mountains the specific features of insolation and the richness of solar light in blue-violet and especially in long-wave UV-rays play a very considerable, if not a decisive role in the change of the morphologic, functional, and biochemical characteristics of plants.

In 1958, Gurskiy, Ostapovich, and Sokolov (1961) began to study the radiation conditions in Pamir. At a height of 3000 m above sea level they detected a high radiation dose in the region of ultra-violet "B", 500 μw/cm^2 and ultra-violet "A", 1200 μw/cm^2. Taking account such high intensity of radiation, the authors suggested that photo-reactivation can take place in the mountains. The latter, as is known, is the restoration of ultraviolet lesions with light of longer wave length. In order to study this problem, Gurskiy et al. (1961) set up experiments where plants were cultivated in natural light and with illumination by SVDSh-250-3 quartz-mercury lamps whose spectrum has ultraviolet "C".

The calculations of the authors showed that a quartz-mercury lamp at a distance of 1 m increases (in the region of ultraviolet "B" during the course of a day) the radiation dose by fourfold in comparison with the natural. In spite of the greater doses of UV, not a single plant died, according to the authors' assertions.

Taking account our further investigations of the effect of UV-radiation on plants in Pamir (Shakhov, Khazanov, Stanko, and Ostapovich, 1962), which were partly carried out together with the Pamir Botanical Garden (L.F. Ostapovich, et al.), it was of interest to approach plant activity in high-mountain regions from the space biology point of view. The conditions of UV-radiation at heights of 4000 to 5000 m or with irradiation by the ultraviolet "C" of quartz-mercury lamps to a certain extent approach the radiation conditions in the upper atmospheric layers and can be called "quasi-cosmic."

But at first it is necessary to dwell on the principles determining the character of our earlier investigations into photo-energetism of plants under conditions of diurnal radiation in the Far North.

Physiologists are accustomed to looking upon plant activity only through a narrow spectral slit--the visible light (400 to 720 mμ). Such a "narrow viewing" is very jealously kept by a number of specialists. In defense of the notion that only a narrow spectral region (visible light) is important for plants, the reasons usually cited are that the near-infrared and ultraviolet regions bounding the visible light will not be important in the physiological characteristics of a plant. Therefore, the concept of a physiological or photosynthetic radiation (400 to 720 mμ) was put forward. It is considered that in the region of near-infrared rays the plant is transparent and they cannot render a substantial effect on the processes taking place in the plant. The short-wave ultraviolet rays have acquired the reputation of being harmful to an organism. But this concept, which is only true for ultraviolet "C", is sometimes extended to ultraviolet "A" and "B", which borders on visible light. The possibility of a positive effect of intense UV-radiation on photosynthesis of plants is disputed or negated.

As a result of underestimating the role of the spectral boundary regions (IR and UV) in the plant activity many important phenomena have escaped us. Due to the physico-technical difficulties of studying the indicated boundary regions, an almost "unknown world" slipped out of the scope of the biologists: the physicochemical changes in plants when irradiated with IR- and UV-rays.

If we take as a whole the extensive problem of the relation between a vegetable organism and radiant energy, then here we can presently say that we see much less than we don't see.

As the studies of our laboratory and of a number of other Soviet and foreign investigators have shown in recent years, plants proved to be more "seeing" than we are accustomed to consider them. They actively perceive radiant energy of spectral regions bordering with light with a high physiological effect, which increases their activity and resistance.

By moving back the spectral slit to both sides of the visible light, thus expanding the scope of our view, we make it possible to study the activity of plants in a wider energy range. It is just this that aroused us in recent years to focus our attention in our investigation on a study of the photoenergy of plants. For this purpose we examined not only the significance of radiant energy of the boundary regions of the optical spectrum per se. We were also interested in the effect obtained from the influence on plants of the energy of the boundary regions together with the spectral regions of visible light. Important in this connection are the regularities of the spectral mutual complementation, spectral mutual exclusion or counteraction; they lay at the foundation of the red-infrared effect, the red-blue effect, the Danilov-Emerson effect, photoadaptation, photoreactivation, and other phenomena.

The ability to pass on resistant offspring is important in the reaction of a vegetable organism to new radiation conditions. If the adaptability of an organism to new radiation, e.g., "quasi-cosmic" conditions increases, it is necessary to know by what means the radiation resistances should be increased.

