

Progress in physiological and genetic research concerning forest tree response to low temperature

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Abstract. Forest trees are a great model for physiological and genetic studies of plant resistance to unfavourable environmental conditions, since the same species can successfully acclimate at different latitudes. Modern biology, such as genomics, transcriptomics, proteomics, etc., significantly facilitates these studies and accelerates the acquisition of new knowledge. This allows for a more effective implementation of conservation measures and the renewal of forest ecosystems.

This review contains information on the latest scientific achievements in the field of acclimatization and tolerance to abiotic stresses, such as cold and frost, of forest trees. There is no doubt that in the course of evolution forest trees developed a complex and dynamic mechanism for controlling the entry into the winter dormancy stage, which allows woody plants to successfully survive in cold and freezing conditions and is initiated long before the beginning of winter. Studying the function of individual genes in forest tree species, however, remains an incredibly difficult task due to large genomes, specific development as well as the lack of standard techniques and routine procedures. In recent years, similarities between the well-studied genetic response to low temperatures of the model plant *Arabidopsis thaliana* and forest trees have been identified, which produced meaningful analogies and allows for issues of functional genetics to be addressed more effectively.

The main goal of this work was to show that findings from forest tree genomics can be effectively used as a tool for the reproduction and protection of important tree species through the identification of the predisposition of specific populations to climate change and their adaptive capacity.

Keywords: adaptation, tolerance, molecular response to stress, woody plants

1. Introduction

Forest ecosystems, including trees, herbs, microorganisms, animals and so on, perform many important productive, protective, social or recreational functions, while at the same time, by creating specific phytoclimatic conditions, these play a major role in climate change mitigation (Neale, Kremer 2011). Both current and predicted natural phenomena, such as prolonged droughts or frosts, excessive salinity or floods, have a negative impact on the growth and vitality of trees, posing a serious threat to the productivity and sustainability of forests worldwide (Salojärvia et al. 2017). The dying out of trees as a result of abiotic stress, including the impact of low temperatures, is predicted to accelerate in the next few decades (Harfouche et al. 2014).

In forest management, one of the most important meteorological phenomena that should be taken into account in breeding practice is the occurrence of frost. Due to its significant negative economic impact, research work relating to the resistance of forest trees to low temperatures (LT) is developing dynamically (Hurme et al. 2000; Gonzalez-Martinez et al. 2006; Salojärvia et al. 2017).

In characterizing frost, not only should the dates of its occurrence or termination be taken into account, but also its duration and the actual number of days with frost. Frost occurs when the average daily temperature is higher than zero and the minimum temperature falls below this value or when the maximum temperature is higher than zero and the minimum temperature has a negative value. Frost that occurs near the ground is referred to as ground frost, while that

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recorded in a meteorological instrument shelter is referred to as hard frost. For plants, late frosts occurring in spring are particularly dangerous because the leaf buds and shoots developing at that time are more sensitive to low temperatures. Forest crops, saplings and nurseries located in an open area, unprotected from ground-level heat radiation losses, are especially threatened by frosts (Wilczyński et al. 2005).

Traditional breeding techniques can effectively improve both quantitative and qualitative characteristics of trees, such as tree height, crown structure or also partial resistance to biotic and abiotic stress. Unfortunately, due to the long life span of trees, slow ontogenetic changes, long maturity, large genome sizes and the lack of well-characterized mutations, using selection methods to improve forest trees is an arduous and slow process (Harfouche et al. 2014).

Trees, despite a number of limitations in the dynamic development of studies on their tolerance to low temperatures, are an interesting research subject. Woody plants in the boreal zone to the Arctic and high mountains can survive long-term exposure to temperatures below 40°C or even -60°C, and laboratory tests have shown that many of these species can survive immersion in liquid nitrogen at -196°C (Strimbeck et al. 2014). In the taiga forest regions of Siberia and Canada, temperatures range from a record low of -64°C to a record high of +36°C, with a total amplitude of 100°C. In these regions, the evergreen *Pinus* pines, *Picea* spruces, *Abies* firs, together with *Larix* larch and several species of angiosperms are exposed to extreme cold, varying light conditions, as well as strong and dry winds in winter (Strimbeck et al. 2014). Plants from boreal and temperate areas are more able to cope with low and freezing temperatures. In recent years, the breeding capacity of some forest tree species has been developed as a result of advances in genetics and plant genomics. Studies of Siberian and Canadian species with full tolerance to extreme temperatures found that tolerance to low temperatures varies depending on the climate of the place of origin of these species, indicating that this is the result of genetically fixed adaptation and is subject to strong genetic control (Strimbeck et al. 2014).

