DOI: https://doi.org/10.17816/ecogen623901
Review Article

# The peculiarities of cell elongation growth of cereal coleoptiles under normal and flooding conditions

Anastasia A. Kirpichnikova [1], Guzel R. Kudoyarova [1, 2],
Vladislav V. Yemelyanov [1], Maria F. Shishova [1]

[1] Saint Petersburg State University, Saint Petersburg, Russia;
[2] Ufa Institute of Biology, Ufa Federal Science Center of the Russian Academy of Sciences, Ufa, Russia

ABSTRACT

The review examines modern knowledge on the mechanisms of the early stages of plant cell elongation growth. Coleoptiles are used as a model object representing juvenile organs of cereal seedlings. Elongation growth is considered to be a protective morphophysiological stage of seedling development during hypogeal germination. The molecular mechanisms of elongation growth include: changes in the properties of the cell wall, activation of proton pumps, as well as aquaporins of plasma membrane and tonoplast. Particular attention is paid to the hormonal system of regulation, including auxin and ethylene. Coleoptiles of rice, a semi-aquatic plant tolerant to oxygen deficiency, demonstrate that the mechanisms of elongation growth are changing intensively under submergence, but they completely ensure cell growth. There is also a redistribution of importance and abundance between phytohormones. The data presented in the review indicate the necessity to continue investigations on the mechanisms of elongation growth under normal and stress conditions.

**Keywords:** submergence; coleoptile; elongation growth; rice (*Oryza sativa* L.).

**To cite this article**
Kirpichnikova AA, Kudoyarova GR, Yemelyanov VV, Shishova MF. The peculiarities of cell elongation growth of cereal coleoptiles under normal and flooding conditions. *Ecological genetics*. 2023;21(4):401–417. DOI: https://doi.org/10.17816/ecogen623901

**Received:** 07.11.2023 **Accepted:** 05.12.2023 **Published:** 24.01.2024

DOI: https://doi.org/10.17816/ecogen623901
Обзорная статья

# Особенности роста растяжением клеток колеоптилей злаков в норме и при затоплении

А.А. Кирпичникова [1], Г.Р. Кудоярова [1, 2], В.В. Емельянов [1], М.Ф. Шишова [1]

[1] Санкт-Петербургский государственный университет, Санкт-Петербург, Россия;
[2] Уфимский институт биологии Уфимского федерального исследовательского центра Российской академии наук, Уфа, Россия

АННОТАЦИЯ

В обзоре рассмотрены современные представления о механизмах реализации начальных этапов роста растяжением растительных клеток на примере клеток колеоптилей — ювенильных органов проростков злаков. Рост растяжением колеоптилей расценивается как защитный морфофизиологический этап развития проростка при подземном прорастании. Рассмотрены такие молекулярные механизмы роста растяжением, как изменение свойств клеточной стенки, активация протонных насосов, а также аквапоринов плазмалеммы и тонопласта. Особое внимание уделено гормональной системе регуляции роста растяжением, в том числе ауксину и этилену. На примере колеоптилей риса — полуводного растения, толерантного к недостатку кислорода, — продемонстрировано, что в условиях затопления механизмы роста в значительной степени меняются, однако полностью обеспечивают рост клеток растяжением. Происходит также перераспределение значимости между фитогормонами. Приведенные в обзоре данные указывают на необходимость продолжения исследований механизмов роста растяжением в норме и в стрессовых условиях.

**Ключевые слова:** затопление; колеоптиль; рост растяжением; рис (*Oryza sativa* L.).

**Как цитировать**

Кирпичникова А.А., Кудоярова Г.Р., Емельянов В.В., Шишова М.Ф. Особенности роста растяжением клеток колеоптилей злаков в норме и при затоплении // Экологическая генетика. 2023. Т. 21. № 4. С. 401–417. DOI: https://doi.org/10.17816/ecogen623901

**Рукопись получена:** 07.11.2023 **Рукопись одобрена:** 05.12.2023 **Опубликована:** 24.01.2024

## BACKGROUND

Elongation growth is a unique stage in plant cell development. It refers to multiple irreversible increases in cell size, mainly along the vertical axis. The intensity of this elongation can be up to a thousandfold [1, 2]. It is thought that during the evolution of plants, this type of growth arose quite early, at the stage of algae development, and represents a compensatory mechanism for an attached lifestyle under conditions requiring constant movement to nutrition sources, such as light, water, and mineral elements [3]. The increasing complexity of the structure and the emergence of various regulatory systems at the whole organism level have led to the subordination of the growth intensity of various organs, as well as the possibility of changing growth processes under the influence of environmental factors [4]. In higher plants, elongation growth is most intense in zones adjacent to the meristems, and the ability of cells to elongate is retained for a relatively short time. Nevertheless, because meristems are constantly functioning, elongation growth is preserved in plants throughout ontogenesis. Through this process, the axial and lateral organs are enlarged. The unequal intensity of elongation growth underlies tropisms, which are plant growth responses to the unilateral influences of various environmental factors.

This process is most noticeable in the growth of the axial organs of the seedling, especially at the germination stage and the subsequent period of formation of the first true leaves, which are responsible for photosynthesis. Elongation growth is especially important during the juvenile development of a seedling under etiolated (in the absence of light) conditions. Deep germination allows the seedling to overcome the soil layer and reach light, which is the main source of energy for photosynthetic organisms.

Studies on the mechanisms of elongation growth have been ongoing more than a century. The first documented interest in this process was the work by Charles and Francis Darwin "The Power of Movement in Plants" [5]. In this study, coleoptiles, the juvenile organs of cereal seedlings, were used as model objects to explore these mechanisms. A huge amount of data in this subject has accumulated. These data indicate the multistage nature of implementation, as well as a multilevel system of regulation of elongation growth in various organs and tissues, as well as in various plant species. The intensity of elongation growth can change under the influence of various stressors. Despite the abundance of experimental results on elongation growth, we are still very far from a detailed understanding of the universal mechanisms underlying this process.

This review presents a comparative analysis of the main mechanisms of elongation growth under normal conditions and under the influence of stress factors, such as lack of oxygen, using the coleoptile of cereals as an example.

## MECHANISMS OF ELONGATION GROWTH IN COLEOPTILE CELLS

The coleoptile of cereals is a juvenile organ of time-limited development, whose main function is to protect the true leaf during germination. It has a cylindrical shape and two vertical conductive bundles in its structure. Chloroplasts can form in the outer cells of the epidermis, whereas the inner layers of cells are characterized by large amyloplasts [6]. The growth of the coleoptile stops when it reaches the soil surface and is exposed to light [7]. At this point, a "breakthrough" of the apex of this organ is occurs, in which the cell death program is initiated [8]. Under normal conditions, by day 4 of development, coleoptiles complete their morphophysiological development program [9, 10].

Seedlings with longer coleoptiles are believed to have many advantages. For example, a long coleoptile ensures seed germination in deeper layers of the soil, which prevents the negative effects of temperature fluctuations, lack of moisture, or even the action of herbicides and rodents, which are characteristic of surface germination [11–13]. However, a comparative analysis of the growth of coleoptiles under normal conditions does not enable unambiguous assessment of parameters, such as stability and final productivity of plants [14, 15]. Apparently, dependence manifests only under the influence of a stress factor.

Thus, the elongation growth of coleoptile cells is a complex process that involves almost all of their compartments (including vacuole, Golgi apparatus, endoplasmic reticulum, and cell wall). The intensity of elongation growth is regulated at the transcriptional and posttranslational levels [16, 17], and is under the control of many external factors.

## ROLE OF THE CELL WALL

It is impossible to understand elongation growth without considering the dynamic processes occurring in cell walls [18–20]. Their importance is mediated by the role of the exoskeleton, which maintains cell shape and protects intracellular compartments from biological, chemical, and physical damage. These structures have two mutually exclusive properties: rigidity to provide cell protection and extensibility to accommodate growth caused by turgor pressure [1, 2]. Cell walls have a multicomponent profile that varies depending on the plant species and development stage [21, 22]. Cellulose microfibrils are the largest polysaccharides in the cell wall. Their location determines the direction of elongation growth.

They interact with molecules of xyloglucans and pectin. This type of cell wall is characteristic of dicotyledonous plants [2]. α-Expansins, a group of small proteins able to modify the bonds between xyloglucan and cellulose molecules, are important for elongation growth [23]. The mechanism of this process is still unclear, because α-expansins themselves do not have their own enzymatic activity. However, expansins initiate a 100-fold elongation of tobacco cells *in vitro* [[1].

Unlike dicotyledonous plants, the primary cell walls of cereals, studied mainly using root cells as examples, are distinguished by having a special type of noncellulosic polysaccharides, which distinguishes them as a special type II [2]. The leading position in their structure is occupied by glucuronoarabinoxylan and glucan with a mixed type of bond. It is assumed that the mechanism of cell wall transformation during elongation growth in cereals displays some traits of this process compared with other flowering plants. High growth rate is consistent with the accumulation of mixed-linkage glucan, whose function is the same as that of type I cell wall pectins [24]. Similarly, the content of glucuronoarabinoxylan, a connecting glycan of the primary cell walls of cereals, increases, and its domain organization also changes [25]. Changes in the properties of the cell wall during elongation growth are accompanied by high expression of a rather large group of genes. Up to 40% of this group consists of genes for expansins and xyloglucan endotransglycosylases, as well as glycosyl transferases, peroxidases, and enzymes for the synthesis of cell wall components [2, 7]. During elongation growth, the protein profiles of cell walls also undergo significant changes [26, 27].

Despite research using the most modern methods, the processes occurring in the cell walls of coleoptiles are mostly still not fully deciphered and there is need to further explore them.

## VACUOLIZATION AND ROLE OF AQUAPORINS

The driving force for growth is turgor pressure, which is predominantly caused by internal osmotic pressure in the vacuolar system [28]. The value of the latter in plant cells usually ranges from 5 to 10 atm and is balanced by the mechanical properties of the cell walls [1, 29]. The accumulation of osmotically active ions and metabolites, such as sugars, organic and amino acids, $K^+$ ions, and other compounds, in the vacuole causes water absorption. The membrane potential, which ensures the transport of these compounds through the tonoplast, is created by two proton pumps, $H^+$-pyrophosphatase and $H^+$-ATPase [30].

Due to cell wall loosening and preservation of osmotic potential, water is intensively absorbed by vacuoles. It is thought that a change in the properties of the cell wall can be perceived as a signal that is detected by receptor-like kinase (LRX/FER) and subsequently leads to a significant increase in the central vacuole [31]. Another connecting factor between the size of the cell and the vacuole can be proteins of the networked (NET) family, which can interact with actin filaments and membranes [32]. *NET4A* mutants significantly change the cell vacuolation intensity during elongation growth [33].

There is no doubt that a sharp increase in the vacuole is accompanied by an intense flow of water into it. Water can penetrate cell membranes directly through the phospholipid bilayer [34]. However, aquaporins (transmembrane proteins responsible for water transport) are predominantly involved in water absorption into the vacuole [35, 36]. The intensive activity of aquaporins was revealed in the composition of the plasma membrane (PIP, plasma membrane intrinsic proteins) and tonoplast (TIP, tonoplast intrinsic proteins) [30, 36]. This is consistent with findings on changes in the hydraulic conductivity of biological plant membranes upon modulation of the amount of aquaporins obtained using molecular genetic methods [37, 38]. Unfortunately, there are no published data on the contribution of aquaporins to the elongation growth of cereal coleoptile cells. However, this contribution is indirectly confirmed by their participation in the growth of adult plant organs [39]. For example, there are differences in dynamics of gene expression between *ZmTIPs* and *ZmPIPs* at the stage after germination [40], which may indicate an unequal representation of aquaporins in the plasmalemma and tonoplast during cell elongation.

Thus, the general increase in the external dimensions of the cell during the elongation growth of coleoptiles is accompanied by intense vacuolization due to an increase in the hydrostatic permeability of some cell membranes.