According to the data of our laboratory, the adaptation of plants through the generations (reproductions) to light conditions, i.e., photo adaptation, is well expressed under conditions of natural diurnal illumination in the Far North. As the plants in the 3rd to 5th generations become adapted, the absorption of radiant energy by the leaves increases. Generally during the summer in the Transpolar region (Kola Peninsula) at a low soil and air temperature, the plants actively absorb radiant energy, especially the near-infrared radiation. The ability of plants to absorb attenuated solar radiation during the light night hours is the cause of diurnal photosynthesis.

Irradiation of plants in the Transpolar region by concentrated solar light with a power of 5 to 10 suns causes burns which pass away in several days probably as a result of the processes of general photoreactivation. Plants irradiated with concentrated light, according to the determinations of our associate S. A. Stanko, had more pigments and more fully absorbed radiant energy. The effect of individual factors of "quasi-cosmic" radiation conditions can imitate the action of concentrated solar light of various intensities and durations on plants.

We suggest that the briefly examined photoenergetic approach in conjunction with an investigation of the influence of ionizing radiation will enable us to explain the action of various "quasi-cosmic" conditions on a plant organism. This should be taken into account when developing quasi-cosmic physiology and biophysics of plants, which are important divisions of Soviet space biology.

The investigation which we carried out in Eastern Pamir (Chechekty, bio-station, 3860 m above sea level) and also with A.V. Gurskiy, L. F. Ostapovich, and Yu. L. Sokolov (Khorog, botanical garden, 2340 m above sea level) confirmed, for high-mountain conditions, the photoadaptation of plants to new radiation conditions which had been detected earlier in the Transpolar region. These investigations deepened the concepts concerning the photoreactivation observed by the named authors and us in Pamir with supplementary irradiation of the plants with quartz-mercury lamps.

Qualitative investigations by Gurskiy and co-workers actually indicate the presence of photoreactivation protecting the plants from damage by large doses of short-wave ultraviolet. At the same time, during adaptation of the plants to the described experimental radiation conditions, their activity as well as the structure of the leaf apparatus underwent profound changes. As an illustration of this we can cite the data which we obtained along with B. M. Golubkova on the chloroplasts of certain wild and cultivated plants inhabiting various heights of Pamir. The plants studied were under both a natural and the above-described "quasi-cosmic" radiation conditions.

In the leaves of Primula (Primula turkestanica (Rgl) White, Fig. 3a) and Swertia (Swertia marginata Schrenk, Fig. 4b) inhabiting the nival belt at a height of 4750 m, the chloroplasts were round, small, compact, with grana rather large with respect to the size of the chloroplasts. The stroma of the chloroplasts contain very small osmiophilic granules. This gives us grounds to make a preliminary (before checking other plants) conclusion that during the historical adaptation of the plants to the temperature-light conditions of the Pamir highlands, small dense chloroplats with extremely minute osmiophilic granules were formed in them. Chloroplasts of such a structure ensure normal photosynthesis in the plants under high-mountain conditions.

Additional irradiation of the agricultural plants with ultraviolet of quartz-mercury lamps (botanical garden, 2340 m above sea level) caused a noticeable change in the submicroscopic structure of the chloroplasts in spite of the evident processes of photoreactivation.

Under natural growing conditions at a height of 2340 m beets had oval chloroplasts of average density with small osmiophilic granules arranged as clusters in the stroma of the plastids (Fig. 4a). Under the effect of UV-irradiation of beets during the growing season, its chloroplasts became more compact, multilayered, somewhat larger, with increased osmiophilic granules (Fig. 4b).

Small round chloroplasts with small grana and osmiophilic granules (Fig. 5a) developed in the leaves of radishes under natural radiation at the same, more than 2-km height. Additional irradiation by artificial ultraviolet severely changed the chloroplast. It becomes considerably larger, looser, with very large osmiophilic granules, which are equal to or larger than the grana (Fig. 5b). Judging by the considerable size of the latter, we can consider that UV-irradiation affects lipid metabolism of the chloroplasts, the lipid bond with the proteins. And since the chloroplasts usually contain up to 20 to 30% lipids, the change noted in their condition should be considered as very important in the metabolism of the chloroplasts. The presence of numerous free lipids in the stroma of the chloroplasts can affect their photoenergetic properties.