The aim of this paper is to review the literature on the functional genetics of the phenomenon of the resistance of forest trees to low temperatures.

2. The physiological response of woody plants to low temperatures (LT)

The tolerance of trees to freezing is closely connected to the phases of the vegetation cycle, and thus, their physiological activity. The meristematic activity of top buds stops in response to shortening day lengths, ending with the cessation of growth and initiation of absolute rest. A distinction is made with relative rest, which results from negative external factors such as low

temperature or oxygen deficiency, and disappears when conditions improve. There is also the phenomenon of deep plant dormancy, caused by changes in the internal plant mechanisms relating to hormonal management or genetic predisposition (Kopcewicz et al. 2012). A few weeks after the cessation of bud growth, the buds enter a state of deep dormancy. Parallel to growth cessation, the tolerance of trees to freezing starts increasing in response to the short day's photoperiod. Prolonged exposure to a short day can lead to a significant increase in tolerance to freezing (Fig. 1) (Welling, Palva 2006).

Most of the life support processes in plants are temperature-dependent. This is associated with the thermal adaptation of enzymatic proteins, the development stage of the plant and its growth conditions (Floryszczak-Wieczorek 2008). Thermal stress occurs when the plant is exposed to the effects of sub-optimal temperatures. The following plants are distinguished on the basis of their ability to adapt to temperature:

- plants that are sensitive to cold and have a tolerance range of +10°C to 0°C; these are generally plants growing in tropical and subtropical climates,
- plants that are sensitive to frost, tolerate temperatures of up to 0°C; these are plants that grow in the temperate zone, but are damaged when the temperature is low enough to cause water to crystallize in the plant cells; such plants include the 'drosophila' of plant genetics – *Arabidopsis thaliana* (L.) Heynh,
- plants that tolerate freezing with a temperature range of -1°C to -70°C; these are usually trees – perennial terrestrial plants, mosses and algae.

Plants that tolerate freezing, especially trees, are able to withstand the crystallization of water outside the cell and the loss of water by cells during freezing after the autumn acclimatization period. The freezing temperature in the cells is reduced by increased cytoplasm density and partial water loss. The formation of ice crystals in the apoplast is not yet a critical and irreversible situation for the cell. Irreversible damage can be observed when the ice crystals form in the symplast. Therefore, resistance to freezing is mainly based on the formation of ice inside the cell. One of the most important defensive mechanisms is the so-called 'frost plasmolysis', which consists of water penetrating into the apoplast and prevents the 'cooling of the liquid' (Kopcewicz et al. 2012). Reactions caused by frost largely resemble conditions corresponding to a water deficit. This results in a conformational change of proteins and abnormal reactions between the cell wall and its membrane. All these processes lead to the cessation of photosynthesis in the plant (Floryszczak-Wieczorek 2008).

Frost mainly damages the cell membrane through ice crystals, leading to an excessive leakage of electrolytes from the tissues (Tuteja 2009). Another reaction to the cold is the phenomenon of membrane depolarization. Calcium channels open up, which in turn increases the concentration of

