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Research article

Stress induced «railway for pre-ribosome export» structure as a new model for studying eukaryote ribosome biogenesis

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Abstract: The article presents the details of the process of structural organization, formation and disassembly of the nucleolus, chromatin condensation during the passage of the cell cycle studied by the method of classical transmission electron microscopy (TEM) in the cells of the meristematic zone of the wheat root. The transformations of peripheral chromosome material (PCM) in telophase, the transformations of the nucleolar nucleolonema in the interphase and prophase, and the chromatin transformations (condensation and decondensation) were studied and analyzed under the conditions of the geomagnetic field, weakened magnetic field and static magnetic field. Using an analysis of the dynamics of structural transformations of proliferating nuclei, we observed a disturbance in the formation of the chromonema and condensed chromatin in the middle interphase, a change in the structural organization of the nucleolus during the transition from late interphase to prophase, as well as a change in the structure of PCM, pre-nucleolus and chromatin in telophase. A schema for the generation of a specific conformation of nucleolonema and chromonema and its influence on the structural organization of chromosomes in anaphase and telophase was proposed. The nature of this structure is discussed. Possible mechanisms of the effect of magnetic field on the nuclear compartment, regulation of chromatin decompactization, export of pre-ribosomal particles under stress, and the fine structure of the nucleolonema are considered.

Keywords: weakened magnetic field; cold; chromonema; nucleolonema; nucleolus; ribosome biogenesis

1. Introduction

It is believed that life on the Earth was formed in the conditions of the liquid phase of water and the influence of magnetic field (MF) that arose more than four billion years ago [1]. Such parameters as temperature, pressure, salt composition, acidity, gas composition of the atmosphere and the aqueous environment underwent significant changes during evolution, sometimes extreme ones [2]. The magnetosphere is very volatile, and its model has little to do with classical notions of the ideal dipole [3]. Thus, on the Earth there are zones with high and low MF strength [4]. Recently, the question of the possibility of survival of living organisms with a reduced or hypomagnetic field [5] gained a particular interest, especially in connection within the protective role of the MF in preventing damage from cosmic irradiation, which makes long space flights hardly feasible. It is supposed that the ability to adapt to such conditions can be embedded in 'evolutionary memory' and will be much in demand for the development of underground, and underwater spaces, as well as for the cultivation of plants and human survival in space stations and biospheric experiments on other planets [6,7].

Magnetosensitivity and magnetoreception in plants is the subject of extensive research [8–10]. The effects of enhancing or inhibiting growth, changes in metabolism, structural organization of organelles, Ca^{2+} compartmentalization as a result of changes in ambient MF were demonstrated [5,9,11,12].

A rather large array of data on the effect of a much weakened magnetic (hypomagnetic) field (WMF) on living organisms was obtained, since such information is important for planning the development of near-Earth space, where the field intensity does not exceed 10−5 Oe [13], with human participation. However, most studies on the effects of WMF on plants were performed at the level of the whole plant or individual organs and tissues. Studies at cell level are fairly few [14–17], and studies of the core of the organization of living matter of eukaryotes—the nucleus of the cell and the carrier of heritable information—chromatin are very rare [13,15]. Moreover, the influence of MFs is generally estimated from the point of view of some physical parameters and biochemical properties [18].

Whereas the visual assessment of changes in the structure of the nucleus and chromatin under the impact of WMF and other MFs have never been performed. The high-resolution microscopy makes possible to observe such vital processes for cell reproduction (division) as condensation and decondensation of chromatin.

Obviously, the degree of chromatin condensation is extremely important for the generative sphere of both plants and animals, especially for the formation of pollen and spermatozoa, which are highly sensitive to the action of MFs [19]. We have previously shown that such a weak stress factor, as slight temperature rise, caused chromatin condensation in human lymphocyte cells [20]. This led to a slowdown of the expression of most proteins, except for the family of heat shock proteins. In addition, the work with lysed human lymphocytes showed that chromatin condensation after exposure to low-frequency 50-Hz MF differed from its state before exposure [21].

Plants, like other living systems, must be resistant to the fluctuations of MFs and should have acquire the mechanisms that allowed them to survive and pass through the natural conditions [5]. The main problem in finding targets of sensitivity to MFs is the assumption of its specificity. Although it is not worthwhile to exclude such an option, it is reasonable to assume that the mechanism of susceptibility and response to changing MF characteristics in living systems, constantly modifying due to mutations and epigenetic regulation, may be non-specific—that is,

random. Most of the currently proposed hypothetical targets can explain some effects selectively only [22,23]. However, the same question is essential for other environmental conditions undergoing fairly strong fluctuations. If we estimate the sensitivity not from the point of view of the target, but from the point of view of the mechanism, then it can be assumed that the mechanism of sensitivity can be the same, but there can be several detectable targets. In this case, it would be interesting to take into account the proposed new model, which can be considered on the assumption of the dependence of the processes of moving gas bubbles and degassing in solutions subjected to a MF [24]. The interaction of water clusters and gas nanobubbles forming in a solution can explain many ambiguous effects of MFs, since it is obvious that taking into account temperature, pressure, gas composition, as well as the effect of organic and inorganic salts in experiments with biological systems is problematic. What makes evident the problem of reproducibility of a number of classical experiments [8,23]. This possible explanation seemed so attractive to us that it prompted us to consider the complex system of highly organized interaction of the chromonema and nucleolonema established by us earlier [15]. Moreover, in this experiment, prolonged shielding from the influence of the geomagnetic field was observed and a low positive temperature was maintained, corresponding to the highest water density 2–4 ℃ [25]. The model of the nucleolus as a dynamic multifunctional domain within the nucleus [26] turned out to be quite attractive, since it implied evolutionary determined, self-organizing, ordered, and highly organized structure, which is capable to subsequent disassembly and assembly after duplication of the nuclear genetic material [27].