Therefore, in spite of the clearly evident photoreactivation, UV-irradiation which approaches cosmic irradiation in intensity, causes deviations in the chloroplast structure, especially in radishes, from the control plants. However, these deviations cannot be considered as pathological changes since they do not disrupt the function of the chloroplasts; the main feature of the submicroscopic structure of chloroplasts, the presence of grana, also is not disturbed. Plants with irradiated chloroplasts, as our investigations showed, contain more chlorophyll *a* and carotenoids (Shakhov, Khazanov, Stanko, Ostapovich, 1962) and have a sufficiently high photosynthetic rate. This indicates the normal operation of the photosynthetic apparatus and, consequently, a high activity of the plant organism.

At the same time it is known that, although the chloroplasts have a relatively high radioresistance (Kuzin and Shabadash, 1959), UV-rays with a wavelength less then 300 mμ usually severely suppress photosynthesis. As Bell and Merinov (1961) suggest, the action of UV-rays is partially localized in the chloroplasts, and the inhibition of photosynthesis in Chlorella which they observed is probably caused by the interaction between UV-quanta and substances of a nucleic nature contained in the chloroplasts.

Therefore, our data on the high rate of photosynthesis with simultaneous illumination of the plants during the daylight hours of the growing period with ultraviolet and long-wave rays also apparently indicate the important role of photoreactivation.

The structural changes of the photosynthetic apparatus, especially the above-mentioned higher content of pigments in the chloroplasts, must affect the ability of the plants to absorb energy of the radiant flux. As a result of the action spectrum of chlorophyll, we usually consider that in the absorption spectrum of a leaf there is a large yellow-green "gap", and in the infrared region the leaves are completely transparent. In our investigations of many years in the Transpolar region it was shown by means of photointegrating instruments that in the Far North the yellow-green absorption maximum for a leaf is not great, and that near-infrared radiation is actively absorbed by a leaf (Shakhov, Stanko, Khazanov, Yakolev, 1959). It turned out that this is also characteristic for high-mountain plants. In our experiments carried out in Pamir together with V. S. Khazan, S. A. Stanko, and D. M. Shishov on a photointegrating instrument with interference filters, we observed that different plants of Pamir quite actively absorb radiant energy throughout the entire spectrum, from the ultraviolet to the infrared regions. For instance, a high absorption of green (78 to 85%), yellow (76 to 86%), and near infrared rays (15 to 25%) is noted in ligneous frutescent plants.

Our previous investigations also established that as plants adapt through the generations to temperature and light conditions of highlands, the ability to absorb energy, especially of green and infrared rays, is increased in leaves. This is nicely illustrated by the new data on Pallidium 4 barley (Table 2).

However, such photoadaptation over the generations was not distinctly determined in the first years of adaptation in all plants which we studied. For Parallelum barley the absorption of radiant energy by leaves of plants of the fifth high-mountain reproduction (generation) in comparison with the first generation is expressed weakly, except for the region of infrared radiation. In plants more labile with respect to variations, an intensification of absorption of solar energy is distinctly seen already in the first reproduction in comparison with the original, i.e., the plants cultivated for the first time in mountains. In subsequent generations this process proceeds more slowly. It is possible that the Parallelum variety (Table 2) belongs to just that group of plants. In other plants the ability of leaves to absorb light during adaptation continues to increase in any case to the 7th generation, which is shown in the work fulfilled together with Khazan, Stanko, and Ostapovich (1962).

Therefore, at a height of 4000 m under conditions of natural UV-irradiation, the imported agricultural plants when resown from year to year adapt to the unique radiation conditions. Thanks to photoadaptation the plants can produce continuously more resistant offspring having higher photoabsorbability.

Additional irradiation with ultraviolet radiation from quartz-mercury lamps also increases the photoabsorbability of leaves (Table 3).

As a result of a two-three month cultivation of plants under "quasi-cosmic" UV-radiation conditions, the plant organism acquires properties making it possible to reflect and transmit radiant energy. Under the effect of high UV-irradiation, the plants can additionally utilize the energy of the green and infrared rays, a large absorption of which is considered dangerous due to the possibility of over-heating the plant. However, under certain conditions of the temperature and radiation conditions, a potential for assimilating a large amount of radiant energy is created in the leaf as the optical system of the plant. As a consequence of such a large "energy capacity" of the leaf the plant can, without dying, be exposed to irradiation of high-energy UV-quanta. Some portion of the absorbed energy of a certain spectral region is consumed for the photoreactivation processes.

