Mechanisms of Antarctic Vascular Plant Adaptation to Abiotic Environmental Factors

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Abstract—Native species of the Antarctic *Deschampsia antarctica* and *Colobanthus quitensis* exist at the limits of survival of vascular plants. Fundamental adaptations to abiotic environmental factors that qualitatively distinguish them from the other vascular plants of extreme regions, namely temperature, ultraviolet radiation hardiness, and their genetic plasticity in the changeable environment are discussed.

INTRODUCTION

Plant adaptation concerns hereditarily fixed constitutive properties typical for plants, regardless of the fact whether they are in stressful conditions not. These properties become apparent on the structural and biochemical level as well. In general, the problem of plant adaptation to abiotic factors is of great ecological importance, since plant ability to adapt to particular conditions is one of factors determining the natural habitat of wild plants and possibility of their introduction [1]. The Antarctic is a unique place to study natural adaptation mechanisms. It is entirely isolated by the South Ocean waters and the Polar Front system, and vascular plants live here in extreme conditions strained to the limits of their possibilities as 99.5% of surface is covered with continent ice and 0.3% of its area is favorable for land ecosystems [2–6]. Such sections include oases of continental or the Eastern Antarctic and also the narrow western coast strip of the Antarctic Peninsula and islands named the maritime Antarctic. If lichen, moss, and algae dominate in severe surroundings, formations of Antarctic grass tundra are spread in more favorable oases of the maritime Antarctic. The formations include two species of native vascular plants—Antarctic hair grass (*Deschampsia antarctica* Desv., Poaceae) and Antarctic pearlworts (*Colobanthus quitensis* Kunth Bartl. Caryophyllaceae) [4, 6–8]. These vascular plants are not fastidious and occupy all favorable places for growing: rocks, hollows and cornices, places with fine clastic stones, beaches, etc. In particular, hair grass grows in separate agglomerations or form thick cover on the surface that is connected with its level of adaptation to conditions of certain habitat. Pearlworts is rather rare, and the reasons for its limited spread are not explained enough [4, 9–13].

Populations of these vascular plants grow on poor or, quite the contrary, overrich with semidecomposed organics soils. They experience effects of severe environmental conditions—low temperature, ultra-violet rays, and moisture deficit. During the direct analysis, we studied some biological peculiarities of Antarctic hair grass [4]. In our work, we pay attention to the contemporary data concerning the reaction of native plants to the main Antarctic abiotic factor because the problems of specific adaptation mechanisms of Antarctic native plants are not clear.

Growing on organic soils. Initial productivity (formation of plant biomass) depends on peculiarities of root nutrition of plants in land ecosystems of high latitudes. In guano-rich areas, the growth of plants differs much in amount of nitrogen, which slowly releases while decomposing because of low temperature. In the maritime Antarctic, *D. antarctica* and *C. quitensis* usually grow in guano-rich territories rich particularly in places of penguin rookery accumulations. This is caused by a high level of nitrate-reductase activity of both species [14]. Thus, the ability to obtain nitrogen on the early stages of its decomposition development proves the success of photosynthesizing plants. Accordingly, one of the adaptive characteristics of *D. antarctica* and *C. quitensis* can be the ability to absorb nitrogen on different stages of its transforma-

tion. But this adaptation is not unique for Antarctic vascular plants.

In the maritime Antarctic, *D. antarctica* is often found in moss areas, especially *Sanionia uncinata* (Hedw.) Loeske, which is a dominant species. At the same time, *D. antarctica* is able to absorb organic matters from soil by 160 times faster than moss growing nearby when temperature increases [14]. Plants *D. antarctica* can absorb small peptides (di-, tripeptides) from soil directly by root hairs. This property gives a significant advantage to hair grass in acclimation in new area but this property is typical for family Poacae on the whole. Plants of family Caryphyllaceae are able to absorb minerals from interstitial water, but root system can cause dissolving of compounds that are unavailable in nonsoluble form [14].

Cold endurance. It is known that vascular plants include most of economic species. And they are characterized by interspecies variability of cold endurance. This fact determines the thorough study of mechanisms of low temperature adaptation of plants that grow in severe climatic conditions [15, 16]. Antarctic plants possess developed avoidance strategy. In particular, this is typical for *C. quitensis*, since this plant seems to be low clump and is mostly found near higher clumps of *D. antarctica* or in hollows between stones avoiding direct influence of unfavorable abiotic factors. In some regions of the maritime Antarctic, *C. quitensis* is only found in some localities that are probably the most protected from unfavorable conditions.