It is known that a nucleolonema is a structure formed by maturing pre-ribosomal particles [28]. While the mechanism of the initial stage of the transcription of ribosomal genes and the processing of rRNA is well studied [29], the formation of the nucleolonema, its qualitative structure and the backbone on which the pre-ribosomal particles are fixed, remain poorly understood. The processes of formation of perichromatin material in telophase [30] and the association of the perinucleolar chromatin and nucleolus at the stage of late interphase and prophase [31] are even less understood. Models and possible mechanisms for the formation of tight interaction of chromosomes and nucleolonema are not reflected in the literature. In the peripheral zone of the nucleolus, the nucleolonema can form large conglomerates, where the sequential arrangement of pre-ribosomal particles at an equal distance, clearly having a linear order, can be clearly seen [32]. What exactly provides the attachment of these particles to an unclear backbone, which today is not obvious, is unknown. The mechanism providing the link between chromatin and nucleolonema is also unclear, especially outside the nucleolus zone. That is why the transformations of these structures can be an extremely interesting model for studying the interaction of these components from two functionally different nuclear domains that are crucial for ribosome biogenesis.

In the present work we aimed to visualize the dynamics of the emergence of association of the nucleolonema with chromonema-like fibers revealed by us earlier in a study describing the effect of shielding of geomagnetic field on the nuclei of root cell meristem of some cereals at low positive temperature 2–4 ℃ [15]. We also tried to systematize the observations received earlier and in this study in order to understand the mechanisms and features of the interaction of DNPs, RNPs, and factors affecting the rearrangement of nuclear domains.

2. Materials and methods

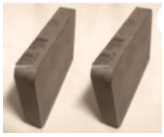
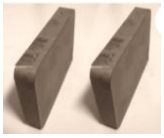
2.1. Plant material and experimental conditions

Winter wheat (*Triticum aestivum* L.) seeds were sterilized for 2 min using 0.2% $KMnO_4$, and then were washed thoroughly by distilled water.

The seeds were laid out on layered double-layer sterile filter paper in Petri dishes for imbibition (5 mL distilled water with 50 seeds in each dish). Imbibition and radicle protrusion took place during the one day at 22–24 ℃. Rolls were twisted from moistened filter paper with a height of 5 cm with 10 seeds in each roll (5 rolls for each experimental impact) and placed vertically in a 50 mL beaker with 20 mL of distilled water. The beakers were placed in experimental conditions for exposure. For the experimental conditions at 22–24 ℃, the duration of exposure was 4 days, at 2–4 ℃ exposure was carried out for 40 days.

To search for the subject of impact of MF in a plant organism, experiments were carried out with exposure WMF and a static magnetic field (SMF) with an induction of 45 μT. The exposure system consisted of: 1) paired composite barium ferrite magnets; 2) spherical shields (Table 1). Characteristic: spherical volumes, consisting of hollow hemispheres, made of raw cast iron with an outer diameter of 30.0 cm, an inner diameter of 24.4 cm, with a wall thickness of 2.8 cm (Table 1). The height of the object location (placed on the carton support) ranged from from 5 cm to 5.5 cm from the lowest point of the sphere. The average values of SMFs are given in Table 1. The maximum heterogeneity of the MF inside the sphere was less than 1 μT. For measurements, a magnetic induction detector TMI-01 (Prokhorov General Physics Institute) with a resolution in SMF 0.1 μT was used.

Table 1. The measurements of the temperature and magnetic field in the different experimental conditions.

Parameters	Geomagnetic field	Geomagnetic field (cold)	Static magnet	Static magnet (cold)	Hypomagnetic chamber	Hypomagnetic chamber (cold)
Exposure	4 d	40 d	4 d	40 d	4 d	40 d
Display	No device	No device				
T, ℃	22–24	2–4	22–24	2–4	22–24	2–4
SMF, μT	45	30	~125×10^3	~125×10^3	6.6	4.4
AMF, nT	<45	<60	<45	<60	<25	<30

2.2. Transmission electron microscope to studying nucleus ultrastructure

We studied the effect caused by action of SMF or shielding of MF. Fragments of wheat plants roots—a part containing an apical meristem were fixed under 4 ℃ at 0.1 M Na-phosphate buffer, pH 7.4

with adding sucrose 15 mg/ml, containing 2.5% glutaraldehyde and 1% osmium postfixation. After dehydration in ethanol solutions (30, 50, 70, 96%) they were placed into absolute 100% ethanol and propylene oxide. Then the samples were treated with resin mixes based on Epon/Araldit with propylene oxide (1/3, 2/5, 1/1, 5/2, 3/1) and were carried into capsules containing resin with catalyst for further polymerization (45 ℃ (24 h) and 62 ℃ (24 h)). For analysis at we used thin sections of wheat meristems roots (microtome LKB-3) after uranyl acetate and lead citrate staining. Visualization was carried out on transmission electron microscope H 500 (Hitachi, Japan). We took for analysis one central root from each of the two plants from different rolls.

2.3. EDTA regressive staining—to visualize DNA containing structures

Bernhard's EDTA regressive staining method differentiates between ribonucleoprotein and deoxyribonucleoprotein particles [33].

Samples are fixed in glutaraldehyde without osmium postfixation. Samples are dehydrated using ethanol and propylene oxide and embedded into Epon/Araldit resin. Thin sections are then stained with 3% aqueous uranyl acetate for 10 min, followed by three washes in distilled water. The sections are then treated with 0.2 M EDTA pH 7.4, for over 15–30 min (timing is may be critical and must be determined experimentally). Grids washed three times in distilled water. This results in preferential removal of uranyl stain from DNA, giving the DNA-containing structures a bleached appearance while RNA-containing particles remain strongly stained.

