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Studies of the Functional Activity of Mitochondria and Cell Ultrastructure of the Coleoptile in Wheat, *Agropyron* and Their Hybrids (Incomplete Amphidiploids) during Decreasing Temperature

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Summary. The structure of the mitochondria and endoplasmic reticulum in the coleoptile of plants (*Triticum aestivum* var. *Lutescens 329*, *Agropyron glaucum*, *Triticum* × *Agropyron* 56-chromosome hybrids, incomplete amphidiploids, TAH, containing 42 wheat chromosomes and 14 chromosomes of genomes D or X of *Agropyron*), which differ in winterhardiness, was studied after exposure to 0° and −4 °C for periods varying from 10 min to 4 days. The functional activity of mitochondria isolated from 3 day old seedlings was also investigated in these cereals. The cells of *Triticum* and *Agropyron* seedlings grown at 23 °C were shown to differ in mitochondrial structure. In the cells of TAH both kinds of mitochondria were found.

On day 4 of exposure to −4 °C, the mitochondria of *Agropyron* cells were not changed; the endoplasmic reticulum formed complex closed cavities. Under similar conditions most wheat mitochondria were destroyed and in the rest no cristae were observed.

Morphometric analysis indicated that the volume of such mitochondria increases by two times, while the surface area of the internal membranes and cristae decreases by 1.54 times. In such cells, the endoplasmic reticulum is represented only by membranes of the smooth type . The structure of the mitochondria and endoplasmic reticulum in the seedling cells of TAH 829, which is more like *Agropyron* in winterhardiness, is similar to that of *Agropyron* cells; in hybrid 822 (more like wheat containing the D genome), changes arise resembling those observed in wheat. The existence of different types of mitochondria in seedling cells of TAH is especially distinct at low temperatures.

The mitochondria of the cereals studied differ in biochemical activity after low temperature treatment (0° and −4 °C). Phosphorylative and oxidative activity of mitochondria of the winterhardy forms (*Agropyron glaucum*, TAH 829) decreases just after the beginning of low temperature treatment. At the same time, the morphology of the mitochondria undergoes reversible changes. The mitochondria of cold-susceptible forms of wintering plants (*Triticum aestivum*, TAH 822) do not conform to this pattern. Under long-term low temperature treatment they display irreversibly damaged mitochondria. It is suggested that the winterhardy forms have high adaptability connected with a rapid protective response of the cell mitochondria and endoplasmic reticulum. This adaptability is regulated by nuclear genes: TAH have different mitochondria in the coleoptile cells; if genome X of *Agropyron* is present, which TAH derives from the male parent, the related mitochondria become more resistant to low temperature treatment.

Much work has been centreed on mitochondria and the endoplasmic reticulum of plants in normal and modified environmental conditions (Semikhatova and Buschuyeva, 1963; Maschansky, Semikhatova and Buschuyeva, 1965; Dexheimer, 1966; Andreeva and Grineva, 1970; Udovenko, Maschansky and Sinitzkaya, 1970; Krasavtzev and Tutkevich, 1970 1971; Kwiatkowska, 1970a, b; Petrovskaya-Baranova, 1971).

It is the general consensus that changes in the structure of mitochondria and reticulum are not specific responses to different treatments, but rather are reflections of the functional state of the organelles (Roodyn and Wilkie, 1968). On the other hand, the impression is gained that mitochondrial cristae of differentiated cells differ in their structure (Carithers and Green, 1972) and that cells at different stages of development vary in mitochondrial inclusions (Cland, 1967; Newcomb, Steer, Hepler and Wergin, 1968; Jonson, 1971). However, these points of view are not contradictory inasmuch as the function of the mitochondria is conditioned by the functional state of the cell, which may be influenced by the degree of differentiation and developmental stage of the organism. The functional state of the cell is determined ultimately by the activity of nuclear genes. It may be suggested that in organisms with different genotypes in conditions when oxidative phosphorylation, one of the main mitochondrial functions, is inactivated, these organelles exhibit a wide pattern of changes.

Studies on the physiological and biochemical causes of winterhardiness in cereals have shown that under Novosibirsk conditions, with temperature fluctuations in the tillering nodes from 0—10 °C, the winterhardiness of rye and *Agropyron* is maintained by the high level of oxidative phosphorylation in the mitochondria of tillering node cells.