The phenomenon of photoreactivation, which can be of space-biological interest according to the concepts being developed here, is almost unstudied in higher plants. Photoreactivation has been studied mainly on viruses, bacteriophages, bacteria, and protozoans. Weis (1952) briefly reported on photoreactivation of growth in unicellular alga Chlamydomonas. Deactivation by ultraviolet and the restoration of the activity of the growth process and the motility of the green alga Platymonas was throughly investigated by Halldal (1961). According to the data of Lyman, Epstein, and Schiff (1961) irradiation of Euglena gracilis with nonlethal doses of UV prevented the formation of chloroplasts in offspring; inhibition of the formation of chloroplasts is reduced by visible light, which causes photoreactivation.

Returning to our electron microscope pictures of the chloroplasts, we note that under "quasi-cosmic" conditions of UV-irradiation there is no complete reversal or absolute reactivation of the photosynthetic apparatus. In leaves of irradiated plants, in spite of the strongly expressed ability for a higher absorption of light, the descendents of the irradiated chloroplasts do not return to the conditions of the chloroplasts in unirradiated (control) plants. Undoubtedly, with the high photoabsorbability of irradiated plants, photoreactivation is expressed sufficiently strongly in order to increase the resistance of the plant to UV-radiation. In this case restoration of the damaged plants apparently leads during development to the creation of new cells and new chloroplasts, which are able to function under "quasi-cosmic" radiation conditions, thus ensuring a high plant activity. It seems to us that with an intense occurrence of the photoreactivation process, i.e., in the presence of a superposed spectral distribution of radiation, the plants acquire the characteristic resistance to UV-rays. Owing to this they can apparently exist for some time under cosmic radiation conditions (for example, in the cabin of a spaceship) without protective filters absorbing the short-wave portions of the spectrum.

Conclusions

1. By combining natural radiation with radiation from artificial sources of ultraviolet, radiation conditions close to those of space can be created in Eastern Pamir.

2. The phenomenon of photoadaptation through the generations and also photoreactivation induced by visible light is distinctly expressed in plants found under such "quasi-cosmic" radiation conditions. These phenomena can be of considerable space-biological importance since plants acquire the ability to withstand, without dying, considerable doses of UV-radiation with high-energy quanta. Here their activity and photosynthesis proceed normally or in certain species are slightly depressed.

3. Under the effect of UV-irradiation, plants develop the ability to utilize more fully the energy of visible light, expecially in the region of green and near-infrared rays.

4. UV-irradiation changes the submicroscopic structure of the chloroplasts and also the lipid metabolism taking place in them.

TABLE 1

Reflection, Transmission and Absorption of Radiant Energy by Leaves of Ligneous-Frutescent Species (Pamir Botanical Gardens, 2340 m Above Sea Level July 1961)

Wave-length, mμ	Syringa Josikaea			Ailanthus altissima			Aesculus hippocastanum			Tilia macrofolia		
	reflection	transmission	absorption	reflection	transmission	absorption	reflection	transmission	absorption	reflection	transmission	absorption
400	2,6	1,1	96,3	3,3	0,6	96,1	2,8	1,8	95,4	3,4	2,0	94,9
433	2,5	1,7	95,8	3,8	1,1	95,1	5,2	1,5	93,3	2,7	2,7	94,6
548	6,3	8,2	85,5	9,4	12,5	78,1	10,3	11,3	78,4	9,6	12,5	77,9
578	8,5	5,5	86,0	5,8	7,8	76,4	7,7	5,4	86,9	6,4	8,8	84,8
621	5,0	3,6	91,4	3,3	3,8	92,9	5,8	5,8	88,4	3,8	7,5	88,7
645	4,2	0,9	94,9	3,5	4,7	91,8	4,5	4,8	90,7	6,4	5,7	87,9
680	4,7	3,2	92,1	2,7	1,2	96,1	3,3	2,4	94,3	4,0	5,4	[illegible]
698	6,9	5,9	87,2	4,4	4,1	91,5	7,4	6,8	85,8	6,1	6,2	87,7
730	34,2	26,4	39,4	34,3	37,0	28,7	30,0	30,0	40,0	27,7	30,0	42,3
800	46,0	33,8	20,2	43,8	41,5	14,9	41,2	34,6	25,2	42,7	41,0	16,3