3. Results

We studied cells in the zone of active proliferation, located above the quiescent center of meristem, in which the processes of differentiation begin (root apex). Cells in this zone have a dense cytoplasm with a large number of ribosomes and, as a rule, do not contain vacuoles characteristic of differentiated plant cells. Normally (geomagnetic field without modifications) the process of transformation of the nucleolus and PCM during the cell cycle progression is well described in the cells of various plants [34,15,35–37]. Nucleolus derived foci (NDF) or peripheral chromosomal material localized in mitosis in the cytoplasm condense around the chromosomes before processing the formation of the nuclear envelope (Figure 1.1a). At this stage, a specific, relatively large domain,—the pre-nucleolus begins to form, which then turns into the typical nucleolus with a pronounced nucleolar lacuna (nucleolar vacuole), fibrillar centers and a granular component forming the nucleolonema on the periphery of nucleolus in the interphase (Figure 1.1b). Further, after DNA duplication, at the end of S phase in pre-prophase, the transformation of the nucleus takes place, which is manifested in chromatin condensation and disassembly of the nucleolus (Figure 1.1c) that is poorly identified in the prophase. After the disappearance of the nuclear membrane and the endoplasmic reticulum the nucleolus materials are distributed in the cytoplasm of the cell [38] and the chromosomes are easily identified in sections as large electron-dense bodies (Figure 1.1d). The action of low positive temperatures (2–4 ℃) causes a change in the structural organization of the nucleus that is accompanied by a retardation of assembly of the pre-nucleolus and PCM and increasing the chromatin packing density, possibly associated with a decrease in the chromatin decondensation rate (Figure 1.2a). Under these conditions, the nucleolus has a looser structure in an interphase; the clearly distinguishable fibrillar centers were observed inside of nucleolus that

probably indicates that this domain does not have a dense structure (possibly due to a change in the synthesis rate of ribosomal genes). The lacuna is identified as a subdomain of irregular shape, and the chromatin is partially decondensed and has a relatively loose structure (Figure 1.2b). In the preprophase nucleus, a change in the structural organization of the nucleolus (amoeboid form) [15,35,36,39] and the formation of irregular outgrowths (rames, sprouts) associated with areas of condensed chromatin adjacent to the nucleolus can be distinguished (the degree of condensation is increased due to changes in chromatin packaging during the transition to mitotic division) (Figure 1.2c). The emerging chromosomes have a dense structure and a more regular form at near-zero temperature than at 22–24 ℃.

We pay special attention to Figures 1.1c and 1.2c, which show partially deactivated nucleoli with a forming dense structure characteristic of late interphase or early prophase. The nucleoli show clear features of enhanced chromatin condensation and characteristic areas of condensed chromatin and nucleolonema separated by a bright halo, which were previously described by us and a number of other authors in wheat, rye, barley [36,37,39,40].

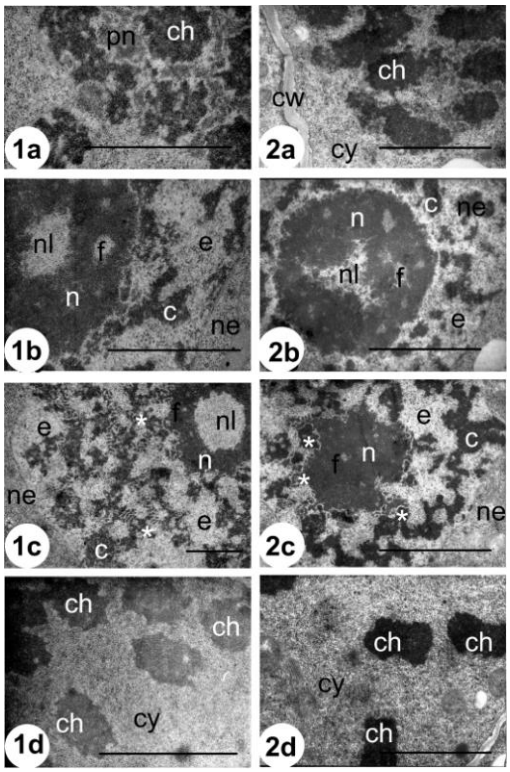


Figure 1. Structural organization of root meristem cells nuclear domains (geomagnetic field condition) at 22–24 ℃ (1a–1d) and low positive temperatures 2–4 ℃ (2a–2d). Phases of the cell cycle: telophase (1a, 2a), middle interphase (1b, 2b), late interphase (pre-prophase 1c, 2c), anaphase (1d, 2d). Notations: pn—pre-nucleolus, ch—chromosome, cw—cell wall, cy—cytoplasm, n—nucleolus, nl—nuclear lacuna, f—fibrillar center, c—condensed chromatin, e—decondensed (euchromatin), ne—nuclear envelope, asterisk—railway pre-ribosome export (associated chromonema and nucleolonema structures). The size of the measuring segment is 1 μm.

It is known that a SMF can influence the degree of chromatin condensation [18]. Figure 2 shows the visual effects of a SMF on chromatin at the optimum temperature of 22–24 ℃ for wheat development and at a low positive temperature of 2–4 ℃. In late telophase, after the formation of the nuclear envelope has been completed, pre-nucleoli are clearly identified with light areas, probably representing emerging fibrillar centers, as well as PCM, located between the partially decondensed chromatin areas. There is also a significant amount of PCM related to the forming nucleoli that associated with the surface of the deconstructing chromosomes (Figure 2.1a). The interphase is represented by the nucleolus with the nucleolar lacunae and fibrillar centers located around. The zones of condensed chromatin have a chromonema-like organization with large zones of euchromatin. A nucleolonema containing a granular component is formed along the periphery of the fibrillar centers in the nucleolus (Figure 2.1b). In the preprophase nucleus, regions of more dense chromatin are formed, associated with both the nuclear envelope and the surface of the nucleolus. The fibrillar centers are shifted to the center of the nucleolus; a large zone of the granular component is formed with a clearly defined boundary between the outgrowths of the nucleolonema and areas of condensed chromatin (Figure 2.1c). Mitotic chromosomes have a typical structure, with the exception of a less precise and more diffuse boundary between the surface of chromosomes and the cytoplasm (Figure 2.1d). At 2–4 ℃ in telophase, CMF causes the formation of a dense material of pre-nucleolus and PCM on the surface of chromatin with large areas of decondensed chromatin (Figure 2.2a). In the interphase the areas of condensed chromatin are located along the surface of the nucleolus, and also are associated with the nuclear envelope. The degree of chromatin condensation corresponds to that of the nucleolonema. The nucleolus has big size with incorrectly located fibrillar centers, and has a large volume of the granular component, forming the large nucleolonema clusters between fibrillar centers and areas of condensed chromatin (Figure 2.2b). In the preprophase nucleus, a big nucleolus of irregular amoeboid form can be observed with multiple outgrowths of the nucleolonema, probably due to the delay in the formation of pre-ribosomes. Condensed chromatin areas are located from the nucleolus to the periphery of the nucleus, apparently in accordance with the occupied chromosomal regions; the chromatin structure at this stage does not correspond to the chromonema-like type (Figure 2.2c). At the end of anaphase, a dense layer of PCM is formed around the chromosomes, and this is probably due to an excess of immature products of the nucleolus functioning formed in previous stages of the cell cycle, which released into the cytoplasm after the disintegration of nuclear membrane when the cell enters mitosis (Figure 2.2d).