Experiments *in vitro* and *in vivo* have indicated that the functional activity of the mitochondria of cells in the tillering nodes of cereals differing in winterhardiness (*Triticum aestivum*, *Agropyron glau-*

cum) and of their hybrids — incomplete amphidiploids with different genome composition — varies and is conditioned by the plant's genotype (Borzkovskaya, Usova and Safonova, 1971).

This paper presents an attempt to elucidate the structure of the mitochondria and of the endoplasmic reticulum of coleoptile cells in these cereals. This study also deals with the functional activity of mitochondria under the action of low temperature on these cereals, which differ in a number of characters, including winterhardiness.

Material and Methods

Cell ultrastructure was studied in the coleoptile cells of wheat (*Tr. aestivum*, var. Lutescens 329), *Agropyron glaucum* and 56-chromosome wheat-*Agropyron* hybrids. The functional activity of their mitochondria was investigated during times of exposure from 10 min to 4 days in a refrigerator at temperatures from 0—4 °C.

The 56-chromosome *Triticum-Agropyron* hybrids (TAH) are incomplete amphidiploids containing 42 wheat and 14 Agropyron chromosomes. The 42-chromosome wheat *Triticum aestivum* (var. Lutescens 329), the maternal form of the TAH, has the following genome composition — $A_tA_tB_tB_tD_tD_t$; the paternal form of this hybrid is *Agropyron glaucum*, which has the genome composition $B_AB_AD_AD_AX_AX_A$ (Vakar, 1935). The 56-chromosome wheat-*Agropyron* hybrids used in this study differed in genome composition: TAH 822 is a hybrid of wheat-intermediate type, containing the entire common wheat karyotype to which is added a D genome of *Agropyron* partially homologous with the D genome of wheat ($A_tA_tB_tB_tD_tD_tD_AD_A$); TAH 829 is an intermediate hybrid with a specific *Agropyron* X genome added ($A_tA_tB_tB_tD_tD_tX_AX_A$) (Yatchevskaya and Laptchenko, 1966). These TAH forms differ in phenotype (TAH 822 is closer to wheat, TAH 829 is more like *Agropyron*) as well as in winterhardiness (TAH 822 is a moderately winterhardy form, TAH 829 is a highly winterhardy form).

In control experiments the seeds were grown at +23 °C. The tops of three days old coleoptiles were cut off, the walls of the coleoptiles were fixed in 6% glutaraldehyde and treated subsequently with 2% OsO_4; in both cases phosphate buffer was used at pH 6.8. Dehydration and embedding in araldite were carried out according to the standard method. Ultrathin sections were obtained with the ultratome Reichert and studied using the electron microscope JEM-7. Quantitative data on the volume and surface area of the mitochondrial internal membranes and cristae, and the surface area of the membranes of the granular and smooth endoplasmic reticulum were obtained by means of morphometric analysis (Weibel, 1969).

The isolation of the mitochondria from the seedlings was performed by the method of Heber et al. (1964) with the modifications we have introduced (Borzkovskaya, Usova and Safonova, 1971). Mitochondrial respiration was determined manometrically in the Warburg apparatus for 15 min at +20 °C. The inorganic phosphorus content was measured according to Fisce—Subbarow. The protein content of the mitochondria was estimated by the method of Lowry.

Results

In similar growth conditions at +23 °C the structural differences between the mitochondria in wheat and *Agropyron* coleoptile cells are clear-cut. Wheat mitochondria have long narrow cristae (fig. 1a), *Agropyron* mitochondrial cristae are characterized by mace-like structures (fig. 1b). In hybrid coleoptile cells, both types of mitochondria are observed. However, in hybrid 822, mitochondria structurally similar to the wheat type (fig. 1c) are more common, whereas cells of hybrid 829 contain more mitochondria similar to those of *Agropyron* (fig. 1d). The endoplasmic reticulum is represented by membranes of the granular and smooth types in the coleoptile cells of all the plants analysed. The cytoplasm of all the cells includes a large number of free ribosomes arranged in polysomes (fig. 1 abcd). In the coleoptile cells of wheat, the mitochondria start to swell 6 hr after treatment at 0 °C. Prolonged exposure significantly affects the structure of these organelles: on the fourth day of exposure to —4 °C some mitochondria are disintegrated, others lose their circular shape and cristae; the endoplasmic reticulum is represented mainly by dilated cavities limited by membranes lacking ribosomes (fig. 2a).