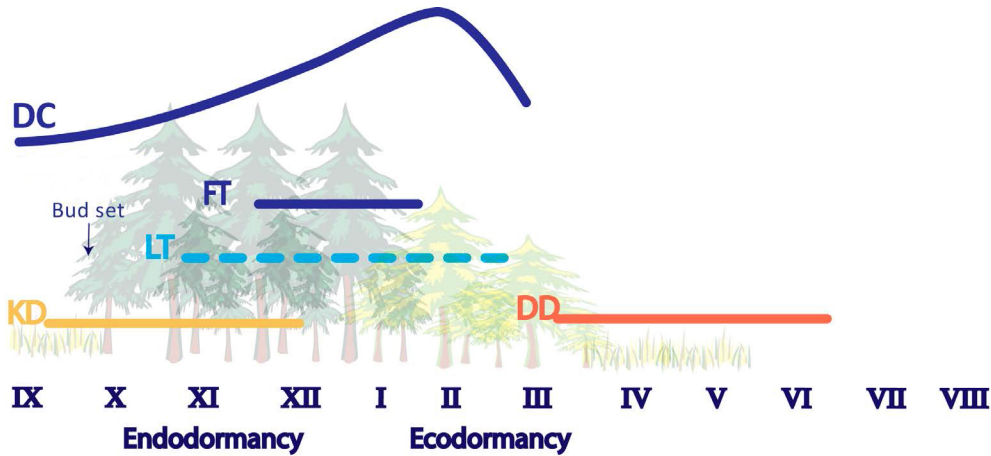


Figure 1. Annual dormancy and freezing tolerance in an adult birch individual during wintering in Poland. DD – long day, KD – short day, LT – low temperature, FT – freezing point temperature. Roman numerals indicate months, DC – dynamics of freezing tolerance, green background color of plants – endodormancy (absolute rest), yellow background color of plants – ecodormancy (relative rest) (Welleng, Palva 2006, adaptation for Poland using <https://www.gismeteo.pl/> and yandex.ru).