## ROLE OF PROTON PUMPS

Intense intracellular changes in a cell during elongation growth demonstrate the importance of homeostatic systems, including the pH-stat system. It is a combination of elements of the buffer capacity of the cytoplasm and the activity of several proton pumps localized on the plasmalemma and tonoplast [41]. There is renewed discussion about the role of protons as an independent signal or secondary messenger in the perception of several factors [42]. Changes in pH can differ in the magnitude of the gradient and in the dynamics of the hydrogen ion content in the three most important compartments, namely, the apoplast, cytosol, and vacuole. The role of apoplast acidification during root growth was further confirmed in a 2023 study [43]. The mechanism of this acidification is closely related to the activation of the plasma membrane $H^+$-ATPase; therefore, it can be considered as a key factor

in determining the pH gradient between the apoplast and cytoplasm. The subsequent stage of elongation growth is directly related to the processes occurring already at the cytosol/vacuole boundary, i.e., the activation of tonoplast proton pumps, which include $H^+$-ATPase and $H^+$-PPase (proton pyrophosphatase). These three transporters/enzymes form the basis of the dynamic pH regulation of plant cells. The main properties of these pumps are discussed below.

## Role of the plasma membrane $H^+$-ATPase

The plasma membrane $H^+$-ATPase belongs to the family of P-type ATPases and is characterized by the formation of a phosphorylated intermediate [30]. It consists of one protein (100 kDa). The enzyme consists of 10 transmembrane domains, which supposedly constitute 20% of the protein. Some of the protein is converted to the apoplast (10%). A significant proportion of the protein is localized in the cytoplasm (70%), which indicates the importance of the cytoplasmic posttranslational regulation of this enzyme [44]. The $H^+$-ATPase of the plasma membrane of plant cells has a more elongated C-terminus, which performs a regulatory autoinhibitory function and can lead to an eightfold increase in the need for ATP while maintaining the number of transported hydrogen ions [45]. In vascular plants, including cereals, the plasma membrane $H^+$-ATPase is encoded by a multigene family, in which five subfamilies are usually distinguished [46, 47]. Unfortunately, no data have yet been obtained on changes in the expression of genes encoding plasma membrane $H^+$-ATPase during elongation growth. It is assumed that the main regulatory processes are associated specifically with posttranslational regulation [48, 30]. The most active mechanisms include phosphorylation/dephosphorylation of amino acid residues at the C-terminus, especially the Thr947 residue. The presence of a phosphate group ensures binding to 14-3-3 proteins and a subsequent decrease in autoinhibition [49].

The hypothesis that the activity of plasma membrane $H^+$-ATPase during elongation growth in coleoptile cells is mediated by a change in the number of enzyme molecules in the membrane has not yet been falsified [50]. Experimental evidence indicates a nonlinear change in the activity of the plasma membrane $H^+$ pump [51–53]. However, a comparative analysis of the genes encoding the plasma membrane $H^+$-ATPase during elongation growth could expand our understanding of the mechanisms of regulation of this enzyme/transporter.

## Role of the tonoplast $H^+$-ATPase

The vacuolar $H^+$-ATPase, which ensures the generation of a proton gradient on the tonoplast, represents a V-type ATPase and has homology with F-type ATPases (ATP synthases) of chloroplasts and mitochondria [54]. It is represented by two domains, namely, the peripheral supramembrane ($V_1$) and membrane integral ($V_0$) domains [30, 55]. The total mass of the complex is approximately 800 kDa [56]. Genes encoding vacuolar $H^+$-ATPase have been identified in all plant genomes sequenced to date. Encoding of vacuolar $H^+$-ATPase subunits can be performed using both single genes and gene families. Phylogenetic analysis suggests that different V-ATPase subunits, which are structural parts of the same protein, evolved differently [57, 58]. There is genus- or even species-specific specialization of isoforms of V-ATPase subunits [59], suggesting the presence of mechanisms for regulating enzyme activity by changing the subunit composition of the enzyme complex [60]. Changes in enzyme activity were recorded upon phosphorylation of subunits and further interaction with 14-3-3 proteins, indicating a complex system of posttranslational regulation [61].

The activity of vacuolar $H^+$-ATPase depends on several environmental factors; therefore, the special name “eco-enzyme” was proposed for the V-ATPase of higher plants [30, 62]. Experimental evidence, although very limited, confirm the importance of this enzyme complex during plant cell ontogenesis, including elongation growth [59]. Changes in the functional activity of V-ATPase during elongation growth were demonstrated using maize coleoptile cells [53]. Proteomic analysis indicated a dynamic decrease in the amount of subunit E when coleoptile growth stopped during etiolated development [5].

## Role of the tonoplast $H^+$-pyrophosphatase

We will conclude this section by considering the properties and functions of another tonoplast proton pump, $H^+$-V-PPase, which uses the energy of pyrophosphate to generate a proton gradient [63, 64]. Recent data indicate the physiological significance of $H^+$-V-PPase [65–67]. Analysis of evolution showed an expansion of the family of genes encoding $H^+$-PPase in angiosperms due to an increase in copy number [68]. The expansion of the number of representatives of the gene family, of course, raises the question of the specificity of their expression in various tissues and cells, depending on the action of various factors. The protein molecule of $H^+$-PPase forms a rosette of 16 transmembrane coils. Both ends of the enzyme molecule (both N- and C-terminal regions) face the vacuole, and its active form is represented by a homodimer [69]. Pyrophosphatase is characterized by posttranslational modification, including the participation of 14-3-3 proteins [70].

V-PPase is present in most plant tissues and cells; however, the amount of this enzyme varies with the tissue [71]. High accumulation of V-PPase mRNA and protein has been reported in shoot apical meristems and leaf primordia, cells characterized by high levels of pyrophosphate. The amount of V-PPase in terms of vacuolar

membrane protein in three-day-old *Arabidopsis* cotyledons was twice as high as that in 10-day-old cotyledons. Similarly, the highest transport activity of this enzyme was demonstrated in the youngest, three-day-old maize coleoptile [53].

To summarize, all of the listed proton pumps are responsible for the generation of an electrochemical gradient of hydrogen ions on the plasmalemma and tonoplast, which ensures the entry of osmotic agents into the cell and vacuole. $H^+$ pumps participate in regulating the intensity of growth processes, including elongation growth of cereal cells. Thus, the work of the plasmalemma $H^+$-ATPase ensures acidification of the cell wall, thereby increasing the elasticity of the latter. However, there are too little data of this kind to conclude about a possible redistribution of the significance of these three pumps during elongation growth.

## ROLE OF THE HORMONAL REGULATION

The above data indicate the involvement of a variety of cell components in the implementation of elongation growth and the consistency of processes occurring at the tissue/organ/organism level. Experimental results indicate the role of the hormonal system in the implementation of elongation growth, which suggests not only the action of individual phytohormones but also the presence of cross-regulation. Elongation growth is regulated by hormones, such as gibberellins, brassinosteroids, and abscisic acid. [72–74]. Nevertheless, the special importance of two phytohormones in controlling the elongation growth of coleoptilism, auxin, and ethylene should be recognized.

### Auxin

In the 1970s, conclusions were made regarding the ability of the phytohormone auxin to induce elongation growth of coleoptile cells of cereals [3, 75]. These conclusions formed the basis of the "acid growth" theory. Taking into account modern ideas, this theory can be briefly represented by the following chain of events: It begins with the activation of plasma membrane $H^+$-ATPase, resulting in cell wall acidification. This, in turn, leads to the activation of many cell wall proteins, namely, xyloglucan endotransglycosylase/hydrolase (XTHs) [76], pectin methylesterase inhibitors (PMEIs) [77], and expansins [78]. Increasing the concentration of protons and the activity of these proteins weakens the interaction between polysaccharides in the cell wall, leading to an increase in the distance between cellulose microfibrils. In some cases, apoplast pH can decrease down to reach 4.0 [79]. Increased operation of the proton pump leads to a change in the membrane potential and, consequently, to the activation of many ion channels, including those for $K^+$ ions [80]. Consequently, osmotically active substances enter the cell. The next stage involves the synthesis of new cellulose microfibrils and the synthesis/secretion of polysaccharides, cell wall matrix proteins, and cell membrane components, which collectively fill the increasing cell surface. The driving force for elongation growth is created by the cell's proton pumps, and the direction is determined by the orientation of the cellulose microfibrils.

The question of the mechanism by which auxin activates the plasma membrane $H^+$-ATPase when auxin is added remains open. The phytohormone entering cells is receptorized with the participation of the F-Box protein TIR1/AFB [81]. This leads to the rapid degradation of Aux/IAA proteins and the release of ARF family transcription factors, leading to a rapid activation of several groups of auxin-specific response genes [82]. However, no transcriptional activation of plasma membrane $H^+$-ATPase genes was detected. Currently, the generally accepted viewpoint is that phosphorylation plays a role in the mechanism of hormonal activation of plasma membrane $H^+$-ATPase [83]. Auxin initiates the activity of the SAUR family protein, which inhibits PP2C. D-phosphatase [84], which leads to an increase in auxin-specific phosphorylation. Another mechanism of action of the hormone may be mediated by activation of auxin kinase (TMK1), which is capable of direct phosphorylation of Thr947, which leads to activation of plasma membrane $H^+$-ATPase and apoplast acidification [85].

The point of view of increasing the proton-transporting activity of plasma membrane $H^+$-ATPase due to an increase in its amount in membrane proteins as a result of changes in the intensity of exo- and endocytosis remains relevant [50]. Auxin-binding protein 1 (ABP1), $Ca^{2+}$ ions, and proteins of the SNARE family may be involved in the implementation of this pathway [86–88].

Further events can be represented as an auxin-induced increase in cell wall elasticity and vacuolization due to intensive water absorption [31].

### Ethylene

The phytohormone ethylene has the opposite effect on the elongation of coleoptiles and seedlings in general. It causes specific morphological changes, which are commonly called the "triple reaction," namely, shortening, thickening, and bending, which increase the mechanical properties of the seedling when growing through soil layers [89]. Using this reaction on a model object (A*rabidopsis* seedlings), the fundamental sequence of the receptor-transduction cascade of this phytohormone was deciphered [90]. The exact opposite process occurs when ethylene affects the growth of rice seedlings; in this case, a significant elongation of juvenile organs, such as coleoptiles and mesocotyls, is recorded [91]. This phenomenon suggests that in rice coleoptiles, there is another mechanism for regulating elongation growth under the influence of ethylene.

In rice coleoptiles, ethylene promotes cell elongation and inhibits cell expansion. Consequently, the coleoptile becomes longer and thinner. Its elongation pushes the shoot tip above the soil surface, and the thinner tip of the juvenile organ reduces mechanical resistance as the seedlings emerge from the soil. The accumulation of two ethylene cascade proteins (OsEIL1 and OsEIL2), specific for rice seedlings, activates the expression of genes involved in the detoxification of reactive oxygen species [91]. These forms, under the influence of ethylene, predominantly accumulate in the apical region of the juvenile organ. In this case, the cell wall properties change because the intensity of expression of the family of genes encoding expansins and peroxidases, including those localized in the cell wall, changes [91].

Unfortunately, there is no evidence to support the possible activation of proton pumps by the action of ethylene on the elongation of coleoptile cells. Nevertheless, there is indirect evidence that indicate the possibility of regulating the expression of genes encoding the subunits of vacuolar $H^+$-ATPase [30]. One of the mechanisms influencing the degree of vacuolization may be the inhibition of the accumulation of organic acids in vacuoles by ethylene, i.e., it causes a change in the balance of osmotically active compounds [92]. Moreover, a possible inhibitory effect of ethylene on the activity of tonoplast aquaporins was established [93]. However, considering that the effect of ethylene on coleoptile cells differs from that on cells of other organs, studies are required that could reveal the ethylene-mediated participation of the listed proteins in the implementation of the elongation growth mechanism specifically in coleoptiles.

## ROLE OF STRESS FACTORS

The effect of external stress factors on elongation growth is diverse. Thus, intensive elongation growth of coleoptile and mesocotyl cells of maize seedlings was recorded during etiolation. In contrast, the action of light leads to rapid inhibition of elongation growth, and this effect depends on the spectral composition of the stimulus. The effect of blue light was more intense than that of red light [7]. Stress factors such as heavy metals, drought, and salinity also have the ability to regulate the intensity of elongation growth [94–96].

Thus, external factors primarily inhibit coleoptile growth, but the reverse process is also noted. An example of this is the germination and primary stage of growth of rice (*Oryza sativa* L.), a representative of the group of semiaquatic plants that can germinate from a depth of up to 35 cm [97].