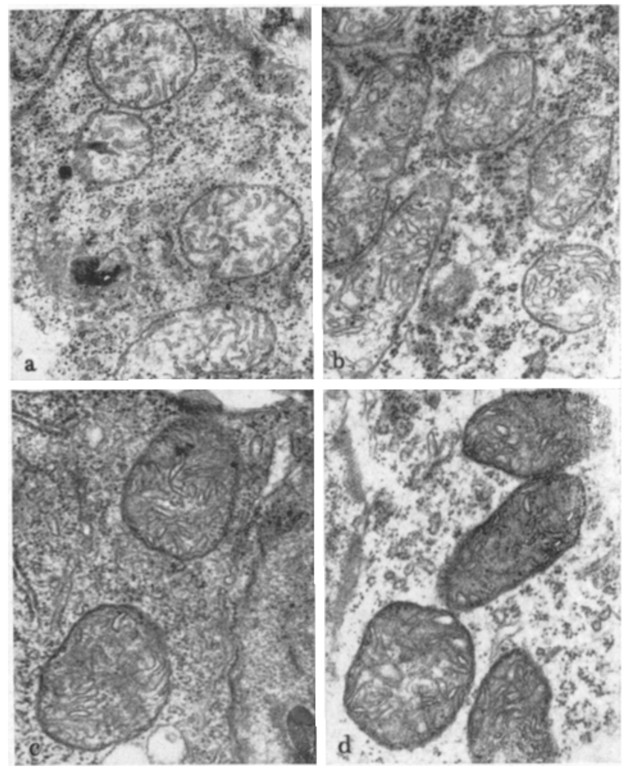

Fig. 1. Mitochondria of coleoptile cells at +23 °C:
a) wheat with long narrow cristae, × 30,000;
b) *A. glaucum* with widened mace-like cristae, × 30,000;
c) TAH 822, mitochondria similar to wheat, × 30,000;
d) TAH 829, mitochondria similar to *Agropyron*, × 30,000

During low temperature treatment, changes in mitochondrial structure in the cells of *Agropyron* seedlings arise earlier than in wheat cells under similar conditions. After 20 min at 0 °C, *Agropyron* mitochondria are swollen, but soon regain their normal appearance. After 4 days at —4 °C the mitochondria retain their typical structure, differing,

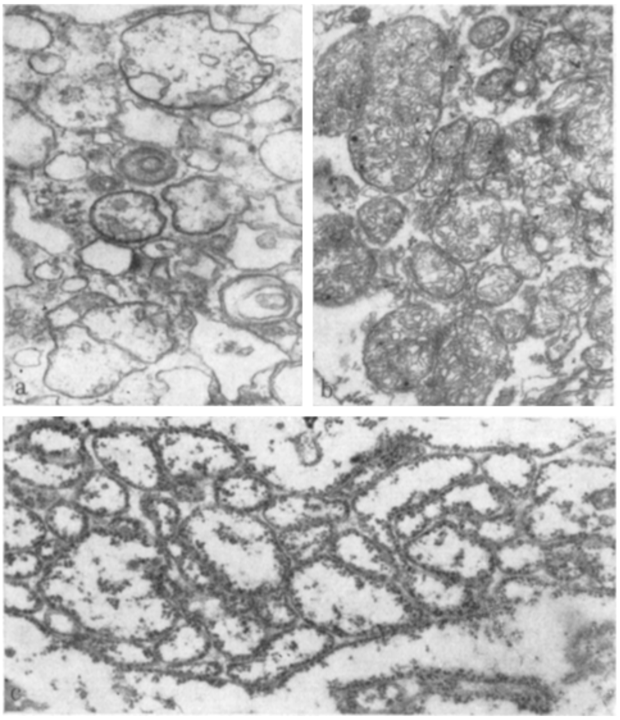

Fig. 2. Mitochondria of coleoptile cells after 4 days of exposure to −4 °C:
a) wheat, no cristae in the mitochondria, × 30,000;
b) *A. glaucum*, slightly swollen cristae, × 30,000;
c) granular endoplasmic reticulum forms complex closed widened cavities, × 50,000

in some cases, in having somewhat larger spacings between the cristae (fig. 2b). The granular endoplasmic reticulum undergoes profound changes and forms closed dilated cavities filled with branching membranes with ribosomes attached to them (fig 2c).