Besides, both plants have specific resistance or endurance mechanism on the level of the whole organism (anatomic changes). The mechanism is maintained by the synthesis of some stress protein classes and also other compounds that provide for plant endurance [17, 18]. Generally, the increase of plant endurance to low temperature is the complex result connected with considerable rearrangement of physiological and biochemical processes and the changes of expression of a great number of genes [19–22].

We found that heat and cold shock cause the changes in gene activity in plant cells and other organisms. Moreover, when temperature decreases, specific genes start functioning and synthesize certain proteins. In addition to a great number of involved enzymes, we isolated some families of proteins that are specifically connected with these processes. According to the scheme of Kolesnichenko et al. [23], at the moment when environmental temperature decreases, the synthesis of stress separating proteins that launch thermogenesis begins. Well-known cold-shock protein 310 (CSP) separates oxidative phosphorylation, which allows the use of oxidative energy for the increase of temperature in plant organs by 4–7°C higher than in the environment (thermogenesis) [24]. This helps plants to maintain positive temperature for some time and prepare for the further decrease of environmental temperature and launch a range of defense reactions, particularly the formation of free fatty acids and free sugars and the synthesis of defensive proteins: antifreeze, dehydrin, and chaperone proteins. They all are multifunctional proteins that regulate processes of translation and transcription and separate oxidation and phosphorylation during low temperature stress [23].

D. antarctica has typical biochemical adaptive mechanisms that are characteristic of plants growing in low temperature [4]. *D. antarctica* and *C. quitensis* can be referred to cryophytes, organisms living in low temperature [25]. In general minimal photosynthesis temperature is liquid freezing point ($-1...-2°C$), and cryophytes photosynthesize in even lower temperature. Thus, for example, *Pinus pumila* photosynthesize under snow at $-7°C$. Antarctic lichen can photosynthesize at $-10°C$ [26]; as for *D. antarctica*, optimal temperature for photosynthesis is $10-12°C$ in natural conditions. For *C. quitensis*, this index value is not clear. Plants *D. antarctica* and *C. quitensis* endure low temperature and drought as well and they are still able to photosynthesize at the freezing point [9].

General cold endurance of *D. antarctica* is much higher ($LD_{50} = -26°C$) than in *C. quitensis* ($LD_{50} = -5°C$) [4, 27].

One of the early reactions to cooling is oxidative stress, which causes disorders of enzyme activity located on chloroplast and mitochondria membranes. Enzymes also cause the processes of oxidative and photosynthetic phosphorylation. Formation of adaptive mechanisms of maintenance of photosynthetic activity in conditions of low temperature is realized on the level of ultra-structural organization and biochemical level of photosynthetic reactions as well [28]. We found that *D. antarctica* undergoes structural changes in cells of leaf mesophil. Chloroplasts have irregular shape with pouches or invaginations inside of organelles and growths to enlarge the chloroplast surface. This increases the productivity of photosynthesis. Leaf mesophil cells of hair grass contain atypical structures as well. They are numerous bladders of different size with concentrically located membranes. These formations are connected with adaptation to climatic conditions of the Antarctic [29]. The data on respective studies on *C. quitensis* are absent.

Earlier, it was mentioned that plants *D. antarctica* and *C. quitensis* have different levels of cold endurance. The difference of antifreeze activity between these plants can reflect the realization of different strategies for freezing prevention, which are found to be successful for existence in the Antarctic [27]. Death of plant cells and an organism on the whole can occur as ice crystals that form in intercellular space take water from cells causing dehydration. Simultaneously, they have mechanical influence on cytoplasm damaging cell structures. Due to antifreeze proteins during severe cold in intercellular space of *D. antarctica*,

small ice crystals are formed that do not damage cells [10, 29–31]. We consider that accumulation of some antifreeze proteins is one of the main adaptive mechanisms [32].