### Lack of oxygen

Under flooding conditions, the availability of oxygen sharply decreases, leading to a significant change in the physiological and biochemical processes recorded in seedlings [36, 98]. With this type of germination (hypo- or anoxic, depending on the flooding duration), germination consists of intensive growth of the coleoptile with almost complete cessation of leaf and root growth [99]. A sharp acceleration in the growth of shoots (including coleoptiles) is associated with one of the strategies of plant adaptation to oxygen deficiency, namely, the avoidance strategy (low-oxygen escape syndrome, LOES).

In rice varieties resistant to flooding, more intense elongation growth of coleoptile cells is registered, which results in a more rapid achievement of the aerobic environment and thereby the supply of oxygen to the entire seedling [15, 100, 101]. The development program of coleoptiles during flooding differs significantly from that under normal conditions (see above). Under these conditions, the aging program slows down, but elongation growth is enhanced [9]. The hypothesis on the role of the coleoptile as a "snorkel," which was proposed in the 1970s [102], has recently received numerous confirmations [103]. It has been established that when flooded, rice coleoptiles can elongate by 6–12 mm per 24 h [10]. Intensive elongation growth was demonstrated for cells of the lower third of rice coleoptiles, whereas this indicator was significantly inhibited near the apex [104]. Additionally, this effect intensified with age but was practically absent in young seedlings just beginning to develop, in which elongation growth proceeded with almost equal intensity along the entire length of the coleoptile. In this regard, it is not surprising that the transcription profile differed significantly between these two zones of the coleoptile and in seedlings of different ages. Genetic mapping analyses revealed several (from 4 to 13) quantitative trait loci (QTL) associated with the development of rice seedlings under flooding [105].

The process of elongation growth under flooding conditions was accompanied by increased expression of genes encoding expansions *EXPA7* and *EXPA12*, as well as genes encoding pectinesterases [104, 106, 107]. Changes in expansin levels certainly influence the state of the cell wall during oxygen deficiency. The activation of soluble peroxidases under flooding conditions may be important [108]. The listed data indicate the mechanisms that increase the elasticity of the cell wall. However, under normoxic conditions, the fundamental mechanism is acidification, which is achieved through activation of the plasma membrane $H^+$-ATPase. Whether this mechanism can be implemented in rice coleoptiles during flooding remains questionable because the lack of oxygen leads to severe energy starvation and, consequently, to the limitation of ATP, the energy substrate for the operation of the plasma membrane proton pump [9, 10, 104]. A different mechanism has been proposed to explain the acidification of cell walls. The elongation of coleoptile cells increased by 8–16 times when solutions saturated

with $CO_2$ were used [109]. However, this mechanism also requires additional confirmation because the $CO_2$ formed during alcoholic fermentation is largely released from plant tissues into the environment [98]. A decrease in the level of ATP in coleoptile cells during germination under flooding conditions is one of the reasons for the decrease in $H^+$-ATPase activity not only on the plasma membrane but also on the tonoplast. The accumulation of lactate because of the activation of lactic acid fermentation leads to acidification of the cytoplasm [98], and this, in turn, activate these proton pumps [110, 111]. Thus, a very dynamic change in the activity of $H^+$-ATPases is noted, which can be modified by the activity of kinases/phosphatases responsible for phosphorylation of the autoinhibitory domain of the plasma membrane $H^+$-ATPase and the subunits of the tonoplast $H^+$-ATPase. The activation of anoxic metabolism is associated with increased activity of some enzymes, including pyruvate phosphate dikinase (PPDK), resulting in the accumulation of pyrophosphate. Therefore, we can assumed that $H^+$-V-PPase is activated. The energy of pyrophosphate hydrolysis is approximately 60% of that of ATP hydrolysis [112]. In aerobically grown rice seedlings, oxygen deficiency activated $H^+$-V-PPase and stimulation of the expression of its encoding genes [113]. Therefore, cells are able to solve several problems, namely, equalizing the pH level of the cytosol, generating an electrochemical potential on the tonoplast, restoring the transport activity of osmolytes into the vacuole, and creating the necessary driving force for water transport [67]. Unfortunately, we did not find literature on changes in the role of aquaporins during elongation growth of rice coleoptile cells, and data on the role of aquaporins in other growing organs of seedlings are contradictory [36]. The genes encoding $H^+$ pumps and aquaporins are not included in the identified QTLs associated with coleoptile growth; therefore, there may be other mechanisms underlying the regulation of elongation growth under flooding conditions.

This review presents the results of an analysis of a recently conducted large-scale study of the promoter region of genes involved in ensuring the germination and growth of rice seedling coleoptiles. Representatives of several families of transcription factors have been identified, namely, MYB, bZIP, AP2/ERF, ARF, WRKY, ZnF, MADS-box, NAC, AS2, DOF, E2F, ARR-B, and HSF [114]. They participate in the regulation of fission processes, elongation growth, and many carbohydrate metabolism genes. Additionally, the rice varieties most resistant to flooding were characterized by the activity of transcription factors such as HY5 (bZIP), GBF3, GBF4 and GBF5 (bZIP), DPBF3 (bZIP), ABF2, ABI5, bHLH, and BES/BZR, which are involved in transduction cascades of phytohormones ethylene, auxin, gibberellin, abscisic, and jasmonic acids. This confirmed that resistance to oxygen deficiency and the maintenance of intensive elongation growth during flooding is determined by several phytohormones [114].

Let us consider the importance of two phytohormones, auxin and ethylene, in the regulation of elongation growth under conditions of oxygen deficiency. The significance of these hormones under normoxic conditions was analyzed as described above. The role of auxin in initiating elongation growth during flooding has been debated for a long time. For example, disruption of the synthesis of this hormone and its polar transport was noted during oxygen starvation in rice [115]. The addition of exogenous auxin did not increase the elongation growth of coleoptiles under anoxic conditions [116]. However, a comparative analysis of rice varieties that differed in coleoptile length showed that the effect of auxin on elongation growth depends on the activity of the AUX1 transporter. Expression of the gene encoding was higher in long-coleoptile rice varieties under flooding [117]. Along with this, a decrease in the expression of the *miR393a* gene was revealed, which negatively regulates the mRNA of the auxin receptor Transport Inhibitor Response 1 (TIR1), which intensifies the phytohormone signaling cascade [118]. Thus, the effect of auxin on the elongation growth of rice coleoptiles under flooding conditions can have an effect of varying intensity, depending both on the participants in the growth response and on the initial genetic characteristics of the plant analyzed, which are inherent in the ability to elongate. In considering the role of ethylene, it should be noted that this gaseous phytohormone is intensively accumulated under conditions of oxygen deficiency [109]. This, in turn, leads to increased expression of *SUB1A* and *SNORKELs* genes [106]. Both hormones belong to the group of transcription factors (Ethylene Responsive Factor of group VII, ERF-VII), a distinctive feature of which is the preservation of the N-terminus of the molecule under conditions of oxygen deficiency. Therefore, these factors do not undergo hydrolysis and thereby participate in the regulation of so-called anaerobic genes [119]. Transcription factors SNORKELs control the strategy of active avoidance of flooding (LOES), in which shoot growth is stimulated, and SUB1A control the strategy of dormancy, or true resistance to hypoxia (low-oxygen quiescence syndrome, LOQS), in which growth is inhibited and adaptation is achieved by changing metabolism [98, 119].

## CONCLUSION

To summarize this review, it is necessary to emphasize the variety of protective functions of a juvenile organ, such as the coleoptile of cereals. The primary function is to protect the seedling leaf as it grows through the soil. This requires intensive elongation of the coleoptile, which is achieved through elongation growth, a more economically advantageous process than cell division.

When light enters the seedling upon reaching the surface, it abruptly stops growth and initiates a program of aging and death of coleoptile cells. In this model, elongation growth depends on acidification of the cell wall, which is mediated by activation of the plasma membrane $H^+$-ATPase and induced by the phytohormone auxin. The change in the hydrogen ion gradient at the apoplast/cytoplasm and cytoplasm/vacuole boundaries is supported by the work of two $H^+$-ATPases, whose functioning is ensured by the synthesis of ATP under conditions of active respiration. Multiple increases in cell length are accompanied by vacuolization, which indicates the active involvement of aquaporins of the plasmalemma and tonoplast in ensuring water transport. The properties of cells in different zones of the coleoptile and their ability to support elongation growth change with age. The role of the phytohormone ethylene, which affects the growth of coleoptiles, is radically different from the influence of other axial organs. High rate of cell growth and softening of the upper part of the coleoptile allows the developing leaf to break easily through its top when emerging from the soil surface. Consequently, by initiating different molecular mechanisms, auxin and ethylene intensify the implementation of coleoptile physiological function.

If stressful conditions develop, the intensity of elongation growth is adjusted. It is largely suppressed by the action of heavy metals, high temperature, drought, and salinity. However, stress factors such as lack of oxygen, on the contrary, can sharply activate growth because of the development of the "avoidance" strategy (LOES). This phenomenon is noted in the coleoptiles of rice, which is a semiaquatic plant well adapted to germination and primary growth under flooded conditions. Metabolic changes (glycolysis and fermentation increase), and a sharp decrease in ATP are partially compensated for by an increase in the level of pyrophosphate; therefore, conditions arise for the activation of the vacuolar $H^+$-PPase instead of intensifying the work of ATPases. The necessary conditions for the initiation of elongation growth (acidification and subsequent increase in the elasticity of cell walls, maintenance of cytoplasmic pH, vacuolization) are achieved by completely different mechanisms. Ethylene assumes major importance in growth regulation. Thus, the protective function of the coleoptile is significantly changed depending on the nature of the stress.

Unfortunately, many peculiarities of the implementation of elongation growth under normal conditions and stress are still far from being fully understood. Recently, special attention is focused on correlating the intensity of coleoptile growth with resistance to unfavorable conditions. Coleoptile length can be used to create special test panels for the development of promising new varieties of rice and other plants that are resistant to flooding.

## ADDITIONAL INFORMATION

**Acknowledgments.** The review is dedicated to the 300th anniversary of Saint Petersburg State University.

**Authors' contribution.** Thereby, all authors made a substantial contribution to the conception of the study, acquisition, analysis, interpretation of data for the work, drafting and revising the article, final approval of the version to be published, and agree to be accountable for all aspects of the study. The contributions of each author: A.A. Kirpichnikova — collection and processing of the material; G.R. Kudoyarova — concept and idea of the study; V.V. Yemelyanov — concept and idea of the study, collection and processing of the material, making final edits; M.F. Shishova — concept and idea of the study, writing the main part of the text, making final edits, funding acquisition.

**Funding source.** This research was funded by the Russian Science Foundation (grant No. 22-14-00096, https://rscf.ru/en/project/22-14-00096/).

**Competing interests.** The authors declare no conflict of interests.

## REFERENCES

**1.** Cosgrove DJ. Plant cell wall extensibility: Connecting plant cell growth with cell wall structure, mechanics, and the action of wall-modifying enzymes. *J Exp Bot*. 2016;67(2):463–476. DOI: 10.1093/jxb/erv511

**2.** Gorshkova TA. Cell wall is a multifunctional structure of a plant. Los' DA, editor. *LXXX Timiryazev readings*. Moscow: Nauka, 2021. 118 p. (In Russ.)

**3.** Field BB. The role of auxin in regulatory systems in plants. Chailakhyan MH. *XLIV Timiryazev readings*. Leningrad: Nauka, 1986. 80 p. (In Russ.)