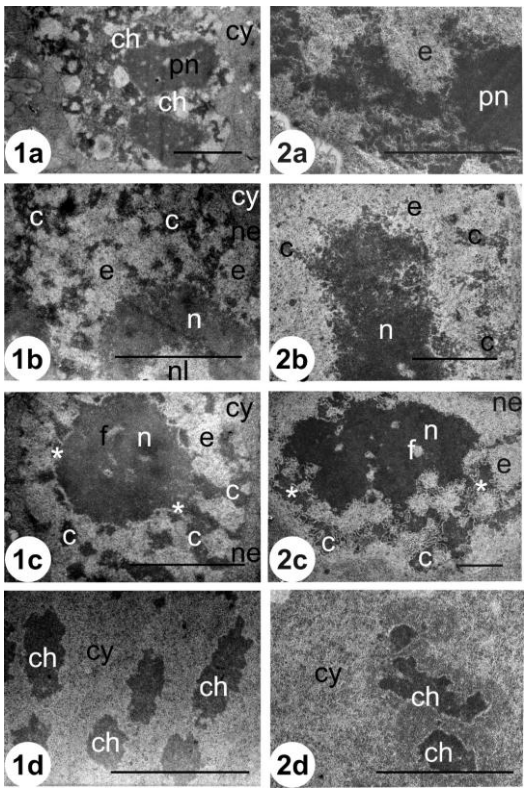


Figure 2. Structural organization of the nuclear domains of the cells of the root meristem after incubation under conditions of external static magnetic field (125 mT) at 22–24 ℃ (1a–1d) and at low positive temperatures 2–4 ℃ (2a–2d). Phases of the cell cycle: telophase (1a, 2a), middle interphase (1b, 2b), late interphase (pre-prophase 1c, 2c), anaphase (1d, 2d). Notations: pn—pre-nucleolus, ch—chromosome, cw—cell wall, cy—cytoplasm, n—nucleolus, nl—nuclear lacuna, f—fibrillar center, c—condensed chromatin, e—decondensed (euchromatin), ne—nuclear envelope, asterisk—railway pre-ribosome export (associated chromonema and nucleolonema structures). The size of the measuring segment is 1 μm.

WMF at 22–24 ℃ leads to a change in the structure of the telophase domains of the forming nucleus: the chromosomes form small decondensation sites associated with PCM, which also has separate light regions and takes part in the formation of pre-nuclei. Most obviously a decondensation affects the zones near by the nuclear envelope (Figure 3.1a). In interphase cells, fibrillar centers are located in the center of a rounded nucleolus with a pronounced area of granular material. The chromatin forms abundant chromonehema-like structures and is identified as small clumps, between which the zones of decondensed chromatin are located (Figure 3.1b). In pre-prophase cells, formed areas of condensed and decondensed chromatin are visible, connecting hypertrophied enlarged nucleolus with nuclear envelope. On the surface of condensed chromosomal regions located the outgrowths of nucleolonema. In the nucleolus a large, loosely located FCs can be observed. They are surrounded by a thick layer of the granular component, which transforms into the fibers of the nucleolonema associated with condensed chromatin (Figure 3.1c). In anaphase cells, the chromosomes have a somewhat loose irregular shape (Figure 3.1d). At 2–4 ℃ in telophase cells one can observe partially decondensed chromosomes and large areas of pre-nucleoli and PCM with a

high degree of chromatin decondensation (Figure 3.2a). In the interphase one can observe the big nucleoli without pronounced fibrillar centers. Some nucleoli have the nucleolonema outgrowths connecting the nucleolus with nuclear envelope. They are always surrounded by thin chromonema-like fibers (Figure 3.2b). The nucleus of preprophase cells contains the big nucleoli with sophisticatedly organized outgrowths of the nucleolonema and chromonema connecting the nucleolus and the nuclear envelope (Figure 3.2c). Chromosomes forming during mitosis have noticeable prominences on their surface. Perhaps this is due to the specific consequences of the action of associates of the nucleolonema and chromonema in pre-prophase nuclei (Figure 3.2d). The action of a SMF at low positive temperatures has impact both on the elements of the nucleolus, PCM, and on the organization of the chromatin and the pre-nucleolus in telophase (Figure 2.1a–2.1d). Thus, the level of chromatin condensation differs from the control, and this is manifested in uneven decondensation of a part of chromatin, an increase in the area of the pre-nucleolus (NPB - nucleolus precursor body) and uneven distribution of PCM and condensed chromatin. The interphase nucleus has an unusual structure and is characterized by large irregular shaped nucleoli. Also, these nucleoli have amoeboid outgrowths. These have no a nucleolar vacuole, and separate, randomly located fibrillar centers are disposed within nucleoli. Chromatin has a chromonema-like organization and partially remains associated with the nucleolus (Figure 2.1b). The organization of the nucleus during the transition from interphase to prophase (pre-prophase) also differs from the control. A large amoeboid nucleolus with a sophisticated network from nucleolonema and chromatin is located inside the nucleus (Figure 2.1d). It can be assumed that a nucleolonema containing pre-ribosomal particles braids all areas of condensed chromatin. However, the light area of the nucleoplasm is structured and contains both various RNPs and decondensed chromatin. The presence of light zones in the nucleolus indicates the decondensation of part of the rDNA or the retention of FCs (Figure 1c). During anaphase, disturbances of the surface structure of chromosomes and the protrusions are observed, indicating a damage of the assembly, as well as a thick layer of PCM (Figure 2.1d) that may correlate with large sizes of the nucleolus in prophase cells and pre-nucleolus in telophase cells (Figure 2.1a,c).