We found that hair grass synthesizes antifreeze protein with weight of 22 kDa (see review [4]), whose one function is to hinder the process of ice formation [23]. Similar proteins are accumulated mostly in conductive and cover tissues, where initial ice formation zones are usually located. The presence of antifreeze proteins in *D. antarctica* is not occasional, since they are a rather widespread adaptive factor of plants, which allows them to endure low temperature [33]. Winter cereals have numerous defensive mechanisms and they efficiently take water from cytoplasm into apoplasts during cold shock, and, thus, avoid formation of ice crystals inside of cells. In particular, antifreeze proteins of hair grass are able to inhibit recrystallisation of water in intercellular space and are encoded by gene IRIPs (Ice recrystallization inhibition proteins) which, however, is not specific only for this plant species (see review [4]). According to our findings in the database NCBI [34], the group of proteins IROPs include seven different proteins. Besides, we found the presence of two more proteins that emerge in response to low temperature (cold). Their attachment to IRIPs is not explained. The difference for the mentioned gene, which is typical for different species, possibly, is that antifreeze protein gene expression occurs in most plants during low temperature acclimatization or hardening. At the same time, we found IRIP-activity in hair grass leaves of unacclimatized plant [35], but it was not confirmed during usage of other analysis method [36].

We conducted the search of sequences (as nucleotides as amino acids) of *C. quitensis* in the public specialized databases and it showed that, currently, there are only seven nucleotide sequences of *C. quitensis* (for two of them, we established or verified attributes, and five are not checked). But none of them is homologous to hair grass gene IRIPs [34]. Verified sequences concern complete sequence of retrotransposon Cassandra TRIM [37] and sequence of gene 18S of ribosome RNA, ITS1-section of gene 5,8S of ribosome RNA, and ITS2-section of gene 28S of ribosome DNA. Unverified chloroplast sequences are partial sequence of K-similar gene, partial sequence of gene tRNA-Leu (*trnL*), complete sequence of intergenic wedge *trnL-trnF* and partial sequence of gene *tRNA-Phe* (*trnF*), partial sequence of genes *PsbZ* (*psbZ*) and *tRNA-Gly* (*trnG*), partial sequences of intergenic wedge *trnQ-rps16* and gene S16 of ribosome protein (*rps16*), and partial sequence similar to dehydrogenase gene NADH of subunit F [38]. Thus, the problem of pearlworts' adaptive system needs further studying.

Dehydration and dehydrins. Low temperature stress is closely connected with cell dehydration and enhanced dehydrin synthesis is characteristic of plants during adaptation. For dehydration of cells under effects of water stress due to high hydrophilism, these proteins prevent water loss and stabilize other proteins [23]. In addition, some dehydrins carry out antifreeze and cryoprotective activity simultaneously, and also take part in the endurance regulation of plant cells to cold stress [39].

We identified genes of dehydrin encoding proteins (with weight of 58, 57, 55, 53, 48, 30, and 27 kDa) of *D. antarctica*. Gene expression of *D. antarctica* is regulated by low temperature, saline, and osmotic stresses. These proteins are accumulated in initial ice formation zones. In *D. antarctica*, we found abscisic acid-dependent and independent methods of dehydrin regulation, but certain mechanism of acid participation in the process of cold-induced gene expression is not clear [40]. They are probably necessary for plant survival under effect of low temperature for long. For *C. quitensis* genes, we did not determine dehydrin encoding proteins, but these plants can survive in the Antarctic. *C. quitensis* can have other mechanisms of survival in conditions of low temperature for long, but explanation of these mechanisms needs further studying (see review [4]).

Kolesnichenko et al. [23] conducted the comparative analysis of six varieties of *Medicago sativa* L. with contrastive frost endurance, which showed that two mRNA—*MsaciA* and *MsaciB*—are accumulated during cold acclimatization. They encode proteins that contain glycerin-rich motives. This confirms that the ability to accumulate proteins similar to MsaciA and MsaciB to a high level can be connected with plant endurance to low temperature. Regarding both Antarctic vascular plants, the data on proteins similar to those mentioned above are absent in the literature.

Most stress proteins are chaperones synthesized de novo, whose number sharply increases under effect of stress factors. Numerous functions of proteins of this family are determined by their chaperone activity. In particular, they are involved in the processes of regular noncovalent arrangement of polypeptides or structures with polypeptides that are not components of newly formed structures. It is considered that molecular chaperone, except for joining and stabilization of other proteins that are unstable in certain conformation conditions, contribute to acquiring of cell endurance, since they take part in accompanying, oligomerous assembly, and transportation into certain subcellular protein compartments or release of them by means of the denaturation method [39]. These hydrophil proteins are formed in cytoplasm under effect of low and high temperatures and accumulate in cell walls. We showed that accumulation in wall cell occurs in *D. antarctica* after temperature stress. This protein has molecular weight of 70 kDa [6]. It helps to transform aggregated or irregularly convolute proteins into solution and vice versa using some cycles of attachment and hydrolysis of adenosine triphosphate [41].