The mean mitochondrial volume does not change in the coleoptile cells of *Agropyron* after 4 days of exposure to −4 °C, while in wheat it increases by more than twice. The most reliable parameter of the functional activity of mitochondria is the surface area of the internal membranes and cristae; this index does not change greatly in the cells of *Agropyron* seedlings, whereas in wheat seedlings it decreases by 1.54 times (fig. 3).

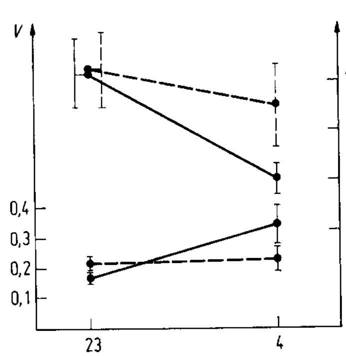

Fig. 3. Mean volume of mitochondria — V (mc³) — and surface area of its internal membranes and cristae — S (mc²) at +23 C and 4 days after exposure to −4 °C. Coleoptile cells:
a) wheat (———);
b) *Agropyron* (— — —)

In hybrid 829, the coleoptile of which is very similar to that of *Agropyron* in winterhardiness, the mitochondria remain unchanged after 4 days of exposure to −4 °C (fig. 4a); the membranes of its granular endoplasmic reticulum, as in *Agropyron* cells, are arranged in convoluted structures forming concentric patterns (fig. 4b). In the seedling cells of the other hybrid (822), the mitochondria have a light matrix and contain very few cristae in these conditions (fig. 4c). As well as the dilated cavities of the endoplasmic reticulum, convoluted concentric patterns of the granular reticulum may be observed (fig. 4d). The heterogeneous structure of cristae in the mitochondrial populations of the coleoptile cells of hybrids, which we have observed at room temperature, was also noted after exposure to temperatures from 0 °C to −4 °C for different periods of time. Thus, after four days of low temperature (−4 °C) treatment, mitochondria with normal and modified structures may be distinguished (fig. 4e).

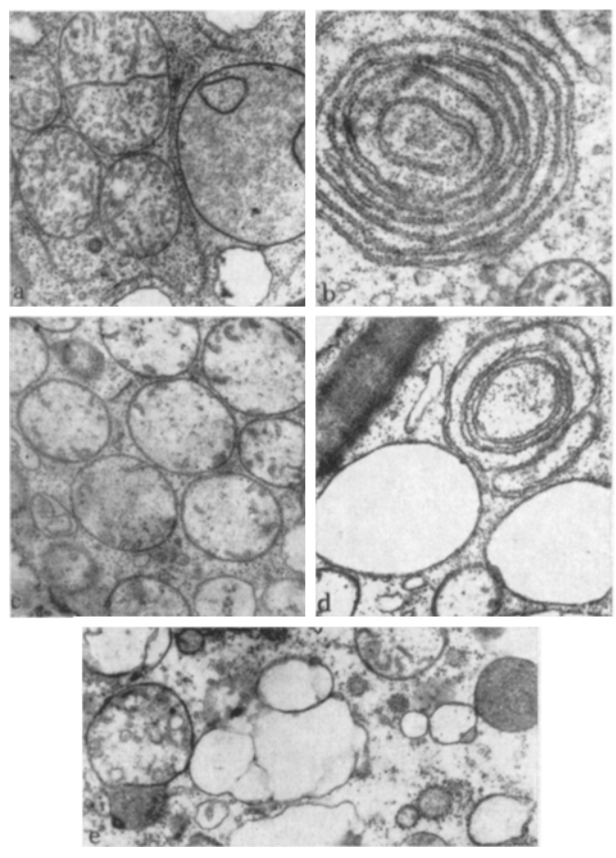

Fig. 4. Coleoptile cells of wheat — *Agropyron* hybrids after 4 days of exposure to −4 °C: TAH 829 a) intact mitochondria, × 30,000; b) complex widened cavities of the granular endoplasmic reticulum, × 30,000; TAH 822 c) mitochondria with light matrix and numerous cristae, × 30,000; d) widened cavity of smooth endoplasmic reticulum and concentrical membranes of the granular endoplasmic reticulum, × 30,000; e) different degree of mitochondrial integrity in a cell of TAH 829, × 30,000