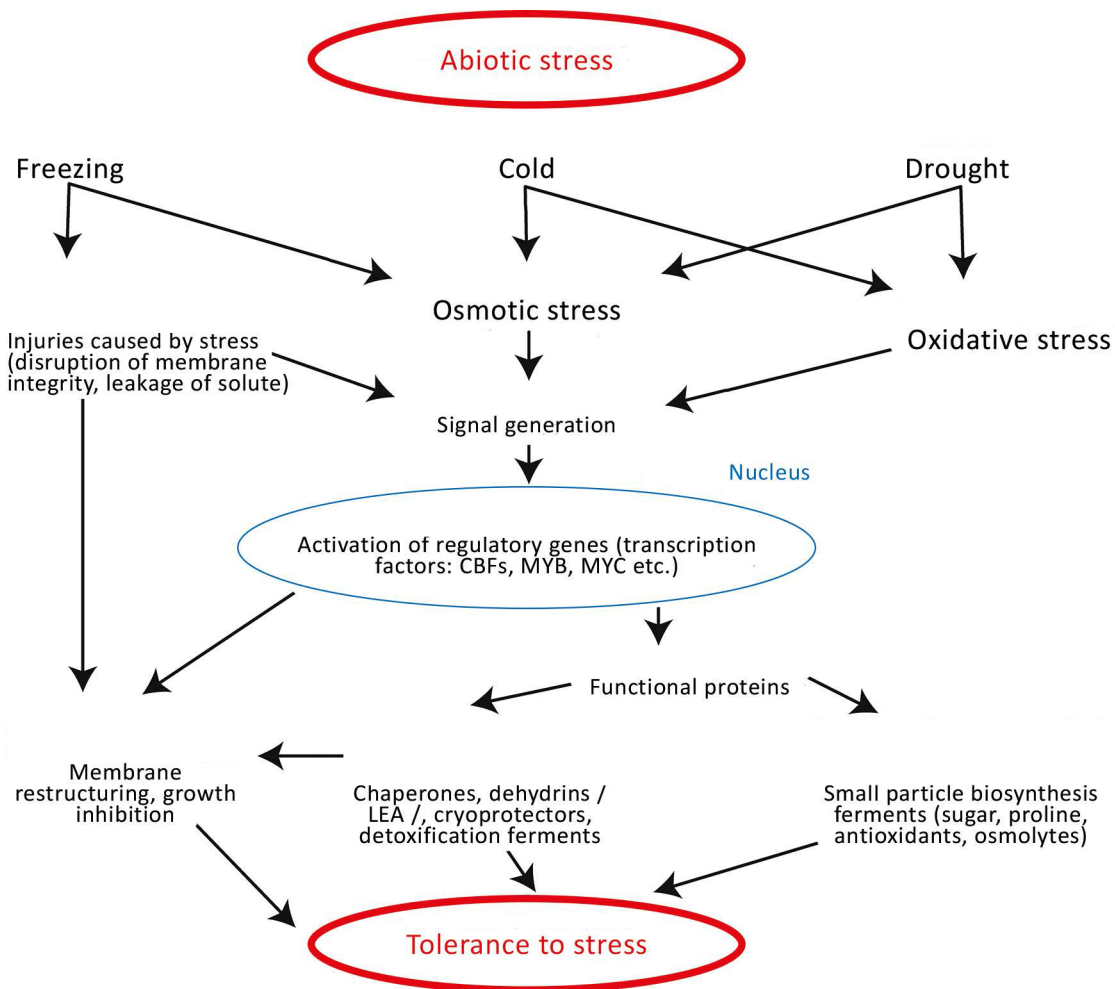


Figure 2. Processes occurring in a plant cell during the abiotic stress response

calcium ions in the cytoplasm. This also applies to the stoma cells, which cause the plant to rapidly wither when opened (Floraszczak-Wieczorek 2008). In general, plants growing in the temperate zone are resistant to cold, but they are threatened by the actions of frost in winter and are therefore forced to develop appropriate defense strategies (Fig. 2).

The cell membrane plays the most important role in low temperature tolerance. Due to its location around the periphery of the cell, it forms the boundary between the external environment and the cytoplasm, participates in ion management and is responsible for water balance. The strength of tolerance largely depends on the stability of the cell membrane, as well as on the ability to adapt, which is influenced by such processes as: changes in membrane properties, hormone levels, sugar content and gene expression. For example, an increase in the content of abscisic acid (ABA) in cells is associated with the resistance of woody plants to cold and frost (Rakowski 2005).

3. The molecular and genetic response of forest trees to LT

The acclimatization of plants to low temperatures is a result of changes in gene transcription (Kimieć et al. 2005). The stress associated with low temperature causes changes in cell metabolism by accelerating the degradation of proteins and slowing down their synthesis. At the same time, new proteins are formed, called stress proteins (Kopcewicz et al. 2012). Classical genetic research has shown that the ability of plants to acclimatize is a quantitative feature, and includes the action of many genes (Tomashow 1999). As already mentioned, one of the main stress factors in cells, resulting from the change of the

water potential in a cell, is dehydration caused by freezing (Wisniewski et al. 2003). Moreover, a cold induced production of a reactive form of oxygen, especially when combined with high light intensity, contributes to even greater membrane damage (Welling, Palva 2006). Therefore, when plant cells acclimatize to the conditions of abiotic stress caused by low temperature, the induction of genes are involved that control membrane stability, biosynthesis of chaperones, strengthening of antioxidant mechanisms and accumulation of sugars and compatible dissolved substances (Tuteja 2009). Numerous changes in the expression of genes during acclimatization to cold conditions (Table 1) have been demonstrated by microarray technology (Fowler, Tomashow 2002; Seki et al. 2002).

Generally, stress-response genes can be divided into two groups: genes that directly participate in protecting cells under stress conditions, and genes that encode components of the signal pathway that regulates gene expressions in response to stress (Tomashow 1999). New tools of functional genomics, widely used in studies on the acclimatization of herbaceous plants to low temperatures, have also been applied in studies on trees entering dormancy and their development of frost tolerance. They include the analysis of the transcriptome and proteome of acclimatizing woody species based on a sequence analysis using the expressed sequence tag (EST) method. This method was used to find several hundred unique transcripts for cold acclimatizing species, that is, blueberries, birch *Betula* spp. and poplar *Populus* spp. It is particularly useful for species whose genome is not yet known, while revealing new genes that may be associated with cold acclimatization and providing an approximate picture of gene expression (Welling, Palva 2006).