**4.** Hilty J, Muller B, Pantin F, Leuzinger S. Plant growth: The what, the how, and the why. *New Phytol*. 2021;232(1):25–41. DOI: 10.1111/nph.17610

**5.** Kutschera U, Deng Z, Oses-Prieto JA, et al. Cessation of coleoptile elongation and loss of auxin sensitivity in developing rye seedlings: A quantitative proteomic analysis. *Plant Signal Behav*. 2010;5(5):509–517. DOI: 10.4161/psb.11210

**6.** Inada N, Sakai A, Kuroiwa H, Kuroiwa T. Three-dimensional progression of programmed death in the rice coleoptile. *Int Rev Cytol*. 2002;218:221–258. DOI: 10.1016/s0074-7696(02)18014-4

**7.** Zhao X, Niu Y, Hossain Z, et al. New insights into light spectral quality inhibits the plasticity elongation of maize mesocotyl and coleoptile during seed germination. *Front Plant Sci*. 2023;14:1152399. DOI: 10.3389/fpls.2023.1152399

**8.** Kawai M, Uchimiya H. Coleoptile senescence in rice (*Oryza sativa* L.). *Ann Bot*. 2000;86(2):405–414. DOI: 10.1006/anbo.2000.1199

**9.** Takahashi H, Saika H, Matsumura H, et al. Cell division and cell elongation in the coleoptile of rice *alcohol dehydrogenase*

*1*-deficient mutant are reduced under complete submergence. *Ann Bot*. 2011;108(2):253–261. DOI: 10.1093/aob/mcr137

**10.** Edwards JM, Roberts TH, Atwell BJ. Quantifying ATP turnover in anoxic coleoptiles of rice (*Oryza sativa*) demonstrates preferential allocation of energy to protein synthesis. *J Exp Bot*. 2012;63(12): 4389–4402. DOI: 10.1093/jxb/ers114

**11.** O'Sullivan PA, Weiss GM, Friesen D. Tolerance of spring wheat (*Triticum aestivum* L.) to trifluralin deep-incorporated in the autumn or spring. *Weed Res*. 1985;25(4):275–280. DOI: 10.1111/j.1365-3180.1985.tb00645.x

**12.** Brown PR, Singleton GR, Tann CR, Mock I. Increasing sowing depth to reduce mouse damage to winter crops. *Crop Prot*. 2003;22(4):653–660. DOI: 10.1016/S0261-2194(03)00006-1

**13.** Rebetzke GJ, Zheng B, Chapman SC. Do wheat breeders have suitable genetic variation to overcome short coleoptiles and poor establishment in the warmer soils of future climates? *Funct Plant Biol*. 2016;43(10):961–972. DOI: 10.1071/FP15362

**14.** Atwell BJ, Waters I, Greenway H. The effect of oxygen and turbulence on elongation of coleoptiles of submergence-tolerant and -intolerant rice cultivars. *J Exp Bot*. 1982;33(5):1030–1044. DOI: 10.1093/jxb/33.5.1030

**15.** Bogdanova EM, Bertova AD, Kirpichnikova AA, et al. Growth and viability of coleoptiles under oxygen deficiency in *Oryza sativa* L. FROM the collection of the federal rice research center. *Agricultural Biology*. 2023;58(3):538–553. DOI: 10.15389/agrobiology.2023.3.538rus

**16.** Huang S, Shingaki-Wells RN, Petereit J, et al. Temperature-dependent metabolic adaptation of *Triticum aestivum* seedlings to anoxia. *Sci Rep*. 2018;8:6151. DOI: 10.1038/s41598-018-24419-7

**17.** Luo H, Hill CB, Zhou G, et al. Genome-wide association mapping reveals novel genes associated with coleoptile length in a worldwide collection of barley. *BMC Plant Biol*. 2020;20:346. DOI: 10.1186/s12870-020-02547-5

**18.** Sharova EI. *Cell wall of plants*. Saint Petersburg: SPbU Publ., 2004. 156 p. (In Russ.)

**19.** Cosgrove DJ. Growth of the plant cell wall. *Nat Rev Mol Cell Biol*. 2005;6(11):850–861. DOI: 10.1038/nrm1746

**20.** Gorshkova TA. *Plant cell wall as a dynamic system*. Moscow: Nauka, 2007. 429 p. (In Russ.)

**21.** Freshour G, Clay RP, Fuller MS, et al. Developmental and tissue-specific structural alterations of the cell-wall polysaccharides of *Arabidopsis thaliana* roots. *Plant Physiol*. 1996;110(4):1413–1429. DOI: 10.1104/pp.110.4.1413

**22.** Goudenhooft C, Siniscalco D, Arnould O, et al. Investigation of the mechanical properties of flax cell walls during plant development: The relation between performance and cell wall structure. *Fibers*. 2018;6(1):6. DOI: 10.3390/fib6010006

**23.** Samalova M, Gahurova E, Hejatko J. Expansin-mediated developmental and adaptive responses: A matter of cell wall biomechanics? *Quant Plant Biol*. 2022;3: e11. DOI: 10.1017/qpb.2022.6

**24.** Gibeaut DM, Pauly M, Bacic A, Fincher GB. Changes in cell wall polysaccharides in developing barley (*Hordeum vulgare*) coleoptiles. *Planta*. 2005;221:729–738. DOI: 10.1007/s00425-005-1481-0

**25.** Kozlova LV, Snegireva AV, Gorshkova TA. Distribution and structure of mixed linkage glucan at different stages of elongation of maize root cells. *Russ J Plant Physiol*. 2012;59(3):339–347. DOI: 10.1134/S1021443712030090

**26.** Li J, Dickerson TJ, Hoffmann-Benning S. Contribution of proteomics in the identification of novel proteins associated with plant growth. *J Proteome Res*. 2013;12(11):4882–48891. DOI: 10.1021/pr400608d

**27.** Niu L, Huang W, Liu L, et al. Differential abundance proteins associated with rapid growth of etiolated coleoptiles in maize. *Plant Direct*. 2021;5(6):e00332. DOI: 10.1002/pld3.332

**28.** Long Y, Cheddadi I, Mosca G, et al. Cellular heterogeneity in pressure and growth emerges from tissue topology and geometry. *Curr Biol*. 2020;30(8):1504–1516.e8. DOI: 10.1016/j.cub.2020.02.027

**29.** Ali O, Cheddadi I, Landrein B, Long Y. Revisiting the relationship between turgor pressure and plant cell growth. *New Phytol*. 2023;238(1):62–69. DOI: 10.1111/nph.18683

**30.** Li Y, Zeng H, Xu F, et al. $H^+$-ATPases in plant growth and stress responses. *Annu Rev Plant Biol*. 2022;73:495–521. DOI: 10.1146/annurev-arplant-102820-114551

**31.** Kaiser S, Scheuring D. To lead or to follow: Contribution of the plant vacuole to cell growth. *Front Plant Sci*. 2020;11:553. DOI: 10.3389/fpls.2020.00553

**32.** Duckney PJ, Wang P, Hussey PJ. Membrane contact sites and cytoskeleton-membrane interactions in autophagy. *FEBS Lett*. 2022;596(17):2093–2103. DOI: 10.1002/1873-3468.14414

**33.** Kaiser S, Eisele S, Scheuring D. Vacuolar occupancy is crucial for cell elongation and growth regardless of the underlying mechanism. *Plant Signal Behav*. 2021;16(8):e1922796. DOI: 10.1080/15592324.2021.1922796

**34.** Deamer DW, Bramhall J. Permeability of lipid bilayers to water and ionic solutes. *Chem Phys Lipids*. 1986;40(2–4):167–188. DOI: 10.1016/0009-3084(86)90069-1

**35.** Kurowska MM. Aquaporins in cereals — important players in maintaining cell homeostasis under abiotic stress. *Genes*. 2021;12(4):477. DOI: 10.3390/genes12040477

**36.** Kudoyarova G, Veselov D, Yemelyanov V, Shishova M. The role of aquaporins in plant growth under conditions of oxygen deficiency. *Int J Mol Sci*. 2022;23(17):10159. DOI: 10.3390/ijms231710159

**37.** Martre P, Morillon R, Barrieu F, et al. Plasma membrane aquaporin play a significant role during recovery from water deficit. *Plant Physiol*. 2002;130(4):2101–2110. DOI: 10.1104/pp.009019

**38.** Hachez C, Zelazny E, Chaumont F. Modulating the expression of aquaporin genes in planta: A key to understand their physiological functions? *Biochim Biophys Acta*. 2006;1758(8):1142–1156. DOI: 10.1016/j.bbamem.2006.02.017

**39.** Wang Y, Zhao Z, Liu F, et al. Versatile roles of aquaporins in plant growth and development. *Int J Mol Sci*. 2020;21(24):9485. DOI: 10.3390/ijms21249485

**40.** Moshelion M, Hachez C, Ye Q, et al. Membrane water permeability and aquaporin expression increase during growth of maize suspension cultured cells. *Plant Cell Environ*. 2009;32(10):1334–1345. DOI: 10.1111/j.1365-3040.2009.02001.x

**41.** Zhou J-Y, Hao D-L, Yang G-Z. Regulation of cytosolic pH: The contributions of plant plasma membrane $H^+$-ATPases and multiple transporters. *Int J Mol Sci*. 2021;22(23):12998. DOI: 10.3390/ijms222312998

**42.** Raghavendra AS, Ye W, Kinoshita T. Editorial: pH as a signal and secondary messenger in plant cells. *Front Plant Sci*. 2023;14:1148689. DOI: 10.3389/fpls.2023.1148689

**43.** Barbez E. Root growth: Orchestrating pH levels in plants. *eLife*. 2023;12:e91025. DOI: 10.7554/eLife.91025

**44.** Palmgren MG. Plant plasma membrane $H^+$-ATPases: Powerhouses for nutrient uptake. *Annu Rev Plant Physiol Plant Mol Biol*. 2001;52:817–845. DOI: 10.1146/annurev.arplant.52.1.817

**45.** Pedersen CN, Axelsen KB, Harper JF, Palmgren MG. Evolution of plant P-type ATPases. *Front Plant Sci*. 2012;3:31. DOI: 10.3389/fpls.2012.00031

**46.** Arango M, Gévaudant F, Oufattole M, Boutry M. The plasma membrane proton pump ATPase: the significance of gene subfamilies. *Planta*. 2003;216(3):355–365. DOI: 10.1007/s00425-002-0856-8

**47.** Toda Y, Wang Y, Takahashi A, et al. *Oryza sativa* $H^+$-ATPase (OSA) is involved in the regulation of dumbbell-shaped guard cells of rice. *Plant Cell Physiol*. 2016;57(6):1220–1230. DOI: 10.1093/pcp/pcw070

**48.** Falhof J, Pedersen JT, Fuglsang AT, Palmgren M. Plasma membrane $H^+$-ATPase regulation in the center of plant physiology. *Mol Plant*. 2016;9(3):323–337. DOI: 10.1016/j.molp.2015.11.002

**49.** Camoni L, Di Lucente C, Pallucca R, et al. Binding of phosphatidic acid to 14-3-3 proteins hampers their ability to activate the plant plasma membrane $H^+$-ATPase. *IUBMB Life*. 2012;64(8):710–716. DOI: 10.1002/iub.1058

**50.** Hager A, Debus G, Edel HG, et al. Auxin induces exocytosis and the rapid synthesis of a high-turnover pool of plasma-membrane $H^+$-ATPase. *Planta*. 1991;185(4):527–537. DOI: 10.1007/BF00202963

**51.** Rudashevskaya EL, Kirpichnikova AA, Shishova MF. Activity of plasma membrane $H^+$-ATPase in coleoptile cells during development of maize seedlings. *Russ J Plant Physiol*. 2005;52(4):504–510. DOI: 10.1007/s11183-005-0074-x

**52.** Rudashevskaya EL, Yakovlev AYu, Yakovleva OV, Shishova MF. Alteration of plasmalemma $H^+$-ATPase activity in maize coleoptile cells at different age of seedlings. *Cell Tissue Biol*. 2009;3(2):143–148. DOI: 10.1134/S1990519X09020059

**53.** Shishova MF, Tankelyun OV, Rudashevskaya EL, et al. Alteration of transport activity of proton pumps in coleoptile cells during early development stages of maize seedlings. *Russ J Dev Biol*. 2012;43(6):342–352. DOI: 10.1134/S1062360412060070

**54.** Ratajczak R. Structure, function and regulation of the plant vacuolar $H(^+)$-translocating ATPase. *Biochim Biophys Acta*. 2000;1465(1–2):17–36. DOI: 10.1016/s0005-2736(00)00129-2

**55.** Sze H, Schumacher K, Müller ML, et al. A simple nomenclature for a complex proton pump: *VHA* genes encode the vacuolar $H^+$-ATPase. *Trends Plant Sci*. 2002;7(4):157–161. DOI: 10.1016/s1360-1385(02)02240-9

**56.** Kabała K, Janicka M. Structural and functional diversity of two ATP-driven plant proton pumps. *Int J Mol Sci*. 2023;24(5):4512. DOI: 10.3390/ijms24054512

**57.** Chen T, Mikhaylova YuV, Shishova MF. Molecular phylogenetic analysis of the tonoplast $H^+$-ATPase subunits. *Russ J Genet Appl Res*. 2017;7(6):592–606. DOI: 10.1134/S207905971706003X

**58.** Lupanga U, Rohrich R, Askani J, et al. The Arabidopsis V-ATPase is localized to the TGN/EE via a seed plant-specific motif. *eLife*. 2020;9:e60568. DOI: 10.7554/eLife.60568

**59.** Schumacher K, Krebs M. The V-ATPase: Small cargo, large effects. *Curr Opin Plant Biol*. 2010;13(6):724–730. DOI: 10.1016/j.pbi.2010.07.003

**60.** Seidel T. The plant V-ATPase. *Front Plant Sci*. 2022;13:931777. DOI: 10.3389/fpls.2022.931777

**61.** Klychnikov OI, Li KW, Lill H, de Boer AH. TheV-ATPase from etiolated barley (*Hordeum vulgare* L.) shoots is activated by blue light and interacts with 14-3-3 proteins. *J Exp Bot*. 2007;58(5):1013–1023. DOI: 10.1093/jxb/erl261

**62.** Lüttge U, Fischer-Schliebs E, Ratajczak R. The $H^+$-pumping V-ATPase of higher plants: A versatile eco-enzyme in response to environmental stress. *Cell Biol Mol Lett*. 2001;6(2A):356–361.

