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The role of plant proteases in the response of plants to abiotic stress factors

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The primary function of proteolytic enzymes is the hydrolysis of peptide bonds. Enzymes responsible for catalyzing this reaction are commonly referred to as proteases. The vast majority of these enzymes belong to the class of hydrolases and operate in aqueous environments. However, there is a distinct group of proteases known as intramembrane proteases, which are integral membrane proteins capable of cleaving peptide bonds in the hydrophobic environment of biological membranes. Proteolysis serves several essential functions in plant cells, ranging from the degradation of damaged and unnecessary proteins to the removal of non-functional protein aggregates. It plays a role in the quality control system for proteins and even releases transcription factors from membrane proteins. Proteolytic processes are indispensable at every stage of plant development and allow for the modification of the cell's protein composition based on developmental needs and environmental requirements. Proteases are also enzymatic components of the cell that facilitate the efficient regeneration of many key metabolic pathways, such as photosynthesis and respiration. The response of plant cells and the entire plant organism to various biotic and abiotic stresses often requires the remodeling of metabolic pathways, the regeneration of key enzymatic complexes, or changes in the protein profile. By participating in all these processes, proteases constitute a crucial element of the cellular response to environmental stresses. The aim of this work is to review the role that individual proteases play in the response of plant cells to abiotic stress factors, such as drought, salinity, cold, temperature, and light.

KEYWORDS

abiotic stress factor, plant proteases, proteolysis, stress response, protein degradation

Proteolysis in plant cells

Proteolysis is a process in which peptide bonds within proteins are broken, resulting in the formation of shorter peptides that can then be further broken down into individual amino acids. Enzymes that catalyze these reactions are known as proteolytic enzymes, also called proteases or peptidases. These terms are often used

interchangeably and refer to any enzyme belonging to the hydrolase class, whose role is to hydrolyze peptide bonds. Proteases are common enzymes throughout the whole world of living organisms from bacteria to humans as well as in the viral particles. Proteolytic enzymes can serve various functions in cells, being involved in the course of multiple metabolic pathways. They also exhibit a wide range of substrate specificity. For instance, pepsin found in the stomach of mammals, facilitating the breakdown of proteins in food, is a relatively non-specific enzyme, which is advantageous in the digestion process. The task of pepsin is to degrade as many protein chains as possible, rather than being substrate specific. In contrast, in terms of enzymatic specificity, the serine protease NS3-4A present in HCV virus particles represents an extreme example. This enzyme plays a crucial role in the virus replication process in chimpanzee hosts and is responsible for cleavage HCV polyprotein at very precisely defined place (Lin, 2006).

Plant proteases perform a variety of functions at every stage of a plant's life. These enzymes are involved in the processes of programmed cell death, plant growth, aging, fruit, and seed ripening, and participate in the process of hydrolysis and mobilization of other proteins accumulated in seeds and cereal grains (Liu et al., 2018; Martinez et al., 2019; Tornkvist et al., 2019). In addition, they play an important role in maintaining the proper course of many metabolic processes, such as respiration and photosynthesis. Finally, proteases play key roles in plant responses to abiotic stress factors (Velasco-Arroyo et al., 2016; Velasco-Arroyo et al., 2018; Gomez-Sanchez et al., 2019; James et al., 2019) and the attack of pathogens (Misas-Villamil et al., 2016; Diaz-Mendoza et al., 2017).

The classification of proteolytic enzymes may be different and depends on the adopted criterion, which may be the structure of the active center of the enzyme, specificity of action, site of cleavage of the polypeptide chain, etc. Taking as the first classification criterion the place within the protein chain where the protease hydrolyzes it, two basic groups of proteases are distinguished. The first group in this approach are exopeptidases that cut the protein sequence at its ends. Exopeptidases can cut off the final amino acids of the protein chain both at the C-end of the protein and at its N-end, hence they are referred to as C- or N-exopeptidases. The second group are endopeptidases that catalyze the process of nucleophilic attack on the carbon atom of the peptide bond located inside the protein chain. As a result of this attack, an unstable complex is formed, the breakdown of which involves the degradation of the peptide bond and the formation of two smaller polypeptide chains (Davies, 1990).