Table 1. The study of functional genomics in woody plants regarding wintering (Welling, Palva 2006 with modifications)

Method	Number of ESTs/genes/and part of the plant	Treatment(s) if specified	Species	Reference
EST sequencing	4406 and 3649 EST sequences from active and dormant cambium, respectively	summer/autumn (active growth/ dormancy)	poplar <i>Populus tremula</i> L.	Schrader et al. (2004)
EST sequencing	17,500 unigenes	12 different libraries	birch <i>Betula pendula</i> Roth.	K. Ojala et al. (unpublished data)
Microarray	2171 ESTs from xylem and shoot tip library	seasonal changes in earlywood–latewood	loblolly pine <i>Pinus taeda</i> L.	Yang, Loopstra (2005)
Microarray	21,840 unigenes from needles from the upper lateral lobes this year	summer/autumn (early winter)	sitka spruce <i>Picea sitchensis</i> (Bong.) Carrière	Holliday et al. (2007)
Microarray	7254 unigenes	shoots were collected every four hours for two days in winter and summer	cryptomeria japonica <i>Cryptomeria japonica</i> (L.f.) D.Don	Nose, Watanabe (2014)

The development of research on the functional genetics of forest trees is a response to the continuous need to develop new and improve existing tools for the protection and management of forest populations. One of the main objectives is to develop mechanisms supporting sustainable forest management. On one hand, these activities are based on promoting and enriching existing genetic diversity in forests. This goal will be achieved by understanding evolution and the development of adaptation possibilities in an evolutionary and ecological context (Neale, Kremer 2011). On the other hand, they also support the selective breeding of forest trees and the pursuit of qualitatively and quantitatively appropriate basic material for forests. The selective and genetic improvement of species, especially those with a short production cycle, is intended to ensure a sustainable supply of wood raw material for the wood processing sector.

Unlike herbaceous plants, trees have no single universal model species and there is no species that dominates economically over other species in the world. This situation certainly hinders progress, but with the development of next generation sequencing (NGS) technology, a large number of target species, often with high genetic diversity, will provide the impetus for structural and functional genomics. Sequencing the genomes of the main species will allow reference samples to be established for thousands of sequences of species of lesser economic importance: cultivated and bio-coenotic (Neale, Kremer 2011). In the studies of frost resistance of forest trees, a promising subject that can serve as a model tree is the silver birch *Betula pendula* Roth. It has a northern range, a short life cycle (initiation of flowering within 1 year), and most importantly, it has a short, sequenced genome (440-Mb) (Salojärvia et al. 2017).

In order to effectively use the results of molecular and genetic analyses to improve the resistance of trees to stress caused by abiotic factors, the signal pathways of plants must be understood in detail, and the genes encoding and regulating the synthesis of key proteins need to be identified. Understanding the molecular and genetic basis of the expression of polygenic traits is an important issue in improving the quality of trees, and is also connected to many other areas. Newer technologies, such as genomic selection (GS) and EcoTILLING now provide new ways to improve knowledge about the various processes occurring in forest trees and the role played by key genes (Harfouche et al. 2014). Knowing and deciphering how forest trees adapt to harsh environmental conditions, especially in the face of predicted climate change, will be a great help in the future to meet the demands of the multifunctional model of sustainable forest management that assumes the coexistence of production functions, while ensuring the continuity and sustainability of forests for future generations.

3.1. CBF (C-repeat Binding Factors) transcription factors

One of the most important regulatory paths of the acclimatization process to cold conditions is the CBF/DREB1 response pathway, which has been widely characterized for *Arabidopsis thaliana*. The *Arabidopsis* genome codes a small group of transcription factors known as CBF1-3 or DREB1 A-C respectively (Kurbidaewa, Novokreshchenova 2011). These proteins have a DNA binding domain, very similar to amino acid sequences and are encoded by genes located on 4 chromosomes (successively: AT4G25490, AT4G25470, AT4G25480) (Kmieć et al. 2005). The induction of CBF1-3 genes occurs within 10–15 minutes after exposure of the plant to low temperatures. Maximum expression is achieved within 2–3 hours and ceases after 24 hours (Gilmour et al. 2004). During the accumulation of DREB1 transcripts, the promoters accumulate the mRNA of the relevant genes with a CRT/DRE (C-repeat/dehydration response element) motif, which is a regulatory DNA sequence of genes encoding protective proteins against stress. The genes are induced by a factor called ‘CBF regulon’. It has been proven to contain 109 genes belonging to several groups (Fowler, Thomashow 2002). The contribution of the ‘CBF regulon’ factor to low temperature acclimatization has been demonstrated in studies where the overexpression of CBFs leads to the constitutive expression of target CBF genes, resulting not only in an increased tolerance of plants to freezing, but also an increased resistance to drought and salt (Kasuga et al. 1999; Gilmour et al. 2004). The CBF protein family, conservative among herbaceous plant species, has been found even in plants unable to acclimatize, such as tomatoes and rice (Thomashow 1999).