**63.** Maeshima M. Vacuolar $H(^+)$-pyrophosphatase. *Biochim Biophys Acta*. 2000;1465(1–2):37–51. DOI: 10.1016/s0005-2736(00)00130-9

**64.** Neuhaus HE, Trentmann O. Regulation of transport processes across the tonoplast. *Front Plant Sci*. 2014;5:460. DOI: 10.3389/fpls.2014.00460

**65.** Ferjani A, Segami S, Horiguchi G, et al. Keep an eye on PPi: The vacuolar-type $H^+$-pyrophosphatase regulates postgerminative development in *Arabidopsis*. *Plant Cell*. 2011;23(8):2895–2908. DOI: 10.1105/tpc.111.085415

**66.** Khadilkar AS, Yadav UP, Salazar C, et al. Constitutive and companion cell-specific overexpression of *AVP1*, encoding a proton-pumping pyrophosphatase, enhances biomass accumulation, phloem loading, and long-distance transport. *Plant Physiol*. 2016;170(1):401–414. DOI: 10.1104/pp.15.01409

**67.** Primo C, Pizzio GA, Yang J, et al. Plant proton pumping pyrophosphatase: The potential for its pyrophosphate synthesis activity to modulate plant growth. *Plant Biol*. 2019;21(6):989–996. DOI: 10.1111/plb.13007

**68.** Zhang Y, Feng X, Wang L, et al. The structure, functional evolution, and evolutionary trajectories of the $H^+$-PPase gene family in plants. *BMC Genom*. 2020;21:195. DOI: 10.1186/s12864-020-6604-2

**69.** Lin S-M, Tsai J-Y, Hsiao C-D, et al. Crystal structure of a membrane-embedded $H^+$-translocating pyrophosphatase. *Nature*. 2012;484(7394):399–404. DOI: 10.1038/nature10963

**70.** Hsu Y-D, Huang Y-F, Pan Y-J, et al. Regulation of $H^+$-pyrophosphatase by 14-3-3 Proteins from *Arabidopsis thaliana*. *J Membr Biol*. 2018;251(2):263–276. DOI: 10.1007/s00232-018-0020-4

**71.** Segami S, Asaoka M, Kinoshita S, et al. Biochemical, structural and physiological characteristics of vacuolar $H^+$-pyrophosphatase. *Plant Cell Physiol*. 2018;59(7):1300–1308. DOI: 10.1093/pcp/pcy054

**72.** Baroncelli S, Lercari B, Cionini PG, et al. Effect of light and gibberellic acid on coleoptile and first-foliage-leaf growth in durum wheat (*Triticum durum* Desf.). *Planta*. 1984;160(4):298–304. DOI: 10.1007/BF00393410

**73.** Yin C-C, Ma B, Collinge DP, et al. Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-

mediated abscisic acid pathway. *Plant Cell*. 2015;27(4):1061–1081. DOI: 10.1105/tpc.15.00080

**74.** Kutschera U, Wang Z-Y. Growth-limiting proteins in maize coleoptiles and the auxin-brassinosteroid hypothesis of mesocotyl elongation. *Protoplasma*. 2016;253(1):3–14. DOI: 10.1007/s00709-015-0787-4

**75.** Rayle DL, Cleland R. Enhancement of wall loosening and elongation by acid solution. *Plant Physiol*. 1970;46(2):250–253. DOI: 10.1104/pp.46.2.250

**76.** Nishitani K, Vissenberg K. Roles of the XTH protein family in the expanding cell. In: Verbelen JP, Vissenberg K, editors. *The expanding cell. Plant cell monographs*. Berlin, Heidelberg, New York: Springer, 2006. Vol. 5. P. 89–116. DOI: 10.1007/7089_2006_072

**77.** Hocq L, Pelloux J, Lefebvre V. Connecting homogalacturonan-type pectin remodeling to acid growth. *Trends Plant Sci*. 2017;22(1):20–29. DOI: 10.1016/j.tplants.2016.10.009

**78.** Cosgrove DJ. Plant expansins: Diversity and interactions with plant cell walls. *Curr Opin Plant Biol*. 2015;25:162–172. DOI: 10.1016/j.pbi.2015.05.014.

**79.** McQueen-Mason S, Durachko DM, Cosgrove DJ. Two endogenous proteins that induce cell wall extension in plants. *Plant Cell*. 1992;4(11):1425–1433. DOI: 10.1105/tpc.4.11.1425

**80.** Du M, Spalding EP, Gray WM. Rapid auxin-mediated cell expansion. *Annu Rev Plant Biol*. 2020;71:379–402. DOI: 10.1146/annurev-arplant-073019-025907

**81.** Dharmasiri N, Dharmasiri S, Estelle M. The F-box protein TIR1 is an auxin receptor. *Nature*. 2005;435(7041):441–445. DOI: 10.1038/nature03543

**82.** Dreher KA, Brown J, Saw RE, Callis J. The *Arabidopsis* Aux/IAA protein family has diversified in degradation and auxin responsiveness. *Plant Cell*. 2006;18(3):699–714. DOI: 10.1105/tpc.105.039172

**83.** Takahashi K, Hayashi K-i, Kinoshita T. Auxin activates the plasma membrane $H^+$-ATPase by phosphorylation during hypocotyl elongation in Arabidopsis. *Plant Physiol*. 2012;159(2):632–641. DOI: 10.1104/pp.112.196428

**84.** Stortenbeker N, Bemer M. The *SAUR* gene family: The plant's toolbox for adaptation of growth and development. *J Exp Bot*. 2019;70(1):17–27. DOI: 10.1093/jxb/ery332

**85.** Lin W, Zhou X, Tang W, et al. TMK-based cell-surface auxin signalling activates cell-wall acidification. *Nature*. 2021;599(7884):278–282. DOI: 10.1038/s41586-021-03976-4

**86.** Kirpichnikova AA, Rudashevskaya EL, Yemelyanov VV, Shishova MF. $Ca^{2+}$-Transport through plasma membrane as a test of auxin sensitivity. *Plants*. 2014;3(2):209–222. DOI: 10.3390/plants3020209

**87.** Fendrych M, Leung J, Friml J. TIR1/AFB-Aux/IAA auxin perception mediates rapid cell wall acidification and growth of Arabidopsis hypocotyls. *eLife*. 2016;5: e19048. DOI: 10.7554/eLife.19048

**88.** Xia L, Mar Marquès-Bueno M, Karnik R. Trafficking SNARE $SYP_{132}$ partakes in auxin-associated root growth. *Plant Physiol*. 2020;182(4):1836–1840. DOI: 10.1104/pp.19.01301

**89.** Liu S, Chen H. Ethylene signaling facilitates plant adaption to physical barriers. *Front Plant Sci*. 2021;12:697988. DOI: 10.3389/fpls.2021.697988

**90.** Binder BM. Ethylene signaling in plants. *J Biol Chem*. 2020;295(22):7710–7725. DOI: 10.1074/jbc.REV120.010854

**91.** Yin C-C, Huang Y-H, Zhang X, et al. Ethylene-mediated regulation of coleoptile elongation in rice seedlings. *Plant Cell Environ*. 2023;46(4):1060–1074. DOI: 10.1111/pce.14492

**92.** Wang J-H, Gu K-D, Zhang Q-Y, et al. Ethylene inhibits malate accumulation in apple by transcriptional repression of *aluminum-activated malate transporter 9* via the WRKY31-ERF72 network. *New Phytol*. 2023;239(3):1014–1034. DOI: 10.1111/nph.18795

**93.** Tungngoen K, Kongsawadworakul P, Viboonjun U, et al. Involvement of *HbPIP2;1* and *HbTIP1;1* aquaporins in ethylene stimulation of latex yield through regulation of water exchanges between inner liber and latex cells in *Hevea brasiliensis*. *Plant Physiol*. 2009;151(2):843–856. DOI: 10.1104/pp.109.140228

**94.** Karcz W, Kurtyka R. Effect of cadmium on growth, proton extrusion and membrane potential in maize coleoptile segments. *Biol Plant*. 2007;51(4):713–719. DOI: 10.1007/s10535-007-0147-0

**95.** González Á, Ayerbe L. Response of coleoptiles to water deficit: Growth, turgor maintenance and osmotic adjustment in barley plants (*Hordeum vulgare* L.). *Agric Sci*. 2011;2(3):159–166. DOI: 10.4236/as.2011.23022

**96.** Nizam I. Effects of salinity stress on water uptake, germination and early seedling growth of perennial ryegrass. *Afr J Biotechnol*. 2011;10(51):10418–10424. DOI: 10.5897/AJB11.1243

**97.** Wu Y-S, Yang C-Y. Comprehensive transcriptomic analysis of auxin responses in submerged rice coleoptile growth. *Int J Mol Sci*. 2020;21(4):1292. DOI: 10.3390/ijms21041292

**98.** Chirkova T, Yemelyanov V. The study of plant adaptation to oxygen deficiency in Saint Petersburg University. *Biol Commun*. 2018;63(1):17–31. DOI: 10.21638/spbu03.2018.104

**99.** Turner FT, Chen C-C, Mccauley GN. Morphological development of rice seedlings in water at controlled oxygen levels. *Agron J*. 1981;73(3):566–568. DOI: 10.2134/agronj1981.00021962007300030037x

**100.** Ismail AM, Ella ES, Vergara GV. Mechanisms associated with tolerance to submergence during germination and early seedling growth in rice (*Oryza sativa*). *Ann Bot*. 2009;103(2):197–209. DOI: 10.1093/aob/mcn211

**101.** Su X, Wu H, Xiang J, et al. Evaluation of submergence tolerance of different rice genotypes at seedling emergence stage under water direct seeding. *OALib J*. 2022;9: e8706. DOI: 10.4236/oalib.1108706

**102.** Kordan HA. Patterns of shoot and root growth in rice seedlings germinating under water. *J Appl Ecol*. 1974;11(2):685–690. DOI: 10.2307/2402218

**103.** Shiono K, Koshide A, Iwasaki K, et al. Imaging the snorkel effect during submerged germination in rice: Oxygen supply via the coleoptile triggers seminal root emergence underwater. *Front Plant Sci*. 2022;13:946776. DOI: 10.3389/fpls.2022.946776

**104.** Narsai R, Edwards JM, Roberts TH, et al. Mechanisms of growth and patterns of gene expression in oxygen-deprived rice coleoptiles. *Plant J*. 2015;82(1):25–40. DOI: 10.1111/tpj.12786

**105.** Hsu S-K, Tung C-W. RNA-Seq analysis of diverse rice genotypes to identify the genes controlling coleoptile growth during submerged germination. *Front Plant Sci*. 2017;8:762. DOI: 10.3389/fpls.2017.00762

**106.** Lasanthi-Kudahettige R, Magneschi L, Loreti E, et al. Transcript profiling of the anoxic rice coleoptile. *Plant Physiol*. 2007;144(1): 218–231. DOI: 10.1104/pp.106.093997

**107.** Magneschi L, Lasanthi-Kudahettige R, Alpi A, Perata P. Expansin gene expression and anoxic coleoptile elongation in rice cultivars. *J Plant Physiol*. 2009;166(14):1576–1580. DOI: 10.1016/j.jplph.2009.03.008

**108.** Lee T-M, Lin Y-H. Peroxidase activity in relation to ethylene-induced rice (*Oryza sativa* L.) coleoptile elongation. *Bot Bull Acad Sin*. 1996;37(4):239–245.