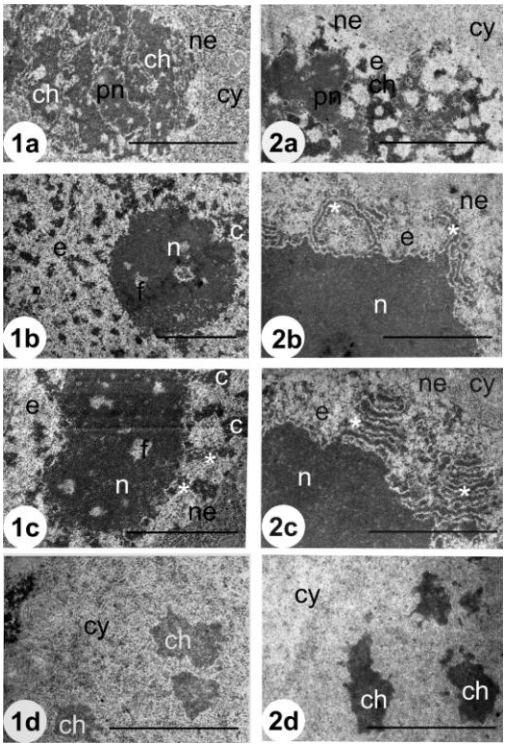


Figure 3. Structural organization of nuclear domains of root meristem cells after incubation under conditions of weakened (shielding) geomagnetic field (6.6 μT) at 22–24 ℃ (1a–d) and low positive temperatures 2–4 ℃ (2a–d). Phases of the cell cycle: telophase (1a, 2a), middle interphase (1b, 2b), late interphase (preprophase 1c, 2c), anaphase (1d, 2d). Notations: pn—pre-nucleolus, ch—chromosome, cw—cell wall, cy—cytoplasm, n—nucleolus, nl—nuclear lacuna, f—fibrillar center, c—condensed chromatin, e—decondensed (euchromatin), ne—nuclear envelope, asterisk—railway pre-ribosome export (associated chromonema and nucleolonema structures). The size of the measuring segment is 1 μm.

A particularly impressive result of the transformations of nucleolonema structures, pre-nucleolus and PCM can be obtained using a combination of WMF and low positive temperatures, and the degree of the effect manifestation depends on the exposure time of 35–40 days (Figure 3.2a, 3.2b, 3.2c, 3.2d), but the effect partly begins to appear already on day 12–14 (data not shown). Thus, in telophase a mesh structure of chromatin with multiple light areas of the nucleoplasm is observed. There is a large area of the pre-nucleolus and a distinct from control conditions the distribution of PCM associated with condensed chromatin (Figure 3.2a). Interphase nuclei have a rounded or close to rounded shape. There are almost no fragments of condensed chromatin in interphase nuclei, but only the fibrils associated with areas, which contain the granular components—nucleolonemae can be observed (Figure 3.2b). In prophase (Figure 3.2c) the amount of condensed chromatin increases. Nevertheless, it remains associated with the nucleolonema that corresponds to the data we previously obtained on barley and rye [15]. When observing chromosomes in anaphase, there are obvious changes in the structural organization of chromosomes in the form of protrusions (outgrowths) of the surface, along which the derivatives of PCM are collected (Figure 3.2d). Probably, violations of the

observed structure can be provided by a disturbance of chromosome condensation in the prophase (Figure 3.2c).

One can observe that the restoration of the form of nuclear domains to the characteristic normal appearance is not full: the loose packing of chromatin in telophase, the retention of the outgrowths of the chromosomes in anaphase. In addition, the recovery of the PCM form, the nucleolus and FCs is not completed. Thus, the observed structural changes in chromosomal conformation could serve as a visual illustration of the recently described effects of epigenetic 'memory' regarding the preservation of the expression properties of a number of genes in further generations when removing stress effects [41].

Our data on the transformation of the nucleolus, peripheral chromosomal material (PCM), pre-nucleolus, taking into account the degree of chromatin condensation, can be presented as a scheme. Activation and suppression of chromatin remodeling and ribosome processing caused by modifications in the conformation and interactions of DNA, RNA and protein molecules, which are induced by various abiotic stresses, are manifested in alterations in quantitative and qualitative mutually-regulating interactions leading to changes in the structural organization. In the inactivation of the nucleus domains, rapid chromatin condensation occurs (Figure 1.1c) with the formation of condensed chromosomes in late interphase and prophase. In addition, the effects of rDNA condensation in the nucleolus (Figures 2.1c, 3.1b and Figure 4(in)), which are identified under particularly severe conditions as nucleolus segregation, can be noted [42]. However, reverse processes can be observed, in which chromatin decondensation is enhanced and chromatin condensation is slowed down and weakly pronounced even in late interphase and prophase. FCs do not have a characteristic spatial configuration or are not detected, and the nucleolus is greatly enlarged and has highly organized outgrowths of nucleolonema (Figure 3.2b, 3.2c and Figure 4, enhanced chromatin decondensation) as previously described [15,34,37,39,43]. The nucleoli in this type of nucleus demonstrate an unusual structure: the fibrillar and granular component form the 'railway for pre-ribosomes'—the threads of nucleolonema associated with the chromonema. Various types of intermediate variants are most often encountered, in which condensed chromatin (in the form of a chromonemal network and larger domains) is detected in the nucleoplasm both in interphase and prophase (Figures 1–3 and Figure 4, moderate chromatin decondensation). The nucleolus (nucleoli) has a nucleolar lacuna (vacuole), characteristic arrangement of fibrillar centers and has a rounded shape. In this case, the nucleolonema is also associated with fragments of condensed chromatin, but normally this is manifested significantly weaker than under the action of stress factors [15,35,36] and become apparent very rarely, due to the small number of cells in the prophase. It is possible that the structure formed jointly by chromonema and nucleolonema can specifically influence the packaging of chromatin in mitotic chromosomes and be essential for the passage of vernalization, the control of dormancy duration, the formation of epigenetic resistance to abiotic stresses. To study this phenomenon, it was necessary to significantly increase the number of cells in the cell cycle stage, which is characterized by the structures revealed by us (transition from interphase to prophase), which normally occurs in 1–3% of cells. In the present study, the number of cells in pre-prophase and prophase was increased to 3–5% when SMF 125 mT (magnets) was applied, and was increased to 6–8% when weakening of the geomagnetic field (WMF due to shielding) was used. In addition, the simultaneous application of a low positive temperature of 2–4 ℃ increased the number of cells in the investigated phase to 10–13% (in the case of magnets) and to 15–22% (in the case of shielding).