Thus, we can assume that this protein ensures low temperature photosynthesis optimum (+12°C) (see [4, 6]). To conclude, *D. antarctica* realizes the method of synthesis of stress proteins typical for other vascular plants, which provide for photosynthetic activity in temperature stress conditions. Also, *D. antarctica* is an important component of defensive reaction of live organisms in response to effect of unfavorable abiotic factors. Respective data concerning *C. quitensis* are absent in the literature.

One more defensive mechanism of plants to low temperature for a period is accumulation of soluble sugars in tissues. Thus, maximum accumulation of saccharose, fructose and glucose in *D. antarctica* leaf tissues is observed before Antarctic winter [42, 43]. Some scientists studied expression of gene encoding saccharose phosphatesynthetase enzyme of *D. antarctica*. We discovered that the activity of mentioned enzyme increases in response to low temperature, but number and level of proper encoding gene expression does not change [44].

Resistance to ultra-violet radiation. *D. antarctica* and *C. quitensis* are well adapted to UV radiation. Thus, under effect of UV-B, the leaves of these plants become smaller and shorter but thicker. We can observe the increased content of photosynthetic pigments there. The life span of *C. quitensis* leaves becomes shorter. UV-B radiation accelerates ripening and favors the increase of a number of blossom cluster and fruit. UV-B radiation does not influence the life span of seeds [45]. In the experiment, we compared plants *D. antarctica* that grew in natural and hothouse conditions (without UV influence) and found that, in natural conditions, *D. antarctica* had 50% less output of total vegetative biomass in comparison with hothouse plants and 47% less than land biomass. The decrease of land biomass growth was the result of the decrease of leaf extension speed (grew shorter leaves) by 29% and the decrease of general leaf area by 59% [46].

It is known that p-coumaric, caffeic, and ferulic acids are predecessors of hydroxycinnamic acid and lutein derivatives, which are dominating flavonoids both in insoluble and soluble extracts from leaves. Concentrations in insoluble p-coumaric and caffeic acids and soluble ferulic acid in *D. antarctica* in conditions of natural UV-B radiation are higher in comparison with hothouse conditions by 38, 48, and 60% correspondingly. This means that flavonoids formed under UV radiation effect can protect cellular structures from damages [46]. This reaction of *D. antarctica* is neither species-specific [17]. Plants *C. quitensis* have photoprotecting properties that can be referred to effect of flavonoids and carotinoids and act as UV-absorbing molecules and antioxidants [47].

Plasticity of genome in extreme living conditions. High plasticity of genome of somatic cells becomes apparent in ontogenesis and is formed on the basis of well-known cellular and molecular defensive mecha-

nisms of plants under effect of stress factors, adaptation, and homeostatic character on the level of separate organism. Plant genome plasticity substantiates totipotency (switching of morphogenetic programs, for example, with the purpose of restoring of damaged organs or organism on the whole) and regulated (adaptive) changeability of genome in ontogenesis (including emergence of genotrophs), and also high frequency of, prima facie, undirected genome changes under the effect of different environmental factors [48−50].

According to the data given in the review [4], *D. antarctica* is characterized by karyotype $2n = 2x = 26$, with formula $10 \text{ m} + 6 \text{ cm} + 8 \text{ st} + 2 \text{ t}$. Chromosome number $2n = 26$ with main number $x = 13$ is generally typical for species of genus *Deschampsia*. And only two species have the main number of chromosomes of 7— *D. atropurpurea* ($2n = 14$) and *D. flexulosa* ($2n = 28$), which belong to separate genera according to the data of molecular taxonomy. We used the methods of C-banding, analysis of restriction spectra of plastid and nuclear DNA, and isozyme spectrum to determine the difference between *D. core*, *D. atropurpurea* and *D. flexuosa*. *C. quitensis* has chromosome set $2n$ with 80 chromosomes. Because of small size of chromosomes, the complete study of karyotype was not conducted. At the same time, karyotype with such number of chromosomes is determined for close species *C. apetalus* and *C. affinus*.