**109.** Ishizawa K, Esashi Y. Gaseous factors involved in the enhanced elongation of rice coleoptiles under water. *Plant Cell Environ*. 1984;7(4):239–245. DOI: 10.1111/1365-3040.ep11589438

**110.** Hager A. *Avena* coleoptile segments: Hyperelongation growth after anaerobic treatment. *Z Naturforsch C*. 1980;35(9):794–804. DOI: 10.1515/znc-1980-9-1022

**111.** Yemelyanov VV, Chirkova TV, Lindberg SM, Shishova MF. Potassium efflux and cytosol acidification as primary anoxia-induced events in wheat and rice seedlings. *Plants*. 2020;9(9):1216. DOI: 10.3390/plants9091216

**112.** Baykov AA, Malinen AM, Luoto HH, Lahti R. Pyrophosphate-fueled $Na^+$ and $H^+$ transport in prokaryotes. *Microbiol Mol Biol Rev*. 2013;77(2):267–276. DOI: 10.1128/MMBR.00003-13

**113.** Carystinos GD, MacDonald HR, Monroy AF, et al. Vacuolar $H(^+)$-translocating pyrophosphatase is induced by anoxia or chilling in seedlings of rice. *Plant Physiol*. 1995;108(2):641–649. DOI: 10.1104/pp.108.2.641

**114.** Mohanty B. Promoter architecture and transcriptional regulation of genes upregulated in germination and coleoptile elongation of diverse rice genotypes tolerant to submergence. *Front Genet*. 2021;12:639654. DOI: 10.3389/fgene.2021.639654

**115.** Pegoraro R, Mapelli S, Torti G, Bertani A. Indole-3-acetic acid and rice coleoptile elongation under anoxia. *J Plant Growth Regul*. 1988;7:85–94. DOI: 10.1007/BF02025378

**116.** Horton RF. The effect of ethylene and other regulators on coleoptile growth of rice under anoxia. *Plant Sci*. 1991;79(1):57–62. DOI: 10.1016/0168-9452(91)90069-K

**117.** Nghi KN, Tondelli A, Vale G, et al. Dissection of coleoptile elongation in *japonica* rice under submergence through integrated genome-wide association mapping and transcriptional analyses. *Plant Cell Environ*. 2019;42(6):1832–1846. DOI: 10.1111/pce.13540

**118.** Nghi KN, Tagliani A, Mariotti L, et al. Auxin is required for the long coleoptile trait in *japonica* rice under submergence. *New Phytol*. 2021;229(1):85–93. DOI: 10.1111/nph.16781

**119.** Bailey-Serres J, Fukao T, Gibbs DJ, et al. Making sense of low oxygen sensing. *Trends Plant Sci*. 2012;17(3):129–138. DOI: 10.1016/j.tplants.2011.12.004

## СПИСОК ЛИТЕРАТУРЫ

**1.** Cosgrove D.J. Plant cell wall extensibility: Connecting plant cell growth with cell wall structure, mechanics, and the action of wall-modifying enzymes // J Exp Bot. 2016. Vol. 67, No. 2. P. 463–476. DOI: 10.1093/jxb/erv511

**2.** Горшкова Т.А. Клеточная стенка — многофункциональная структура растения // LXXX Тимирязевские чтения / под ред. Д.А. Лося. Москва: Наука, 2021. 118 с.

**3.** Полевой В.В. Роль ауксина в системах регуляции у растений // XLIV Тимирязевские чтения / под ред. М.Х. Чайлахяна. Ленинград: Наука, 1986. 80 с.

**4.** Hilty J., Muller B., Pantin F., Leuzinger S. Plant growth: The what, the how, and the why // New Phytol. 2021. Vol. 232, No. 1. P. 25–41. DOI: 10.1111/nph.17610

**5.** Kutschera U., Deng Z., Oses-Prieto J.A., et al. Cessation of coleoptile elongation and loss of auxin sensitivity in developing rye seedlings: A quantitative proteomic analysis // Plant Signal Behav. 2010. Vol. 5, No. 5. P. 509–517. DOI: 10.4161/psb.11210

**6.** Inada N., Sakai A., Kuroiwa H., Kuroiwa T. Three-dimensional progression of programmed death in the rice coleoptile // Int Rev Cytol. 2002. Vol. 218. P. 221–258. DOI: 10.1016/s0074-7696(02)18014-4

**7.** Zhao X., Niu Y., Hossain Z., et al. New insights into light spectral quality inhibits the plasticity elongation of maize mesocotyl and coleoptile during seed germination // Front Plant Sci. 2023. Vol. 14. ID 1152399. DOI: 10.3389/fpls.2023.1152399

**8.** Kawai M., Uchimiya H. Coleoptile senescence in rice (*Oryza sativa* L.) // Ann Bot. 2000. Vol. 86, No. 2. P. 405–414. DOI: 10.1006/anbo.2000.1199

**9.** Takahashi H., Saika H., Matsumura H., et al. Cell division and cell elongation in the coleoptile of rice *alcohol dehydrogenase 1*-deficient mutant are reduced under complete submergence // Ann Bot. 2011. Vol. 108, No. 2. P. 253–261. DOI: 10.1093/aob/mcr137

**10.** Edwards J.M., Roberts T.H., Atwell B.J. Quantifying ATP turnover in anoxic coleoptiles of rice (*Oryza sativa*) demonstrates preferential allocation of energy to protein synthesis // J Exp Bot. 2012. Vol. 63, No. 12. P. 4389–4402. DOI: 10.1093/jxb/ers114

**11.** O'Sullivan P.A., Weiss G.M., Friesen D. Tolerance of spring wheat (*Triticum aestivum* L.) to trifluralin deep-incorporated in the autumn or spring // Weed Res. 1985. Vol. 25, No. 4. P. 275–280. DOI: 10.1111/j.1365-3180.1985.tb00645.x

**12.** Brown P.R., Singleton G.R., Tann C.R., Mock I. Increasing sowing depth to reduce mouse damage to winter crops // Crop Prot. 2003. Vol. 22, No. 4. P. 653–660. DOI: 10.1016/S0261-2194(03)00006-1

**13.** Rebetzke G.J., Zheng B., Chapman S.C. Do wheat breeders have suitable genetic variation to overcome short coleoptiles and poor establishment in the warmer soils of future climates? // Funct Plant Biol. 2016. Vol. 43, No. 10. P. 961–972. DOI: 10.1071/FP15362

**14.** Atwell B.J., Waters I., Greenway H. The effect of oxygen and turbulence on elongation of coleoptiles of submergence-tolerant and -intolerant rice cultivars // J Exp Bot. 1982. Vol. 33, No. 5. P. 1030–1044. DOI: 10.1093/jxb/33.5.1030

**15.** Богданова Е.М., Бертова А.Д., Кирпичникова А.А., и др. Показатели роста и устойчивости к дефициту кислорода у колеоптилей *Oryza sativa* L. из коллекции Федерального научного

центра риса // Сельскохозяйственная биология. 2023. Т. 58, № 3. С. 538–553. DOI: 10.15389/agrobiology.2023.3.538rus

**16.** Huang S., Shingaki-Wells R.N., Petereit J., et al. Temperature-dependent metabolic adaptation of *Triticum aestivum* seedlings to anoxia // Sci Rep. 2018. Vol. 8. ID 6151. DOI: 10.1038/s41598-018-24419-7

**17.** Luo H., Hill C.B., Zhou G., et al. Genome-wide association mapping reveals novel genes associated with coleoptile length in a worldwide collection of barley // BMC Plant Biol. 2020. Vol. 20. ID 346. DOI: 10.1186/s12870-020-02547-5

**18.** Шарова Е.И. Клеточная стенка растений. Санкт-Петербург: Изд-во СПбГУ, 2004. 156 с.

**19.** Cosgrove D.J. Growth of the plant cell wall // Nat Rev Mol Cell Biol. 2005. Vol. 6, No. 11. P. 850–861. DOI: 10.1038/nrm1746

**20.** Горшкова Т.А. Растительная клеточная стенка как динамичная система. Москва: Наука, 2007. 429 с.

**21.** Freshour G., Clay R.P., Fuller M.S., et al. Developmental and tissue-specific structural alterations of the cell-wall polysaccharides of *Arabidopsis thaliana* roots // Plant Physiol. 1996. Vol. 110, No. 4. P. 1413–1429. DOI: 10.1104/pp.110.4.1413

**22.** Goudenhooft C., Siniscalco D., Arnould O., et al. Investigation of the mechanical properties of flax cell walls during plant development: The relation between performance and cell wall structure // Fibers. 2018. Vol. 6, No. 1. ID 6. DOI: 10.3390/fib6010006

**23.** Samalova M., Gahurova E., Hejatko J. Expansin-mediated developmental and adaptive responses: A matter of cell wall biomechanics? // Quant Plant Biol. 2022. Vol. 3. ID e11. DOI: 10.1017/qpb.2022.6

**24.** Gibeaut D.M., Pauly M., Bacic A., Fincher G.B. Changes in cell wall polysaccharides in developing barley (*Hordeum vulgare*) coleoptiles // Planta. 2005. Vol. 221. P. 729–738. DOI: 10.1007/s00425-005-1481-0

**25.** Kozlova L.V., Snegireva A.V., Gorshkova T.A. Distribution and structure of mixed linkage glucan at different stages of elongation of maize root cells // Russ J Plant Physiol. 2012. Vol. 59, No. 3. P. 339–347. DOI: 10.1134/S1021443712030090

**26.** Li J., Dickerson T.J., Hoffmann-Benning S. Contribution of proteomics in the identification of novel proteins associated with plant growth // J Proteome Res. 2013. Vol. 12, No. 11. P. 4882–48891. DOI: 10.1021/pr400608d

**27.** Niu L., Huang W., Liu L., et al. Differential abundance proteins associated with rapid growth of etiolated coleoptiles in maize // Plant Direct. 2021. Vol. 5, No. 6. ID e00332. DOI: 10.1002/pld3.332

**28.** Long Y., Cheddadi I., Mosca G., et al. Cellular heterogeneity in pressure and growth emerges from tissue topology and geometry // Curr Biol. 2020. Vol. 30, No. 8. P. 1504–1516.e8. DOI: 10.1016/j.cub.2020.02.027

**29.** Ali O., Cheddadi I., Landrein B., Long Y. Revisiting the relationship between turgor pressure and plant cell growth // New Phytol. 2023. Vol. 238, No. 1. P. 62–69. DOI: 10.1111/nph.18683

**30.** Li Y., Zeng H., Xu F., et al. $H^+$-ATPases in plant growth and stress responses // Annu Rev Plant Biol. 2022. Vol. 73. P. 495–521. DOI: 10.1146/annurev-arplant-102820-114551

**31.** Kaiser S., Scheuring D. To lead or to follow: Contribution of the plant vacuole to cell growth // Front Plant Sci. 2020. Vol. 11. ID 553. DOI: 10.3389/fpls.2020.00553

**32.** Duckney P.J., Wang P., Hussey P.J. Membrane contact sites and cytoskeleton-membrane interactions in autophagy // FEBS Lett. 2022. Vol. 596, No. 17. P. 2093–2103. DOI: 10.1002/1873-3468.14414

**33.** Kaiser S., Eisele S., Scheuring D. Vacuolar occupancy is crucial for cell elongation and growth regardless of the underlying mechanism // Plant Signal Behav. 2021. Vol. 16, No. 8. ID e1922796. DOI: 10.1080/15592324.2021.1922796

**34.** Deamer D.W., Bramhall J. Permeability of lipid bilayers to water and ionic solutes // Chem Phys Lipids. 1986. Vol. 40, No. 2–4. P. 167–188. DOI: 10.1016/0009-3084(86)90069-1

**35.** Kurowska M.M. Aquaporins in cereals — important players in maintaining cell homeostasis under abiotic stress // Genes. 2021. Vol. 12, No. 4. ID 477. DOI: 10.3390/genes12040477