Endopeptidases are a very broad group of proteolytic enzymes that differ, among other things, in the structure of their active site. Taking these differences into account, six main types of endopeptidases can be distinguished: aspartic, cysteine, glutamine, serine, threonine endopeptidases and metalloendoproteases. The different structure of the active center is associated with a slightly different mechanism of nucleophilic attack on the protein's peptide bond, however, all these enzymes catalyze proteolysis reactions using a water molecule and operate only in an aquatic environment in contrast to a separate group consists of the so-called intramembrane proteases that are able to catalyze the reaction of

breaking peptide bonds within biological membranes, i.e. in an extremely lipophilic environment (Wolfe and Kopan, 2004).

Oligopeptidases, which are distinguished as a subgroup of endopeptidases, are enzymes capable of cleaving short amino acid chains, but are unable to digest entire, large protein molecules. This property results from the structure of oligopeptidases themselves, whose active site is located at the end of a narrow cavity where only smaller peptides can reach. The size of the peptide that is the substrate for the protease is crucial in the process of the so-called "docking", i.e., attaching the substrate to the active center of the protease. However, the spatial structure of the potential substrate is also important for the possibility of catalysis of the hydrolysis reaction itself. In some cases, the structure of the peptide may inhibit the activity of catalyzing enzymes (Jacchieri et al., 2009).

In addition to the properties of the potential substrate, size, spatial structure or amino acid sequence of the peptide, environmental conditions are an important factor influencing the activity of proteases. Thus, the activity of some cytosolic oligopeptidases depends on the current redox status of the environment. An example is zinc timet oligopeptidases - TOP, belonging to the M3 type of metalloproteases, present in both animal and plant cells. TOP is an enzyme whose activity is regulated by the concentration of hydrogen peroxide. Studies on the human embryonic kidney cell line HEK293 have shown that increasing the concentration of hydrogen peroxide in cells leads to an increase in the activity of TOP protease, which reaches its maximum activity at a hydrogen peroxide concentration of 1.2nM (Icimoto et al., 2017).

Plants throughout their lives are exposed to a range of unfavorable environmental factors. Abiotic stress factors include primarily drought, salinity, cold, high temperature, excessive radiation, pesticides, and heavy metals. These factors interact with plants, often leading to a series of unfavorable functional and structural changes. However, during evolution, plants have developed a range of mechanisms called adaptations that allow them to minimize or tolerate the effects of stress. Plant proteases play an extremely important role in these processes, degrading damaged proteins that hinder the efficient functioning of specific metabolic pathways. Thus, proteases contribute to the efficient regeneration of metabolic pathways or their redirection to other paths better suited to changed environmental conditions (Figure 1 and Table 1).

Peptides produced as a result of protease activity can also regulate the production of reactive oxygen species (Möller and Sweetlove, 2010) and thus participate in signal transduction pathways generated by reactive oxygen species. Proteases are therefore involved in the transmission of information over long distances between different tissues and organs. Proteases are involved in this aspect, among other things, in regulatory processes associated with abscisic acid (Schaller, 2004; van der Hoorn, 2008; Kato and Sakamoto, 2010; Kidric et al., 2014; van Wijk, 2015; Diaz-Mendoza et al., 2016; Sharma and Gayen, 2021).

The regulation of various plant developmental processes, starting from seed germination and the mobilization of storage materials, and extending to the formation and development of specific cell organelles, such as plastids, requires the activity of