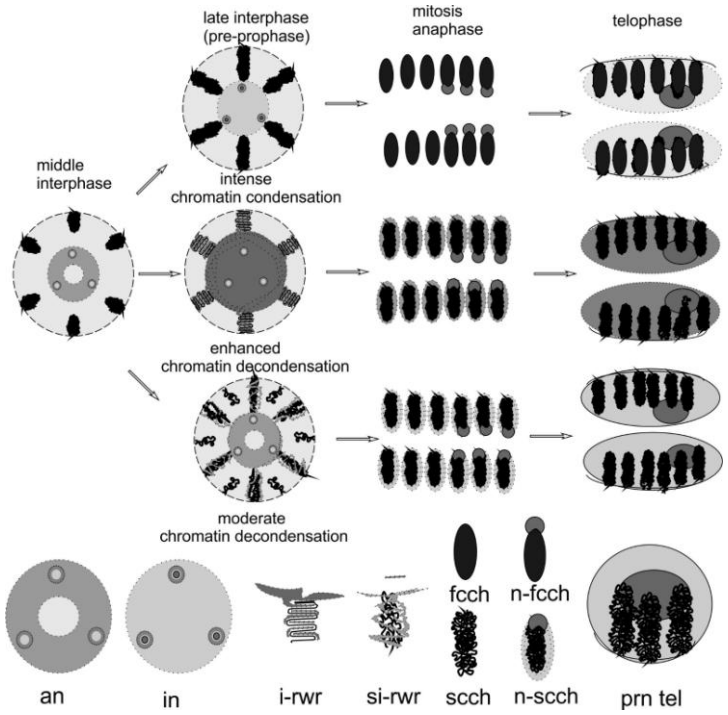


Figure 4. Dynamic structures of nuclear domains at different stages of the cell cycle under the action of abiotic factors, depending on the level of chromatin condensation. Notations: *an*—active interphase nucleolus, *in*—inactive interphase nucleolus, *i-rwr*—inactive railway pre-ribosome export, *si-rwr*—semi-inactive railway pre-ribosome export, *fcch*—full condensed chromosome, *scch*—semi-condensed chromosome, *n-fcch*—nucleolus organizer containing the full condensed chromosome, *n-scch*—nucleolus organizer containing the semi-condensed chromosome, *prn tel*—pre-nucleolar body, forming nucleolus organizer containing the condensed chromosome in telophase nucleus.

Abiotic environmental factors have a significant impact on the duration of the various phases of cell cycle [44,45]. Since in order to study the nucleolus and the sophisticatedly organized structures of chromonema and nucleolonema, and also the amoeboid structure of nucleolus revealed by us, it was necessary for the investigated root tissue to have quite a lot of cells at the necessary stage of the cell cycle, which could be achieved using physical effects such as cold [39], pH action [35,36] and some modifications of the MF. Previously, the most interesting transformations of the nucleolonema and chromonema were described by us with the simultaneous application of two stress factors [15].

The features of chromatin condensation in prophase cause deviations in the structure of mitotic chromosomes, which we identified during application of various exposures that probably affects the formation of PCM and nucleolus derived foci (NDF) in anaphase (Figures 1.1d, 1.2.d, 2.1d, 2.2d, 3.1d, 3.2d; Figure 4, chromosome anaphase). It is obvious that the consequences of changes in the chromosome packing, pre-nucleolus formation, and the association of PCM with chromatin in such cases will have easily visualized differences (Figures 1.1a, 1.2a, 2.1a, 2.2a, 3.1a, 3.2a; Figure 4) related with the size of the nucleolus in prophase and the amount of PCM in telophase. Thus, we present our vision of the influence of factors of a physical nature on the processes of transformation and interaction of chromatin, nucleolus and PCM in the nuclei of eukaryotes.

4. Discussion

The transformation of chromatin, nucleolus and peripheral chromosome material (peripheral chromosome layer) intensively studied for more than 50 years [46,47]. However, its composition, principle of formation, configuration, and dynamic conversions despite many successes [26], are still unclear. To identify the transformations, we chose the previously tested rigid reversible effects of an abiotic nature that accompanied the development of cells during evolution: fluctuations of the MF, temperature, and acidity [15,35,36,39]. In this study, we chose the root cells of wheat as a target. Since these cells are in an actively proliferating state, it is possible to reliably determine the necessary phases of the cell cycle, in which the nuclear domains can be easily identified: fibrillar and granular components and chromatin.

The sensitivity of chromatin condensation to external stimuli and disturbance of ribosome formation processes, manifesting in the appearance of nucleolonema and chromonema associates, suggest that nucleolus and PCM proteins can play an important role in this process. Possible candidate proteins can be Ki-67 [48,49], Nop53 [50], fibrillarin [51], p53 [52] and other proteins identified in the nucleolus and PCM. However, to date, more than 700 proteins have been identified in the composition of the nucleolus [53] that greatly complicates the search for targets.