However, recent molecular and genetic studies clearly show that lowering the temperature leads to the activation of a similar process of signal transmission and expression of orthologous genes both in herbaceous and woody plants. Benedict et al. (2006) cloned the orthology of genes of the CBF family *Arabidopsis thaliana* (AtCBFs) from *Populus balsamifera* L. Studies on the expression of the AtCBFs genes of the poplar have shown their ability to transmit increased tolerance to low temperatures and other abiotic stresses. Experiments with cDNA microarrays allowed genes to be identified that increase their expression by the overexpression of AtCBF1 in this species. A strong similarity of the CBF regulon was found between the poplar and radish and differences between leaf and shoot regulons were identified. Thus, Benedict et al. (2006) were able to demonstrate that the regulation of genes affected by the freezing of wild poplar leaves was similar to the poplar with the transgenic AtCBF gene. However, the varying expression of PtCBF paralogues and different gene groups responding to CBFs in temporal (leaf) and solid (stem) tissues suggests that as a result of the evolution of winter dormancy in perennial plants, the role of these genes in different tissues of woody species may vary.

3.2. Dehydrins

In research on the acclimatization to cold conditions, the most widely analysed proteins are dehydrins, due to their abundance and expected role in protecting cells from dehydration. Several dehydrin genes in their promoter contain LTRE/DRE/CRT (an element of the reaction to low temperature and drought) (Welling, Pavla 2006), which is recognized by CBF transcription factors. In addition, some dehydrins accumulate in response to ABA, the level of which increases due to osmotic stress, including frost (Kurbidaeva, Novokreshchenova 2011). To date, the orthologous genes of abscisic acid response participants (NCED, PYL, etc.) and the deactivation of reactive oxygen species (GPX, GST and GSR) (Du et al. 2018) have been identified in the *Pinus massoniana* transcriptome. In recent years, the physiological role of adaptation-related dehydrins has been actively studied, and although the exact function of most dehydrins has not yet been explained, it has been found that they have a hydrophilic structure that determines the water binding function in the cell and prevents the formation of ice crystals (Graether, Boddington 2014).

The study showed seasonal variability in the expression of dehydrin genes and protein content in different woody plants. This level is high in winter and low in the period of active growth (Welling, Pavla 2006). To analyse the factors that regulate the appearance of dehydrin during wintering, the gene expressions for different environmental conditions were studied. Most dehydrin in woody plant tissues is induced in response to LT or influenced by the shortening day length and then LT (Cooke et al. 2012). In addition, dehydrin was shown to be induced in dormant tissue in response to approaching the freezing point, but only after the tissue had thawed (Welling, Pavla 2006). In *Betula* spp. birch cells, dehydrins were clearly expressed in autumn in response to the short day, and in the middle of winter in response to low temperatures and frost (Welling, Pavla 2006).

After an active growth period at the beginning of summer, trees start to prepare for winter long before unfavourable conditions appear (Welling, Pavla 2006). Schrader et al. (2004) used the cryosection method to isolate purified cambial meristem cells from the woody plant *Populus tremula* during active growth and dormancy. They demonstrated that genes of the PttCBFs family, as well as those of the PttLEA family (Late Embryogenesis Abundant, dehydrins), are more pronounced in poplar meristems grown in the field in response to the short day that may indirectly affect the expression of frost resistance genes during acclimatization. As Puhakainen et al. suggest (2004), the short day also has a direct effect on genes induced by low temperature. It has been shown that it increases the induction of birch dehydrin genes controlled by CBF (Puhakainen et al. 2004). This issue has been extensively analysed

on the example of the model plant *Arabidopsis thaliana*, for which it has been shown that the expression of the CBF1 gene is dependent on diurnal rhythms (Lee, Thomashow 2012).