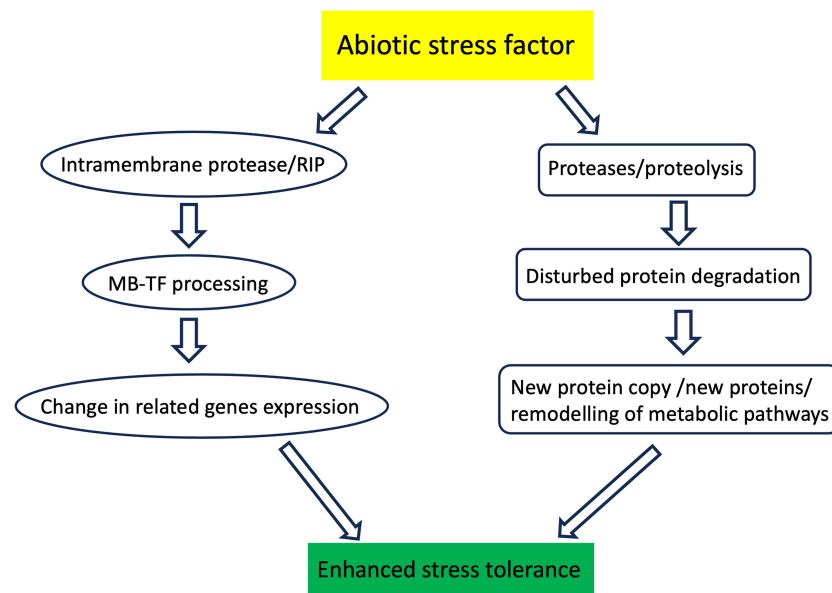


FIGURE 1

Schematic representation of the plant proteases action during stressful conditions. Intramembrane proteases cleave the protein transcription factor anchored in the biological membrane. This process, called regulatory intramembrane proteolysis (RIP), enables the activation of transcription factors and, ultimately, changes in the expression of related genes. The other proteases degrade proteins damaged during plant stress exposure. Degraded proteins are replaced with new functional copies. Proteases also degrade unnecessary proteins, which also enables remodeling the metabolic pathways.

proteases (Schaller, 2004; van der Hoorn, 2008; Kato and Sakamoto, 2010; Kidric et al., 2014; van Wijk, 2015; Diaz-Mendoza et al., 2016; Sharma and Gayen, 2021).

Furthermore, intramembrane proteases are suspected of degrading small polypeptides anchored in biological membranes, leading to the release of their fragments that can function as transcription factors or elements of polymerase-stabilizing complexes (Adamiec et al., 2017; Adamiec et al., 2018). Such activity is associated with changes in the gene expression profile. This process is so significant that it has been described as intramembrane regulatory proteolysis.

The main goal of this study is to examine the role that plant proteases play in the response of plants to abiotic stress factors, such as drought, salinity, low and high temperatures, and excessive light intensity.

Drought

Drought, much like excessive water, is considered as one of the main causes of reduced yields and plant survival, especially in the case of crops such as corn, rice, and wheat (Furlan et al., 2016).

Lack of rainfall and high temperatures that increase evaporation intensity led to a situation in which the amount of transpired water by the plant exceed its capacity to its absorption by the roots. The consequence of such a situation is the occurrence of osmotic stress within the plant (Bray, 1997). Water deficit in cells results in structural and functional changes in cell walls and

cell membranes, altering their permeability and disrupting basic metabolic pathways such as photosynthesis and cellular respiration (Kumar et al., 2018; Kapoor et al., 2020). One of the most common consequences of drought in plants, as well as other stresses, is secondary oxidative stress, caused by the generation of large quantities of reactive oxygen species (ROS), which damage both proteins and nucleic acids as well as lipids (de Carvalho, 2008). Naturally, over the course of evolution, plants have developed protective mechanisms to minimize the damage caused by drought.

One of the initial responses of plants to emerging soil water deficit is the synthesis of abscisic acid (ABA), which is subsequently transported to the leaves where it induces the closure of stomata (Moloi and Ngara, 2023). This restricts water loss from the leaves. However, stomatal closure is associated with limited gas exchange, thereby inhibiting the supply of CO₂ to the mesophyll cells. As a result, there is a decrease of CO₂ assimilation and the photosynthetic electron transport chain, leading to the generation of increased levels of ROS that need to be scavenged by the cellular machinery; otherwise, damage to lipids, proteins and nucleic acids may occur (Wang et al., 2003; Sharma et al., 2012; Moloi and Ngara, 2023). However, ABA is not the only hormone participating in a plant's response to drought. The literature extensively describes the involvement of other hormones such as jasmonic acid, ethylene, gibberellins, cytokinins, and auxins in the comprehensive response to drought stress (Moloi and Ngara, 2023).