Recently it was shown that as the induction of a MF in a hypomagnetic chamber is weakened, the magnitude of the redox potential of the aquatic environment is increased, and its oxidative properties are enhanced [54]. The authors suggested that the slowdown of biochemical processes with a sharp decrease in the MF from the normal level caused a slowdown in seed growth, which suggests that the determining factor in the action of a lower geomagnetic field is probably a change in the state of the aqueous environment [54]. On the other hand, the environmental conditions such as temperature, humidity and others, can change the pH of the soil solution, which can significantly affect the plant roots [55]. In addition to the influence on water, other mechanisms of magnetoreception are currently being actively discussed [22,56,57]. Historically, the first mechanisms of magnetic biological effects associated the primary target with biologically relevant ions Ca^{2+}, Mg^{2+}, and others, and with the resonance phenomenon,—the cyclotron resonance and parametric resonance [58]. However, these mechanisms have insuperable drawbacks from the physical point of view [59]. Moreover, these mechanisms do not explain the biological effects of a SMF, in particular, of hypomagnetic conditions, where the geomagnetic field is weakened by two or more orders of magnitude [10]. Interestingly, in recent years, attention has been attracted to the effects of hypomagnetic fields [17,60,61] due to the planned manned flights to the Moon and Mars and possible biomedical applications.

Today, most researchers working in the field of magnetic navigation of animals agree that the plausible mechanism of magnetoreception is photosensitive reactions involving spin-correlated radical pairs [62]. Particularly significant is the discrepancy between the mechanism of radical pairs and the effects of hypomagnetic fields less than 1 μT observed in many laboratories [10], as well as effects with a selectivity in the magnitude of SMF [10,63], alternating MF [21,64] and frequency of alternating MF [65]. In addition, a number of authors believe that, perhaps, the primary effect of an electromagnetic field on water systems may be the synchronous polarization of all unstable micro- and nanobubbles in water [24] or the resulting effects, such as a change in pH and an increase in reactive oxygen species [66–68]. However, one of the most promising concepts currently under consideration is the mechanism based on the interference of rotational quantum states of molecular

groups [69]. The interference of quantum states is accompanied by an inhomogeneity of the probability density of different angular positions of the molecular group and, thus, regulates the relative probabilities of the molecular group in different angular positions, in which rotation occurs with biomolecules possessing a magnetic moment or their fragments. Thus, the most probable target of MF in a cell are some fundamental processes common to all living organisms, such as the process of gene expression, including replication, transcription, translation and so on. All these concepts can be considered both separately and in combinations [22,23]. However, the mechanism of reactions of organic molecules and the aqueous phase as the main sensitive elements of living systems remain unclear.

The mediated effect of the MF was previously studied at the level of growth reactions, morphology, and biochemistry. Currently, many works shed light the obvious effects of primary reactions characteristic of other abiotic influences, manifested in changes in the genome activity. For example, it has been shown that the acting of weak SMFs induces changes in the expression of a number of genes [16,61,70,71].

Of particular interest are studies of the influence of the magnetic field on the dynamics of the cell cycle [72]. It was found that a change in the characteristics of a static and alternating MF can significantly change the mitotic index, which is a characteristic manifestation of stress impact. Hence, the change of this parameter indirectly indicates an alteration in the distribution of cells in the cell cycle and can be explained by a shift in the duration of the phases, for example, by blocking the cell cycle [73].

The nucleolus is the largest nuclear domain involved in the staged processes of biosynthesis of ribosomes [34,38,74]. These processes begin with the transcription of ribosomal genes (rDNA), proceed to the processing of rRNA and the further assembly of pre-ribosomal particles with the participation of many ribosomal and accessory proteins, and complete with the formation of large and small ribosome subunits for exporting them from the nucleus to the cytoplasm [50]. On ultrathin sections prepared by standard procedures, most of the nucleoli exhibit concentric arrangement of the three types of components, defined as fibrillar centers (FC), dense fibrillar component (DFC) and granular component (GC). In addition to these three main components, perinucleolar condensed chromatin can also be often seen [75]. The nucleolus is a dynamic organelle involved in the cell cycle. The materials included in its composition gradually disappear in prophase, and are again collected in telophase [76] (Figure 4). The question concerning to the details of the formation and relocation of the nucleolar material remains controversial. Numerous studies describe the location of the nucleolar components through conventional TEM, immuno-and cytochemical staining for TEM, immunofluorescent staining, etc. [27,40,77–79]. In telophase, the nucleolar components move to the chromosomes, and then gradually reassemble, forming PCM and pre-nucleolus [48,80,81]. A more complete understanding of the details of the process remains unexplored. It is unclear how PCM or nucleolar material forms the nucleolonema, and what is the mechanism of the gradual separation of pre-ribosomal particles from nucleoli? Also, the probable physical mechanisms of the movement of nucleolus materials during assembly and disassembly, as well as during the processing of ribosomes, are not assessed.

In general, the process of ribosome biogenesis (Figure 5, upper row) begins with the decondensation of rDNA in the fibrillar center and the subsequent synthesis of pre-rRNA at the border with a dense fibrillar component, where further processing of rRNA occurs, as established in all eukaryotes [38,82]. Next, the formation of pre-ribosomal particles takes place and after the

attachment of 5S RNA (synthesized in the nucleoplasm), these are transformed into a large and small pre-ribosomal particles [52], which then continue to mature and finally are exited into the cytoplasm, as believed independently of each other [83].