TABLE 2

Reflection, Transmission and Absorption of Radiant Energy by Barley Leaves Over the Generations (Chechekty, 3860 m Above Sea Level July, 1961)

Wave-length, mμ	Pallidum 4						Parallelum					
	1st reproduction			7th reproduction			1st reproduction			5th reproduction		
	reflection	transmission	absorption	reflection	transmission	absorption	reflection	transmission	absorption	reflection	transmission	absorption
400	1,5	0,2	98,3	3,0	0,3	96,7	2,8	0,0	97,2	2,4	0,1	97,5
433	2,7	3 3	94,0	5,5	0,3	94,2	4,9	0,3	94,8	4,1	0,3	95,6
548	14.0	10,5	75,5	9,2	8,8	82,0	11,4	12,0	76,6	9,5	12,0	78,5
578	11,2	7,5	81,3	9,3	5,1	85,6	8,5	8,3	83,2	7,1	11,8	81,1
621	8,1	4,5	87,4	6,7	3,1	90,2	6,8	5,7	87,5	5,5	8,0	86,5
645	6,2	4,0	89,8	5 8	4,0	90,2	5,9	5,2	88,9	3,9	7,0	89,1
660	6,5	2,2	91,3	4,6	1,3	95,1	5,5	2,1	92,4	3,4	3,8	92,8
698	9,0	7,2	83,8	7,8	4,2	88,0	7,4	5,9	86,7	5,5	8,0	86,5
730	32 8	29,0	38,2	28,7	28,0	43,3	32,5	25,8	41,7	22,6	34,6	42,8
860	44,1	48,5	7,4	35,8	41,5	22,7	38,9	43,0	18,1	31,2	44,0	24,8

TABLE 3

Reflection, Transmission and Absorption of Radiant Energy by Beet Leaves with Additional UV-Irradiation at 2340 m Above Sea Level

wave-length, mμ	control plant			Irradiated plant		
	r*	t*	a*	r*	t*	a*
400	4,8	0,6	94,6	4,8	0,2	95,0
433	4,8	1,4	93,8	5,1	0,3	94,6
548	17,9	14,0	68,1	10,0	8,3	81,7
578	11,0	7,8	81,2	8,9	5,4	85,7
621	8,5	4,8	86,7	6,4	3,9	89,7
645	8,0	3,3	88,7	6,5	1,6	91,9
660	7,5	1,4	91,1	6,0	0,8	93,2
698	10,1	4,2	85,7	7,7	3,3	89,0
730	33,3	29,8	36,9	28,7	28,2	43,1
860	47,5	43,0	10,0	43,0	39,0	18,0

* r= reflection t= transmission a= absorption

Fig. 3. Chloroplasts of plants cultivated at 4750 m above sea level. a) Primula turkestanica, 7000X; b) Swertia marginata, 7000X.

Fig. 4. Chloroplasts of beets grown at 2340 m above sea level from plants: a) unirradiated by additional UV, 7000X; b) irradiated with additional UV from quartz-mercury lamps, 7000X.

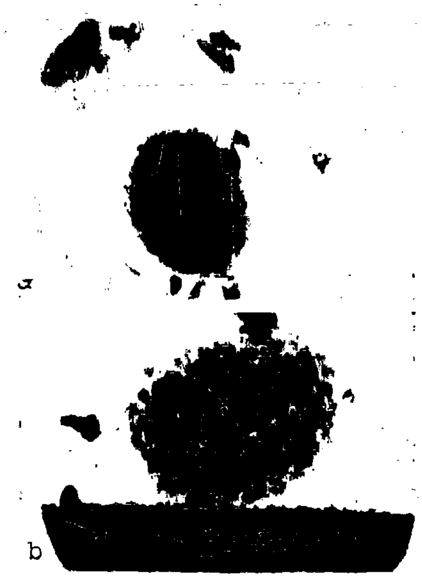

Fig. 5. Chloroplasts of radish cultivated at 2340 m above sea level from plants: a) unirradiated with additional UV, 7000X; b) irradiated with additional UV from quartz-mercury lamps, 7000X.

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