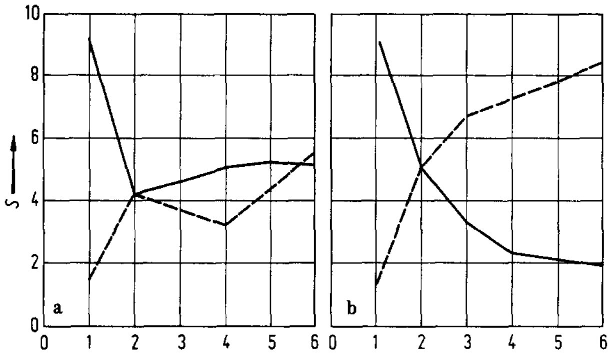

Fig. 5. Membrane surface area of endoplasmic reticulum (Sp mc²/mc³) of cell cytoplasm in the coleoptile of TAH 829 (a) and TAH 822 (b) after exposures of different duration to −4 °C: ——— the granular endoplasmic reticulum; — — — the smooth endoplasmic reticulum. Abscissa: 1) +23 °C. 2–6) −4 °C: 10 min, 1 hr, 6 hr, 24 hr, 4 days

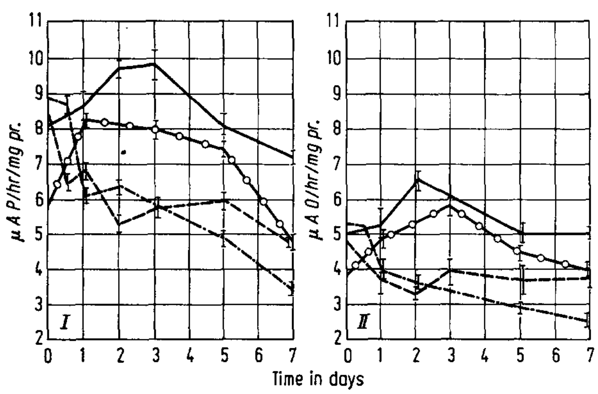

Fig. 6. Phosphorylative (I) and oxidative (II) mitochondrial activity in seedlings at 0 °C (in mc AP and mc AO per mg mitochondrial protein per hr).

——— *Tr. aestivum*; —o—o TAH 822; —·—· TAH 829; — — — *A. glaucum*

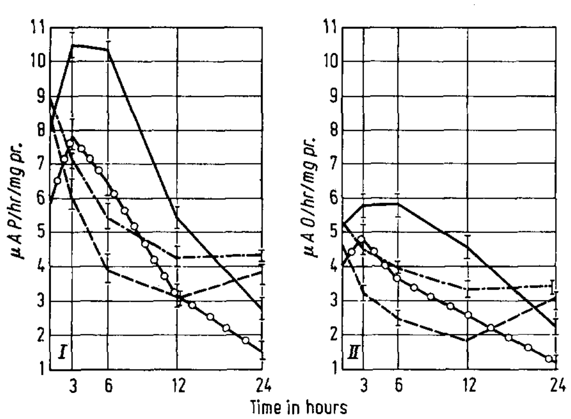

Fig. 7. Phosphorylative (I) and oxidative (II) mitochondrial activity in seedlings at −4 °C (mc AP and mc AO per mg mitochondrial protein per hr).

——— *Tr. aestivum*; —o—o TAH 822; —·—· TAH 829; — — — *A. glaucum*

The surface areas of granular and smooth endoplasmic reticulum were analysed morphometrically in TAH after different periods of exposure to 0 °C to −4 °C. It was found that in both hybrids the granular endoplasmic reticulum decreases and the smooth one increases. These changes differ in the two hybrids. In the coleoptile cells of hybrid 829 (similar to *Agropyron*), the surface area of membranes of both types of reticulum is the same on the fourth day of exposure to −4 °C. In the cells of hybrid 822, which is similar to wheat, the smooth endoplasmic reticulum increases by 6.4 times and the granular decreases by 4.5 times (fig. 5).

The results of studies of respiration and phosphorylation rates of mitochondria under low temperature (0°–4 °C) in the seedlings are schematically presented in figs. 6 and 7.