**36.** Kudoyarova G., Veselov D., Yemelyanov V., Shishova M. The role of aquaporins in plant growth under conditions of oxygen deficiency // Int J Mol Sci. 2022. Vol. 23, No. 17. ID 10159. DOI: 10.3390/ijms231710159

**37.** Martre P., Morillon R., Barrieu F., et al. Plasma membrane aquaporin play a significant role during recovery from water deficit // Plant Physiol. 2002. Vol. 130, No. 4. P. 2101–2110. DOI: 10.1104/pp.009019

**38.** Hachez C., Zelazny E., Chaumont F. Modulating the expression of aquaporin genes in planta: A key to understand their physiological functions? // Biochim Biophys Acta. 2006. Vol. 1758, No. 8. P. 1142–1156. DOI: 10.1016/j.bbamem.2006.02.017

**39.** Wang Y., Zhao Z., Liu F., et al. Versatile roles of aquaporins in plant growth and development // Int J Mol Sci. 2020. Vol. 21, No. 24. ID 9485. DOI: 10.3390/ijms21249485

**40.** Moshelion M., Hachez C., Ye Q., et al. Membrane water permeability and aquaporin expression increase during growth of maize suspension cultured cells // Plant Cell Environ. 2009. Vol. 32, No. 10. P. 1334–1345. DOI: 10.1111/j.1365-3040.2009.02001.x

**41.** Zhou J.-Y., Hao D.-L., Yang G.-Z. Regulation of cytosolic pH: The contributions of plant plasma membrane $H^+$-ATPases and multiple transporters // Int J Mol Sci. 2021. Vol. 22, No. 23. ID 12998. DOI: 10.3390/ijms222312998

**42.** Raghavendra A.S., Ye W., Kinoshita T. Editorial: pH as a signal and secondary messenger in plant cells // Front Plant Sci. 2023. Vol. 14. ID 1148689. DOI: 10.3389/fpls.2023.1148689

**43.** Barbez E. Root growth: Orchestrating pH levels in plants // eLife. 2023. Vol. 12. ID e91025. DOI: 10.7554/eLife.91025

**44.** Palmgren M.G. Plant plasma membrane $H^+$-ATPases: Powerhouses for nutrient uptake // Annu Rev Plant Physiol Plant Mol Biol. 2001. Vol. 52. P. 817–845. DOI: 10.1146/annurev.arplant.52.1.817

**45.** Pedersen C.N., Axelsen K.B., Harper J.F., Palmgren M.G. Evolution of plant P-type ATPases // Front Plant Sci. 2012. Vol. 3. ID 31. DOI: 10.3389/fpls.2012.00031

**46.** Arango M., Gévaudant F., Oufattole M., Boutry M. The plasma membrane proton pump ATPase: the significance of gene subfamilies // Planta. 2003. Vol. 216, No. 3. P. 355–365. DOI: 10.1007/s00425-002-0856-8

**47.** Toda Y., Wang Y., Takahashi A., et al. *Oryza sativa* $H^+$-ATPase (OSA) is involved in the regulation of dumbbell-shaped guard cells of rice // Plant Cell Physiol. 2016. Vol. 57, No. 6. P. 1220–1230. DOI: 10.1093/pcp/pcw070

**48.** Falhof J., Pedersen J.T., Fuglsang A.T., Palmgren M. Plasma membrane $H^+$-ATPase regulation in the center of plant physiology // Mol Plant. 2016. Vol. 9, No. 3. P. 323–337. DOI: 10.1016/j.molp.2015.11.002

**49.** Camoni L., Di Lucente C., Pallucca R., et al. Binding of phosphatidic acid to 14-3-3 proteins hampers their ability to activate the plant plasma membrane $H^+$-ATPase // IUBMB Life. 2012. Vol. 64, No. 8. P. 710–716. DOI: 10.1002/iub.1058

**50.** Hager A., Debus G., Edel H.G., et al. Auxin induces exocytosis and the rapid synthesis of a high-turnover pool of plasma-membrane $H^+$-ATPase // Planta. 1991. Vol. 185, No. 4. P. 527–537. DOI: 10.1007/BF00202963

**51.** Rudashevskaya E.L., Kirpichnikova A.A., Shishova M.F. Activity of plasma membrane $H^+$-ATPase in coleoptile cells during development of maize seedlings // Russ J Plant Physiol. 2005. Vol. 52, No. 4. P. 504–510. DOI: 10.1007/s11183-005-0074-x

**52.** Rudashevskaya E.L., Yakovlev A.Yu., Yakovleva O.V., Shishova M.F. Alteration of plasmalemma $H^+$-ATPase activity in maize coleoptile cells at different age of seedlings // Cell Tissue Biol. 2009. Vol. 3, No. 2. P. 143–148. DOI: 10.1134/S1990519X09020059

**53.** Shishova M.F., Tankelyun O.V., Rudashevskaya E.L., et al. Alteration of transport activity of proton pumps in coleoptile cells during early development stages of maize seedlings // Russ J Dev Biol. 2012. Vol. 43, No. 6. P. 342–352. DOI: 10.1134/S1062360412060070

**54.** Ratajczak R. Structure, function and regulation of the plant vacuolar H(+)-translocating ATPase // Biochim Biophys Acta. 2000. Vol. 1465, No. 1–2. P. 17–36. DOI: 10.1016/s0005-2736(00)00129-2

**55.** Sze H., Schumacher K., Müller M.L., et al. A simple nomenclature for a complex proton pump: *VHA* genes encode the vacuolar $H^+$-ATPase // Trends Plant Sci. 2002. Vol. 7, No. 4. P. 157–161. DOI: 10.1016/s1360-1385(02)02240-9

**56.** Kabała K., Janicka M. Structural and functional diversity of two ATP-driven plant proton pumps // Int J Mol Sci. 2023. Vol. 24, No. 5. ID 4512. DOI: 10.3390/ijms24054512

**57.** Chen T., Mikhaylova Yu.V., Shishova M.F. Molecular phylogenetic analysis of the tonoplast $H^+$-ATPase subunits // Russ J Genet Appl Res. 2017. Vol. 7, No. 6. P. 592–606. DOI: 10.1134/S207905971706003X

**58.** Lupanga U., Rohrich R., Askani J., et al. The Arabidopsis V-ATPase is localized to the TGN/EE via a seed plant-specific motif // eLife. 2020. Vol. 9. ID e60568. DOI: 10.7554/eLife.60568

**59.** Schumacher K., Krebs M. The V-ATPase: Small cargo, large effects // Curr Opin Plant Biol. 2010. Vol. 13, No. 6. P. 724–730. DOI: 10.1016/j.pbi.2010.07.003

**60.** Seidel T. The plant V-ATPase // Front Plant Sci. 2022. Vol. 13. ID 931777. DOI: 10.3389/fpls.2022.931777

**61.** Klychnikov O.I., Li K.W., Lill H., de Boer A.H. TheV-ATPase from etiolated barley (*Hordeum vulgare* L.) shoots is activated by blue light and interacts with 14-3-3 proteins // J Exp Bot. 2007. Vol. 58, No. 5. P. 1013–1023. DOI: 10.1093/jxb/erl261

**62.** Lüttge U., Fischer-Schliebs E., Ratajczak R. The $H^+$-pumping V-ATPase of higher plants: A versatile eco-enzyme in response to environmental stress // Cell Biol Mol Lett. 2001. Vol. 6, No. 2A. P. 356–361.

**63.** Maeshima M. Vacuolar H(+)-pyrophosphatase // Biochim Biophys Acta. 2000. Vol. 1465, No. 1–2. P. 37–51. DOI: 10.1016/s0005-2736(00)00130-9

**64.** Neuhaus H.E., Trentmann O. Regulation of transport processes across the tonoplast // Front Plant Sci. 2014. Vol. 5. ID 460. DOI: 10.3389/fpls.2014.00460

**65.** Ferjani A., Segami S., Horiguchi G., et al. Keep an eye on PPi: The vacuolar-type $H^+$-pyrophosphatase regulates postgerminative development in *Arabidopsis* // Plant Cell. 2011. Vol. 23, No. 8. P. 2895–2908. DOI: 10.1105/tpc.111.085415

**66.** Khadilkar A.S., Yadav U.P., Salazar C., et al. Constitutive and companion cell-specific overexpression of *AVP1*, encoding a proton-pumping pyrophosphatase, enhances biomass accumulation, phloem loading, and long-distance transport // Plant Physiol. 2016. Vol. 170, No. 1. P. 401–414. DOI: 10.1104/pp.15.01409

**67.** Primo C., Pizzio G.A., Yang J., et al. Plant proton pumping pyrophosphatase: The potential for its pyrophosphate synthesis activity to modulate plant growth // Plant Biol. 2019. Vol. 21, No. 6. P. 989–996. DOI: 10.1111/plb.13007

**68.** Zhang Y., Feng X., Wang L., et al. The structure, functional evolution, and evolutionary trajectories of the $H^+$-PPase gene family in plants // BMC Genom. 2020. Vol. 21. ID 195. DOI: 10.1186/s12864-020-6604-2

**69.** Lin S.-M., Tsai J.-Y., Hsiao C.-D., et al. Crystal structure of a membrane-embedded $H^+$-translocating pyrophosphatase // Nature. 2012. Vol. 484, No. 7394. P. 399–404. DOI: 10.1038/nature10963

**70.** Hsu Y.-D., Huang Y.-F., Pan Y.-J., et al. Regulation of $H^+$-pyrophosphatase by 14-3-3 Proteins from *Arabidopsis thaliana* // J Membr Biol. 2018. Vol. 251, No. 2. P. 263–276. DOI: 10.1007/s00232-018-0020-4

**71.** Segami S., Asaoka M., Kinoshita S., et al. Biochemical, structural and physiological characteristics of vacuolar $H^+$-pyrophosphatase // Plant Cell Physiol. 2018. Vol. 59, No. 7. P. 1300–1308. DOI: 10.1093/pcp/pcy054

**72.** Baroncelli S., Lercari B., Cionini P.G., et al. Effect of light and gibberellic acid on coleoptile and first-foliage-leaf growth in durum wheat (*Triticum durum* Desf.) // Planta. 1984. Vol. 160, No. 4. P. 298–304. DOI: 10.1007/BF00393410

**73.** Yin C.-C., Ma B., Collinge D.P., et al. Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-mediated abscisic acid pathway // Plant Cell. 2015. Vol. 27, No. 4. P. 1061–1081. DOI: 10.1105/tpc.15.00080

**74.** Kutschera U., Wang Z.-Y. Growth-limiting proteins in maize coleoptiles and the auxin-brassinosteroid hypothesis of mesocotyl elongation // Protoplasma. 2016. Vol. 253, No. 1. P. 3–14. DOI: 10.1007/s00709-015-0787-4

**75.** Rayle D.L., Cleland R. Enhancement of wall loosening and elongation by acid solution // Plant Physiol. 1970. Vol. 46, No. 2. P. 250–253. DOI: 10.1104/pp.46.2.250

**76.** Nishitani K., Vissenberg K. Roles of the XTH protein family in the expanding cell. In: The expanding cell. Plant cell monographs / ed. by J.P. Verbelen, K. Vissenberg. Berlin, Heidelberg, New York: Springer, 2006. Vol. 5. P. 89–116. DOI: 10.1007/7089_2006_072

**77.** Hocq L., Pelloux J., Lefebvre V. Connecting homogalacturonan-type pectin remodeling to acid growth // Trends Plant Sci. 2017. Vol. 22, No. 1. P. 20–29. DOI: 10.1016/j.tplants.2016.10.009

**78.** Cosgrove D.J. Plant expansins: Diversity and interactions with plant cell walls // Curr Opin Plant Biol. 2015. Vol. 25. P. 162–172. DOI: 10.1016/j.pbi.2015.05.014.