An example of the current trends and rapid progress in functional genomics research in forestry is the Scots pine *Pinus sylvestris* L. The species, despite its important ecological and economic role as well as its extensive range in Europe and Asia (Wachowiak et al. 2014), has remained out of the orbit of research possibilities for years due to its huge genome. Recently, thanks to the rapid development of technology, it has been possible to change the nucleotide in the haplotypes in several gene-candidates' response to LT of selected European Scots pine populations exhibiting a disparity in cold tolerance. Significant variation in the allelic frequency structure of haplotypes was detected in seven locations of the dehydrin gene family, including *dhn1* and *dhn3* (Wachowiak et al. 2009), and *abaR* (abscisic acid-responsive protein), which is the orthologue of the *AtGUN5* gene. Its product was identified as a potential component involved in the signal reception between the chloroplast and the cell nucleus during the acclimatization of plants to low temperatures (Wachowiak et al. 2009; Kindgren et al. 2015).

4. Summary

The high intra-population variability of trees provides excellent opportunities to understand the molecular basis of the functioning of plant organisms (Neale et al. 2013), including their response to changes in environmental conditions. It is very difficult to understand the functions of individual genes in forest tree species due to the size of their genomes, developmental specificity, as well as the lack of standardized methods and ready-made procedures routinely used in the genetic research of herbaceous species (Neale et al. 2013). A better understanding of the many life processes of trees is being made possible by the tools of functional and comparative genetics. In woody plants, the proteomic changes in the early acclimatization process of the leaves of *Populus* sp. (Renaut et al. 2004) and the bark of *Prunus persica* (Renaut et al. 2008) has been characterized, achieving similar results to herbaceous plant species. The introduction of modern technologies in such sciences as proteomics and metabolomics, supported by the results of many years of work on the physiological, biochemical and genetic changes occurring during acclimatization and dormancy, allowed many major molecular agents to be identified. Understanding the functioning of genetic mechanisms regulating the reactions of woody organisms to low temperatures will enable a functional analysis of these components to be conducted in vitro and in vivo, both separately and jointly.

In the future, one of the main and priority research tasks in forest tree genomics will be the development of new and high-throughput phenotyping technologies (Neale, Kramer 2011)

to clarify and define the components of phenotypic variability. Current and ongoing projects sequencing the genome of forest trees are limited to about 40 species, mainly to 4 families out of 100, that is: *Pinaceae* (pines, spruces and firs), *Salicaceae* (poplars and willows), *Myrtaceae* (eucalyptus) and *Fagaceae* (oaks, chestnuts and beeches). They are not conducted on a large scale, as is the case with the human genome, simple herbaceous plants or insects (Neale et al. 2013), but advances in sequencing efficiency and cost have enabled the first projects of the large (~ 20 Gbp) genomes of many coniferous tree species (Street 2019). Currently, the TreeGenes database (Wegrzyn et al. 2008) is the most comprehensive source for the comparative genome analyses of forest trees.

In light of the increasing pressure on forests around the world, the need for tools to provide accurate genetic information on trees will increase, both in the areas of forest management, conservation and improvement (Staton et al. 2015). Genomic resources can be used as tools for breeding and preserving important tree species by identifying the predisposition of individual populations to climate change and estimating their adaptation potential (Segelbacher et al. 2010; Sork et al. 2013). The results obtained in the research on the response of plants to LT can help us understand and predict the impact of global warming on individual tree species and entire forest ecosystems, especially in boreal regions (Strimbeck et al. 2015). It is believed that global warming is expected to be greatest in winter and at higher latitudes, which will tangibly impact dormancy phenology and tolerance of LT (Kramer et al. 2000).

Conflict of interest

The authors declare no potential conflicts of interest.

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Contribution of the authors

M.N. – concept, literature review, manuscript writing; K.S. – literature review, manuscript writing; M.K. – literature review, manuscript writing, editing.