Drought stress is a triggering factor for the upregulation of many genes encoding proteases belonging to various classes.

TABLE 1 Plant proteases involved in the response to abiotic stress factors.

protease	type of protease	activity	Cell compartment	stress	species	References
ASPG1	Aspartyl-type	Reduced stomatal density and aperture	Nucleus of guard cells	drought	<i>A. thaliana</i> ; <i>Coffea</i>	Yao et al., 2012; Sebastian et al., 2020; Fernandes et al., 2021
AtFtsH	Zn ²⁺ -containing metalloprotease	Degradation of PsbA, Lhcb1, Lhcb2	chloroplasts	Drought, low temperature, high light	<i>A. thaliana</i>	Sakamoto et al., 2002; 2003; Yu et al., 2004; Luciński and Jackowski, 2013; Kato and Sakamoto, 2018
FtsH1	Zn ²⁺ -containing metalloprotease	Degradation of PsbA	chloroplasts	high light	<i>A. thaliana</i>	Lindahl et al., 2000
FtsH2/FtsH3	Zn ²⁺ -containing metalloprotease	Degradation of PsbA	chloroplasts	high light	<i>Synechocystis</i> spp.	Krynicka et al., 2015
FtsH11	Zn ²⁺ -containing metalloprotease	Maintaining the proper function of PSI and PSII	chloroplasts	High temperature	<i>A. thaliana</i>	Chen et al., 2018
FtsH4	Zn ²⁺ -containing metalloprotease	Protecting from protein aggregation; maintaining the hydrogen peroxide and auxin homeostasis	mitochondria	High temperature	<i>A. thaliana</i>	Zhang et al., 2014; Maziak et al., 2021
Deg2	Serine-type	Degradation of Lhcb6, PsbA	chloroplasts	Salinity, high temperature, high light	<i>A. thaliana</i>	Chassin et al., 2002; Kapri-Perdes et al., 2007; Luciński et al., 2011
Deg5/Deg8	Serine-type	Degradation of PsbA	chloroplasts	High light	<i>A. thaliana</i>	Kapri-Perdes et al., 2007
Deg1	Serine-type	Degradation of PsbA	chloroplasts	High light	<i>A. thaliana</i>	Kley et al., 2011
Deg10	Serine-type	Root elongation, seed production	mitochondria	High temperature	<i>A. thaliana</i>	Huber et al., 2019
HtrA2	Serine-type	Degradation of misfolded proteins	Plastids, cell wall	Salinity, high temperature	<i>Halotheca</i> sp.	Patipong et al., 2020
LON4	Serine-type	maintaining mitochondrial homeostasis	mitochondria	drought	<i>A. thaliana</i>	Pinti et al., 2016; Sharma and Gayen, 2021
ClpD1	Serine-type	degradation of damaged proteins in plastids	chloroplasts	drought	<i>A. thaliana</i>	Kato and Sakamoto, 2010; Ali and Baek,

(Continued)

TABLE 1 Continued

protease	type of protease	activity	Cell compartment	stress	species	References
Clp complex	Serine-type	Removing of aggregated and improperly folded proteins	chloroplasts	High temperature	<i>A. thaliana</i>	Moloi and Ngara, 2023; Lee et al., 2007; Nishimura and van Wijk, 2015; Sharma and Gayen, 2021
RD19	Papain-like, cysteine-type	Degradation of oxidized proteins	Extracellular space; vacuole	salinity	<i>A. thaliana</i>	Koizumi et al., 1993; van der Hoorn, 2008
RD21	Papain-like, cysteine-type	Degradation of oxidized proteins	Extracellular space; vacuole	salinity	<i>A. thaliana</i>	van der Hoorn, 2008
Cyp15	Papain-like, cysteine-type	Degradation of oxidized proteins	cell wall	salinity	<i>Pisum sativum</i>	Jones and Mullet, 1995
OMA1		Protecting from protein aggregation	mitochondria	High temperature	<i>A. thaliana</i>	Maziak et al., 2021