The data on the oxidative and phosphorylating activities of mitochondria isolated from seedlings after exposure to 0 °C for 7 days (fig. 6) show that the mitochondria of the seedlings of wheat 'Lutescens 329' and *Agropyron glaucum* react differently to low temperature. In wheat mitochondria respiration and phosphorylation rates increase with decreasing temperature and the peak is reached on the third day of exposure (the level of biochemical activity of the mitochondria increases by about 25% compared with the control). Further exposure of the seedlings to 0 °C causes a gradual decrease in the oxidative and phosphorylating activities of the mitochondria, though their level was not lower than in the control even after 5 days of low temperature treatment. A slight decrease is observed only on the seventh day.

In the contrary, in the mitochondria of *Agropyron glaucum* there is a rapid decrease in both phosphorylation and respiration rates at 0 °C. In 6 hr, low temperature exposure decreases the phosphorylation rate by 12% compared with the control, in 12 hr it decreases it by 26%. Respiration rate decreases more slowly, by 11% in 12 hr. Low temperature treatment of seedlings for 2 days induces further decreases in the rates of mitochondrial respiration (34%) and phosphorylation (37%) compared with the control. Prolonged exposure to 0 °C for 7 days has no further effect on mitochondrial activity which remains at the same level to the end of the experiment.

The reaction pattern displayed by the mitochondria isolated from TAH seedlings after exposure to 0° C, is of interest here. Fig. 6 shows that the curves of changes in respiration and phosphorylation rates of these hybrids are midway between the curves of wheat and *Agropyron*. It is also noteworthy that the mitochondria of the more winterhardy hybrids 829 react to low temperature like those of *Agropyron*, while the reaction of the mitochondria of the less winterhardy TAH 822 is similar to those of wheat.

The analysis of the data obtained indicates that changes in the biochemical activity of mitochondria at 0 °C include only shifts in the oxidation rate of succinate, without significant alterations in the coupling of oxidation and phosphorylation, since increased or decreased respiration rates (fluctuations being negligible) are paralleled by corresponding changes in the rate of phosphorylation. The changes in mitochondrial reaction to decreased temperature are more distinct at −4 °C. Fig. 7 depicts the changes in the oxidation and phosphorylation of mitochondria during exposure to −4 °C.

The first point to be noted is that the curves in fig. 6 and 7 are similar. As at 0 °C, during the first hours of exposure to −4 °C (up to 6 hr) both respiration and phosphorylation rates in the mitochondria of wheat seedlings increase. With further exposure (up to 12 hr) there is a sharp decrease in mitochondrial activity, particularly in the phosphorylating rate (by approximately 32%); 24 hr of treatment lowers it by 60% compared with the control.

Unlike wheat mitochondria, exposure to −4 °C produced a drastic fall during the first hours in oxidative and phosphorylating activities of *Agropyron* mitochondria. During the first hours of −4 °C exposure, respiration and phosphorylation are strongly depressed (50% by 6 hr compared with the control). Subsequent exposure of *Agropyron* seedlings to −4 °C produced no changes in the biochemical activity of the mitochondria.

The curves reflecting the oxidative and phosphorylating rates in TAH hybrids, like those produced by exposure to 0 °C, occupy an intermediate position between *Triticum* and *Agropyron*, with the reaction pattern of the mitochondria to −4 C in TAH 829 being similar to that of *Agropyron* and in TAH 822 resembling that of wheat.

It may be concluded that the initial response of seedling mitochondria to low temperature (0° to −4 °C) is the change in their functional activity. In *Agropyron glaucum* and TAH 829 (with X genome of *Agropyron*), this change consists of a decrease in the rates of oxidation and phosphorylation, while in wheat 'Lutescens 329' and TAH 822 (with D genome of *Agropyron*), enhanced biochemical activity is observed first. The mitochondria of the more winter-hardy forms have a rather high P/0 coefficient which does not change after prolonged exposure to low, though not damaging, temperatures. This is, perhaps, because mitochondria belong to structures whose cells bear high functional loads. To withstand these loads, the mitochondria probably have considerable functional reserves at their disposal to enable them to maintain, or promptly restore, their normal state (Udovenko, Maschansky and Sinitzkaya, 1970).