There are data on the presence of aneuploidy cells in meristem of some plants and even particular aneuploidy plants *D. antarctica*. The studies of appendage roots of *D. antarctica* from the islands of Galindez, Piterman and Barselot (area of Akademik Vernadsky Ukrainian Antarctic Station, maritime Antarctic) proved our findings. Besides, we discovered mixoploidy (polysomaty) of this species. Also number of chromosomes in cells of meristem of root tip is significant—from 10 to 68 chromosomes [51]. Thus, *D. antarctica* of this region does not demonstrate mixoploidy regarding a number of chromosomes compared with generic number and it is characterized by the presence of aneuploidy.

Species formation inside of the genus irrespective of areal (and, in most cases, specimens of genus *Deschampsia* are adapted to conditions of cold humid meadows) is not accompanied with the change of chromosome number. Except for diploid sets, some species are characterized by polyploidization and aneuploidization. Karyological variations of species of genus *Deschampsia*, particularly *D. caspitosa*, are caused by fusion of smaller chromosomes with further polyploidization. This process is rather widespread among plants [52]. We found Poaceae features of ecological differentiation connected with the level of plant ploidy. At the same time, diploid plants had lower indices of realization of potential ecological niche than polyploid ones. The level of such realiza-

tion and ploidy increased [53]. Probably, such a tendency is the basis for creation of species forms with tetraploid ($n = 13$) karyotype, for example, *D. obensis*, *D. mackenziana*, and *D. mildbraedii*. In general, we found that polyploidization can cause separation of endemic forms in specific conditions of increase [54−57]. There is no data on aneuploidy in *C. quitensis* in the literature.

We also conducted cytological analysis of *D. caespitosa* from populations of the northern part of Lake Ontario (Canada), which proved the presence of aneuploids and variation of diploid number of chromosomes from 18 to 26. Besides, specimens with $2n = 26$ have additional or so-called B-chromosomes. The role of B-chromosomes, which were also detected in *D. wibeliana*, is not discussed [58]. However, scientists recently consider that B-chromosomes maintain endurance of many species of organisms in unfavorable natural conditions. Certainly, B-chromosomes appear resulting in main chromosome changeability and can influence adaptive plant potential, which becomes apparent not only by particular changes of plant phenotype with B-chromosomes but also with the increase of genome changeability level. This increases plant population polymorphism by unfavorable conditions of habitat [56]. By the way, B-chromosomes have been recently discovered in *D. antarctica* that grow on the Darboux Island (unpublished results of joint studies of the Department of Cell Population Genetics of the Institute of Molecular Biology and Genetics, National Academy of Sciences of Ukraine and the Laboratory of the Institute of Molecular Biology, Russian Academy of Sciences).

D. antarctica is characterized by general low content of DNA (10 pg). This means that *D. antarctica* is a plant preadapted to development in cold conditions. The data on amount of DNA in *C. quitensis* is absent. However, low DNA content is generally typical for other species that are adapted to low temperature. In other words, DNA content can be regarded as one of the factors of geographical spreading [59].

In addition to the change of chromosome number in plant meristems that live in a severe environment, we can observe the phenomena of ontogenetic polyploidy. Vascular plants are characterized by polyploidy of different tissues and organs of plant bodies: polysomaty [49−51]. The analysis of DNA content in cell nuclei of leaf parenchyma and epidermis of plants from different populations of the Argentine Islands showed reliable differences on the basis of these indices between plants from different habitats [59]. Thus, according to the index of DNA amount in nucleus (concerning the level of ploidy of somatic cells) specimens of genus *Deschampsia* and also populations of *D. antarctica* compose a complex heterogeneous complex. Ploidy and the amount of DNA may substantially which we think has an adaptive value [50, 51, 58, 59]. It coincides with the concepts on mechanisms

and reasons of phenomena described by other authors. They connect the established aneusomatic character with influence of different environmental factors, particularly temperature. But similar data on *C. quitensis* is absent in the literature.

CONCLUSIONS

The comparative analysis of adaptive mechanisms of native Antarctic plants *Deschampsia antarctica* and *Colobanthus quitensis* to severe environmental conditions demonstrates a range of generally accepted adaptation ways owing to basic genetic plasticity, which do not distinguish the given species between other vascular plants. Despite the difference in adaptive strategies of these species, they are generally equally adaptive. The reasons why perlworts are not rather spread, are not probably connected with basic adaptive mechanisms but survival methods for this species and habitation in particular regions in the past historical epochs.

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