Available data show that in many species, the organs in which the expression of genes encoding specific proteases increases are leaves and roots (Moloi and Ngara, 2023). In *A. thaliana* and in *Coffea*, one of the key enzymes determining the plant's drought resistance is the aspartyl protease guard cell, ASPG1 (Yao et al., 2012; Fernandes et al., 2021). Overexpression of this protein is associated with lower stomatal density and reduced stomatal aperture, resulting in increased drought tolerance in such plants (Sebastian et al., 2020). The increased drought resistance effect in *A. thaliana* is also observed in plants overexpressing the LON4 protein (Li et al., 2010), which is believed to play a significant role in maintaining mitochondrial homeostasis under drought conditions. LON4 is an ATP-dependent serine protease located in mitochondria. The nuclear gene encoding this protease shows increased expression under drought conditions (Pinti et al., 2016; Sharma and Gayen, 2021). It has long been known that the early response of *A. thaliana* to dehydration also includes the induction of the expression of ClpA and ClpB proteins (Kiyosue et al., 1993). These proteins are part of the larger Clp protease complex, which recognizes and degrades misfolded or damaged proteins. ClpA is a chaperone-like protein, which is responsible for substrate recognition, while ClpB is described as a disaggregase, facilitating the disaggregation of previously misfolded or aggregated proteins.

In the leaves of drought tolerant varieties of Barley and Wheat, an increase in the content of ClpP proteases is observed (Ashoub et al., 2013; Chmielewska et al., 2016), as well as ClpD1 protease in the case of Rice (Wu et al., 2016). ClpD1 plays an important role in the degradation of damaged proteins in plastids (Kato and Sakamoto, 2010; Ali and Baek, 2020; Moloi and Ngara, 2023), and it is encoded by the nuclear so-called gene *OsClpD1*, which is induced under drought conditions (Wu et al., 2016). In the leaves of drought-resistant Barley varieties, an increase in the expression of the metalloprotease FtsH1 was also observed (Wang et al., 2015). FtsH1 is a part of the chloroplast heterocomplex FtsH "Type A," along with FtsH5. This complex participates in the repair of damaged polypeptide PsbA (D1 protein), a component of the photosystem II reaction center (Yu et al., 2004). FtsH heterocomplex in *A. thaliana* has been found to be responsible for the degradation of the desiccation related damaged of photosystem II (PSII) polypeptides - Lhcb1 and Lhcb2 (Luciński and Jackowski, 2013).

Drought tolerance in Wheat is also associated with the cysteine protease SUMO (small ubiquitin-like modifier), an enzyme commonly found in plants and yeast (Le Roux et al., 2019). Additionally, in the leaves of drought-resistant Wheat varieties, increased expression of alpha-type proteasome protein (Faghani et al., 2015), as well as type II metacaspases and leucine aminopeptidases, is noted (Ford et al., 2011). In the case of leucine aminopeptidase, it is observed that its levels do not return to their previous levels after drought stress subsides, but they remain increased (Ford et al., 2011). Since leucine aminopeptidase participates in the activation of some proteins and metabolic turnover, some authors suggest that its increased level upon rehydration may be the result of an important role of this peptidase in the processes of changing the protein composition of cells regenerating after drought stress (Moloi and Ngara, 2023).

Salinity

Salinity is one of the most significant environmental factors responsible for a substantial decrease in the chemical potential of soil solution water. This can lead to situations where plants lose the ability to efficiently take up water from the soil. High soil salinity results in changes in the structure and permeability of cell membranes, leading to disruptions in ion balance within cells (Shah et al., 2017). Furthermore, deficiencies in mineral nutrients and secondary oxidative stress occur due to the excessive generation of ROS, resulting in damage to nucleic acids and overproduction of oxidized proteins. This salinity-induced genotoxicity is also associated with a decrease in photosynthetic efficiency and disturbances in the mitochondrial electron transport chain (Sharma and Gayen, 2021).