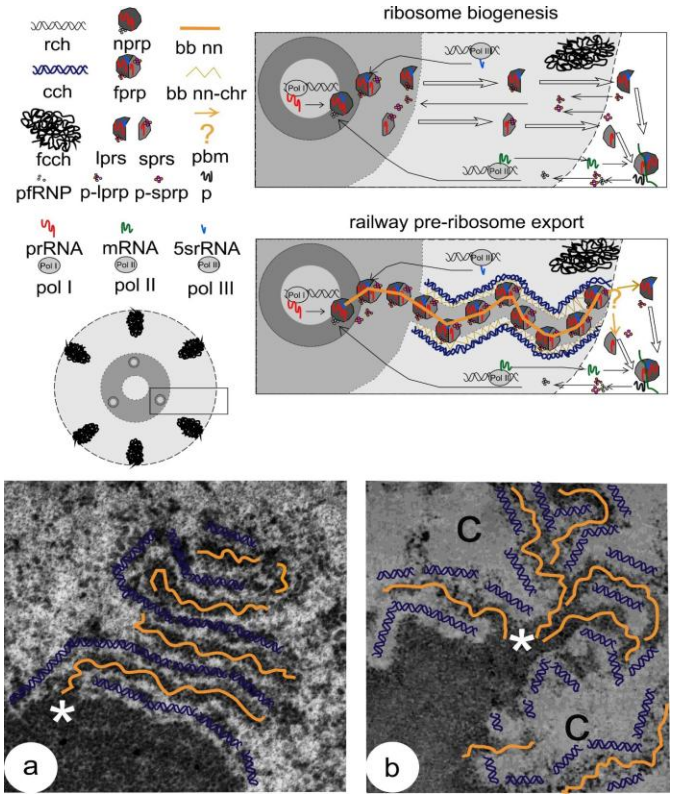


Figure 5. Features of biogenesis and structural elements involved in the bioscience of ribosomes in normal conditions and under the abiotic effects of a stressful nature. Notations: *rch*—relaxed chromatin, *cch*—condensed chromatin (chromonema-like structure), *fcch*—full condenced chromatin domain, *nprp*—new pre-ribosome particle, *fprp*—full assembled pre-ribosome particle, *lprs*—large subunit pre-ribosome subunit, *sprs*—small subunit pre-ribosome subunit, *bb nn*—backbone of nucleolonema, *bb nn-chr*—backbone between nucleolonema and chromonema-like fiber, *pbm*—pre-ribosome binding material, *pmRNP*—protein of RNP folding, *p-bprp*—protein of large pre-ribosome subunit, *p-sprp*—protein of small pre-ribosome subunit, *p*—protein, *prRNA*—pre-ribosomal RNA, *mRNA*—messenger RNA, *5SrRNA*—5S ribosomal RNA, *Pol I*—RNA polymerase I, *Pol II*—RNA polymerase II, *Pol III*—RNA polymerase III. *a*—schema of the association of nucleolonema with chromonema-like fiber on TEM nucleolus fragment contrasting by uranyl acetate and lead citrate nucleolus fragment, *b*—schema of the association of nucleolonema with chromonema-like fiber on TEM nucleolus fragment after Bernhard's EDTA regressive staining—to visualize DNA containing structures.

However, under the action of stress, the pattern of the process obviously changes (Figure 1.2, Figure 4, Figure 5, bottom row). The disturbance is manifested in the formation of outgrowths of the nucleolonema, which is a coil fiber, containing highly organized granular material that is connected

both with each other and leading to a change in shape from round to amoeboid (Figure 5, bottom row). The outgrowths of nucleolus are associated with a chromonema thread, and in all cases a light border and thin fibers connecting RNA and DNA, and containing nucleoprotein structures are identified between them (Figure 5, bottom row, a, b). Such associated structures extend from the nucleolus to the periphery of the nucleus (Figure 1.1c, 1.2c, 2.1c, 2.2b, 2.2c, 3.1c, 3.2c). It seems that such outgrowths of the nucleolus are like 'railway' for the delivery of maturing pre-ribosomal particles to the nuclear envelope and further to the outside.

It is obvious that the physical interactions and molecular mechanisms responsible for this process are extremely important. Since the connections that form and maintain such long elements of the nucleolonema must be very stable and homogeneous. Hence, a certain molecular structure, namely the thread we visualized, to which pre-ribosomal particles are attached, must have such properties. This will help to understand the nature of the linkage of the nucleolonema and the chromonema. One suitable component of such a structure would be Ki-67 protein [49]. The physical cause of chromatin decondensation and the joint influence of temperature and pH on the water fraction and indirectly on the structure and functions of biomolecules also remain unclear. The possible reason could be the suppositional alteration in pH in the aqueous encirclement of biological supramolecular complexes caused by a change in the MF and application of low positive temperatures, while the decrease in diffusion of gases and reduction of their availability for the regulation of biochemical reactions takes place.

Our data suggest that a possible explanation for the surprising effect of changing the usual pattern of transformation of the structural organization of a nucleolonema in late interphase and early prophase may be delayed processing of ribosomes observed under stress (Figure 5, bottom row) [26]. This observed pattern seems to be related to the specific effect of binding the chromatin surface with the nucleolonema (Figure 1.1c, 1.2c, 2.1c, 2.2b, 2.2c, 3.1c, 3.2c; Figure 4), similar to what is formed in telophase (Figure 1.1a, 1.2a, 2.1a, 2.2a, 3.1a, 3.2a; Figure 4). Investigations of the transforming of nucleolar material and PCM in the cell cycle were undertaken repeatedly, however, our detailed study allowed us to use a new, easily reproducible interesting approach when using the combined action of cold and WMF and SMF.

5. Conclusion

This approach allowed a significant increase in the number of cells with an altered phenotype of nucleolus in the pre-prophase of cell cycle. This, in turn, provides an opportunity to investigate in detail the phenomenon of 'railway' for pre-ribosomal particles, which is an association of nucleolonema and chromonema, and to study transformations of the nucleolus and PCM in the cell cycle using molecular, biochemical and cytological methods. In addition, the patterns of interaction of the nucleolar material with the processes of chromosome compactization/decompactization may be promising models for visualizing epigenetic phenomena.

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Conflict of interest

The authors declare no competing financial interests.

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