**79.** McQueen-Mason S., Durachko D.M., Cosgrove D.J. Two endogenous proteins that induce cell wall extension in plants // Plant Cell. 1992. Vol. 4, No. 11. P. 1425–1433. DOI: 10.1105/tpc.4.11.1425

**80.** Du M., Spalding E.P., Gray W.M. Rapid auxin-mediated cell expansion // Annu Rev Plant Biol. 2020. Vol. 71. P. 379–402. DOI: 10.1146/annurev-arplant-073019-025907

**81.** Dharmasiri N., Dharmasiri S., Estelle M. The F-box protein TIR1 is an auxin receptor // Nature. 2005. Vol. 435, No. 7041. P. 441–445. DOI: 10.1038/nature03543

**82.** Dreher K.A., Brown J., Saw R.E., Callis J. The *Arabidopsis* Aux/IAA protein family has diversified in degradation and auxin responsiveness // Plant Cell. 2006. Vol. 18, No. 3. P. 699–714. DOI: 10.1105/tpc.105.039172

**83.** Takahashi K., Hayashi K.-I., Kinoshita T. Auxin activates the plasma membrane $H^+$-ATPase by phosphorylation during hypocotyl elongation in Arabidopsis // Plant Physiol. 2012. Vol. 159, No. 2. P. 632–641. DOI: 10.1104/pp.112.196428

**84.** Stortenbeker N., Bemer M. The *SAUR* gene family: The plant's toolbox for adaptation of growth and development // J Exp Bot. 2019. Vol. 70, No. 1. P. 17–27. DOI: 10.1093/jxb/ery332

**85.** Lin W., Zhou X., Tang W., et al. TMK-based cell-surface auxin signalling activates cell-wall acidification // Nature. 2021. Vol. 599, No. 7884. P. 278–282. DOI: 10.1038/s41586-021-03976-4

**86.** Kirpichnikova A.A., Rudashevskaya E.L., Yemelyanov V.V., Shishova M.F. $Ca^{2+}$-Transport through plasma membrane as a test of auxin sensitivity // Plants. 2014. Vol. 3, No. 2. P. 209–222. DOI: 10.3390/plants3020209

**87.** Fendrych M., Leung J., Friml J. TIR1/AFB-Aux/IAA auxin perception mediates rapid cell wall acidification and growth of Arabidopsis hypocotyls // eLife. 2016. Vol. 5. ID e19048. DOI: 10.7554/eLife.19048

**88.** Xia L., Mar Marquès-Bueno M., Karnik R. Trafficking SNARE $SYP_{132}$ partakes in auxin-associated root growth // Plant Physiol. 2020. Vol. 182, No. 4. P. 1836–1840. DOI: 10.1104/pp.19.01301

**89.** Liu S., Chen H. Ethylene signaling facilitates plant adaption to physical barriers // Front Plant Sci. 2021. Vol. 12. ID 697988. DOI: 10.3389/fpls.2021.697988

**90.** Binder B.M. Ethylene signaling in plants // J Biol Chem. 2020. Vol. 295, No. 22. P. 7710–7725. DOI: 10.1074/jbc.REV120.010854

**91.** Yin C.-C., Huang Y.-H., Zhang X., et al. Ethylene-mediated regulation of coleoptile elongation in rice seedlings // Plant Cell Environ. 2023. Vol. 46, No. 4. P. 1060–1074. DOI: 10.1111/pce.14492

**92.** Wang J.-H., Gu K.-D., Zhang Q.-Y., et al. Ethylene inhibits malate accumulation in apple by transcriptional repression of *aluminum-activated malate transporter 9* via the WRKY31-ERF72 network // New Phytol. 2023. Vol. 239, No. 3. P. 1014–1034. DOI: 10.1111/nph.18795

**93.** Tungngoen K., Kongsawadworakul P., Viboonjun U., et al. Involvement of *HbPIP2;1* and *HbTIP1;1* aquaporins in ethylene stimulation of latex yield through regulation of water exchanges between inner liber and latex cells in *Hevea brasiliensis* // Plant Physiol. 2009. Vol. 151, No. 2. P. 843–856. DOI: 10.1104/pp.109.140228

**94.** Karcz W., Kurtyka R. Effect of cadmium on growth, proton extrusion and membrane potential in maize coleoptile segments // Biol Plant. 2007. Vol. 51, No. 4. P. 713–719. DOI: 10.1007/s10535-007-0147-0

**95.** González Á., Ayerbe L. Response of coleoptiles to water deficit: Growth, turgor maintenance and osmotic adjustment in barley plants (*Hordeum vulgare* L.) // Agric Sci. 2011. Vol. 2, No. 3. P. 159–166. DOI: 10.4236/as.2011.23022

**96.** Nizam I. Effects of salinity stress on water uptake, germination and early seedling growth of perennial ryegrass // Afr J Biotechnol. 2011. Vol. 10, No. 51. P. 10418–10424. DOI: 10.5897/AJB11.1243

**97.** Wu Y.-S., Yang C.-Y. Comprehensive transcriptomic analysis of auxin responses in submerged rice coleoptile growth // Int J Mol Sci. 2020. Vol. 21, No. 4. ID 1292. DOI: 10.3390/ijms21041292

**98.** Chirkova T., Yemelyanov V. The study of plant adaptation to oxygen deficiency in Saint Petersburg University // Biol Commun. 2018. Vol. 63, No. 1. P. 17–31. DOI: 10.21638/spbu03.2018.104

**99.** Turner F.T., Chen C.-C., Mccauley G.N. Morphological development of rice seedlings in water at controlled oxygen levels // Agron J. 1981. Vol. 73, No. 3. P. 566–568. DOI: 10.2134/agronj1981.00021962007300030037x

**100.** Ismail A.M., Ella E.S., Vergara G.V. Mechanisms associated with tolerance to submergence during germination and early seedling growth in rice (*Oryza sativa*) // Ann Bot. 2009. Vol. 103, No. 2. P. 197–209. DOI: 10.1093/aob/mcn211

**101.** Su X., Wu H., Xiang J., et al. Evaluation of submergence tolerance of different rice genotypes at seedling emergence stage under water direct seeding // OALib J. 2022. Vol. 9. ID e8706. DOI: 10.4236/oalib.1108706

**102.** Kordan H.A. Patterns of shoot and root growth in rice seedlings germinating under water // J Appl Ecol. 1974. Vol. 11, No. 2. P. 685–690. DOI: 10.2307/2402218

**103.** Shiono K., Koshide A., Iwasaki K., et al. Imaging the snorkel effect during submerged germination in rice: Oxygen supply via the coleoptile triggers seminal root emergence underwater // Front Plant Sci. 2022. Vol. 13. ID 946776. DOI: 10.3389/fpls.2022.946776

**104.** Narsai R., Edwards J.M., Roberts T.H., et al. Mechanisms of growth and patterns of gene expression in oxygen-deprived rice coleoptiles // Plant J. 2015. Vol. 82, No. 1. P. 25–40. DOI: 10.1111/tpj.12786

**105.** Hsu S.-K., Tung C.-W. RNA-Seq analysis of diverse rice genotypes to identify the genes controlling coleoptile growth during submerged germination // Front Plant Sci. 2017. Vol. 8. ID 762. DOI: 10.3389/fpls.2017.00762

**106.** Lasanthi-Kudahettige R., Magneschi L., Loreti E., et al. Transcript profiling of the anoxic rice coleoptile // Plant Physiol. 2007. Vol. 144, No. 1. P. 218–231. DOI: 10.1104/pp.106.093997

**107.** Magneschi L., Lasanthi-Kudahettige R., Alpi A., Perata P. Expansin gene expression and anoxic coleoptile elongation in rice cultivars // J Plant Physiol. 2009. Vol. 166, No. 14. P. 1576–1580. DOI: 10.1016/j.jplph.2009.03.008

**108.** Lee T.-M., Lin Y.-H. Peroxidase activity in relation to ethylene-induced rice (*Oryza sativa* L.) coleoptile elongation // Bot Bull Acad Sin. 1996. Vol. 37, No. 4. P. 239–245.

**109.** Ishizawa K., Esashi Y. Gaseous factors involved in the enhanced elongation of rice coleoptiles under water // Plant Cell Environ. 1984. Vol. 7, No. 4. P. 239–245. DOI: 10.1111/1365-3040.ep11589438

**110.** Hager A. *Avena* coleoptile segments: Hyperelongation growth after anaerobic treatment // Z Naturforsch C. 1980. Vol. 35, No. 9. P. 794–804. DOI: 10.1515/znc-1980-9-1022

**111.** Yemelyanov V.V., Chirkova T.V., Lindberg S.M., Shishova M.F. Potassium efflux and cytosol acidification as primary anoxia-induced events in wheat and rice seedlings // Plants. 2020. Vol. 9, No. 9. ID 1216. DOI: 10.3390/plants9091216

**112.** Baykov A.A., Malinen A.M., Luoto H.H., Lahti R. Pyrophosphate-fueled $Na^+$ and $H^+$ transport in prokaryotes // Microbiol Mol Biol Rev. 2013. Vol. 77, No. 2. P. 267–276. DOI: 10.1128/MMBR.00003-13

**113.** Carystinos G.D., MacDonald H.R., Monroy A.F., et al. Vacuolar $H(^+)$-translocating pyrophosphatase is induced by anoxia or chilling in seedlings of rice // Plant Physiol. 1995. Vol. 108, No. 2. P. 641–649. DOI: 10.1104/pp.108.2.641

**114.** Mohanty B. Promoter architecture and transcriptional regulation of genes upregulated in germination and coleoptile elongation of diverse rice genotypes tolerant to submergence // Front Genet. 2021. Vol. 12. ID 639654. DOI: 10.3389/fgene.2021.639654

**115.** Pegoraro R., Mapelli S., Torti G., Bertani A. Indole-3-acetic acid and rice coleoptile elongation under anoxia // J Plant Growth Regul. 1988. Vol. 7. P. 85–94. DOI: 10.1007/BF02025378

**116.** Horton R.F. The effect of ethylene and other regulators on coleoptile growth of rice under anoxia // Plant Sci. 1991. Vol. 79, No. 1. P. 57–62. DOI: 10.1016/0168-9452(91)90069-K

**117.** Nghi K.N., Tondelli A., Vale G., et al. Dissection of coleoptile elongation in *japonica* rice under submergence through integrated genome-wide association mapping and transcriptional analyses // Plant Cell Environ. 2019. Vol. 42, No. 6. P. 1832–1846. DOI: 10.1111/pce.13540

**118.** Nghi K.N., Tagliani A., Mariotti L., et al. Auxin is required for the long coleoptile trait in *japonica* rice under submergence // New Phytol. 2021. Vol. 229, No. 1. P. 85–93. DOI: 10.1111/nph.16781

**119.** Bailey-Serres J., Fukao T., Gibbs D.J., et al. Making sense of low oxygen sensing // Trends Plant Sci. 2012. Vol. 17, No. 3. P. 129–138. DOI: 10.1016/j.tplants.2011.12.004

## AUTHORS' INFO

**Anastasiia A. Kirpichnikova;**
ORCID: 0000-0001-5133-5175; eLibrary SPIN: 9960-9527;
e-mail: nastin1972@mail.ru

**Guzel R. Kudoyarova,** Dr. Sci. (Biology), Professor;
ORCID: 0000-0001-6409-9976; eLibrary SPIN: 6130-3083;
e-mail: guzel@anrb.ru

**Vladislav V. Yemelyanov,** Cand. Sci. (Biology), Assistant Professor;
ORCID: 0000-0003-2323-5235; eLibrary SPIN: 9460-1278;
e-mail: bootika@mail.ru

***Maria F. Shishova,** Dr. Sci. (Bioligy), Professor;
address: 7/9 Universitetskaya emb., 199034, Saint Petersburg, Russia;
ORCID: 0000-0003-3657-2986; eLibrary SPIN: 7842-7611;
e-mail: mshishova@mail.ru

## ОБ АВТОРАХ

**Анастасия Алексеевна Кирпичникова;**
ORCID: 0000-0001-5133-5175; eLibrary SPIN: 9960-9527;
e-mail: nastin1972@mail.ru

**Гюзель Радомесовна Кудоярова,** д-р биол. наук, профессор;
ORCID: 0000-0001-6409-9976; eLibrary SPIN: 6130-3083;
e-mail: guzel@anrb.ru

**Владислав Владимирович Емельянов,** канд. биол. наук, доцент;
ORCID: 0000-0003-2323-5235; eLibrary SPIN: 9460-1278;
e-mail: bootika@mail.ru

***Мария Федоровна Шишова,** д-р биол. наук, профессор;
адрес: Россия, 199034, Санкт-Петербург, Университетская наб., д. 7/9; ORCID: 0000-0003-3657-2986; eLibrary SPIN: 7842-7611;
e-mail: mshishova@mail.ru

* Corresponding author / Автор, ответственный за переписку