Discussion

Studies of the cell structure in the coleoptile of 3 day-old seedlings differing in winterhardiness have shown that the structure of their mitochondrial cristae is different. It seems that mitochondrial structure is species specific. This feature is, probably, not markedly expressed at +23 °C because it is not the optimal temperature for the seedlings of these plants. At low temperatures these differences become particularly marked. This is confirmed by morphometric data: in *Agropyron* mitochondria the surface area of the internal membranes and cristae of the mitochondria remains unchanged after 4 days of exposure to −4 °C, while in wheat mitochondria it decreases by 1.54 times.

It has been demonstrated that mitochondrial changes in different organisms are similar and represent transient structural changes accompanying increased functional activity in extreme conditions (Maschansky, 1961; Maschansky et al., 1965; 1971). The range of these changes depends upon the physiological and biochemical processes taking place in the organism. The data we have obtained on mitochondrial structure under conditions of low temperature suggest that the genetical system of the mitochondria is not quite autonomous, in spite of the presence of DNA, and depends upon the genome of the nucleus. The mitochondria of wheat, *Agropyron* and their hybrids are functionally inactive after 4 days of exposure to −4 °C. The more intact structure of the organelles in coleoptile cells of *Agropyron* and wheat-*Agropyron* hybrids (particularly of hybrid 829), where their energy supplying functions are inactivated, prompts the idea that the seedlings of these plants possess genetically determined mechanisms which block the processes of oxidative phosphorylation at low temperatures. In consequence, mitochondrial ultrastructure is left intact and these structures are able to resume their functions as soon as circumstances become favourable. In contrast, at low temperatures the functional activity of wheat mitochondria increases at first (Borzkovskaya, Usova, and Safonova, 1971), which leads subsequently to the partial or total impairment of their structure.

The protective mechanisms providing the integrity of mitochondria in the cells of *Agropyron* seedlings certainly depend upon plant genotype. This is substantiated by the wide variety of changes in the mitochondria of coleoptile cells in TAH, in which such mechanisms presumably do not operate with high precision.

The existence of different mitochondria in coleoptile cells of hybrids indicates that mitochondrial structure and its integrity are controlled directly by the nuclear genome, whose protective mechanism acts only upon "related" mitochondria, i.e. on mitochondria of similar origin.

Noteworthy is the close relationship between mitochondrial structure and the state of the endoplasmic reticulum. The formation of dense accumulations of granular endoplasmic reticulum representing coiled dilated cavities, enclosing membranes of granular reticulum, is interpreted as an adaptive mechanism protecting the protein-synthesizing apparatus from unfavourable conditions. The integrity of the granular endoplasmic reticulum and of the fine structure of the mitochondria in *Agropyron* and TAH 829 (with the X genome of *Agropyron*) at decreased rates of oxidative phosphorylation is evidence for the existence of protective mechanisms maintaining cell homeostasis at low temperatures. The formation of coiled bodies in the endoplasmic reticulum has been established by a number of workers (Dexheimer, 1966; Andreeva and Grineva, 1970; Wrischer, 1965; Petrowskaya-Baranova, 1972). Two alternative explanations have been proposed: One (Dexheimer, 1966) is that this type of structure is indicative of decreased protein synthesis; the other implies that this structure is associated with enhanced protein synthesis in the cell (Björkman, 1968; Lowry and Sussman, 1968; Petrovskaya-Baranova, 1972).

The data obtained in this study are consistent with the former explanation. Since the dense coiled bodies in the endoplasmic reticulum were observed in the cells of seedlings with inactivated, though structurally quite intact, mitochondrial structure, it is difficult to imagine that an increase in protein synthesis occurs when oxidative phosphorylation is abolished. Moreover, morphometric analysis indicates that the membrane of the granular endoplasmic reticulum has a smaller surface area in hybrids at low temperature. Dense coiled bodies consisting of granular endoplasmic reticulum appear in the cells of the seedlings concomitantly with the decrease in surface area of the granular endoplasmic reticulum. This observation is in line with the concept that the activity of the protein-synthesizing apparatus of the cell is reduced. It is hardly conceivable that cell protein synthesis is increased, while the contrary appears plausible. We consider the formation of dense coiled bodies as an adaptive mechanism preserving cell structure.

Another suggestion is possible. In extreme conditions cell compartmentalization is particularly evident: when total protein synthesis is decreased, separate regions of cell cytoplasm are capable of synthesizing more protein. In these regions complex dense bodies arise consisting of granular endoplasmic reticulum.

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