Plants have evolved a range of adaptations to minimize the negative effects of excessive salinity. The plant's response includes both enzymatic and non-enzymatic reactions. Accumulation of proline, sugars, and other osmotically active compounds is one of the elements that lower the water potential of the cell sap and extend the cell's ability to take up water in unfavorable osmotic conditions.

Since salinity induces a strong synthesis of ROS in plant cells, there is a need for the degradation of oxidized proteins. Cysteine proteases play a significant role in these processes (van der Hoorn, 2008), especially proteins RD19 and RD21 belonging to the papain-like cysteine protease family. A strong induction of the expression of genes encoding them has been observed under salinity stress conditions (Koizumi et al., 1993). It is suggested that changes in the osmotic potential of cells are the direct stimulus for the alteration in the expression levels of genes RD19 and RD21. The levels of RD19 and RD21 did not change significantly under low or high-temperature conditions or in the presence of ABA (Koizumi et al., 1993). Another cysteine protease whose levels significantly increase in response to high salt concentrations in the environment is Cyp15 from *Pisum sativum*. The activity of this protease is linked to changes in the levels of various mRNA molecules under salt stress conditions (Jones and Mullet, 1995).

A separate class of proteases involved in the response to high salinity is serine proteases. It has been shown that under conditions of high salinity in the cyanobacterium species *Halotheca* sp., there is a significant increase in the expression of the gene encoding the protease HtrA2 (Deg). This enzyme is responsible for the degradation of misfolded proteins (Patipong et al., 2020). Protease HtrA2 has an optimum pH of 8.0 and remains active under conditions of high salt concentration and high temperature. This protein was detected in both the soluble protein fraction and within the cell membrane and thylakoid membranes. Exposure of cells to high salt stress and high-temperature stress caused a significant change in the subcellular localization of HtrA2. Under such conditions, the protein mostly localized to the cell membrane (Patipong et al., 2020). In higher plants, within the thylakoid membranes of chloroplasts, there are also cysteine, ATP-independent proteases like Deg (Huesgen et al., 2005; Huesgen et al., 2006; Sun et al., 2007; Chi et al., 2012; Schuhmann et al., 2012; Butenko et al., 2018). One of them is Deg2, which is involved in the

degradation of the Lhcb6 polypeptide under salt stress conditions (Luciński et al., 2011). The Lhcb6 polypeptide is part of the minor antenna complexes of PSII and plays an important role in the formation of PSII-LHCII supercomplexes. The absence of Lhcb6 is associated with the preferential formation of C2S2-type supercomplexes and an increase in non-photochemical quenching of chlorophyll a fluorescence (Illikova et al., 2021). Therefore, protease Deg2 may play a significant role in maintaining the proper composition of PSII-LHCII supercomplexes and the efficiency of photosynthesis under salt stress conditions.

Low temperature

The stress associated with low temperatures is most commonly considered as chilling (for temperature ranges from 0°C to slightly below 15°C) and freezing (below 0°C). Prolonged exposure of plants to low temperatures results in the inhibition or slowing down of development, a decrease in growth rate, and a drop in productivity. Low temperatures significantly affect the efficiency of basic metabolic pathways such as respiration and photosynthesis. Therefore, the ability to cope with low temperatures is crucial for most plants living on Earth. The photosynthetic conversion of light into energy stored in chemical bonds and CO₂ assimilation are processes that are highly temperature dependent. Low temperatures reduce the efficiency of reactions within PSII and decrease the synthesis of the large subunit of Rubisco, the enzyme directly responsible for CO₂ assimilation in the Calvin-Benson cycle (Sharma and Gayen, 2021). Such changes necessarily imply a decrease in photosynthesis efficiency.

There are several proteases located in the chloroplasts, which mostly belong to FtsH, Deg, and Clp and play a significant role in a range of processes related to the quality control of chloroplast proteins and in maintaining chloroplast homeostasis (van Wijk, 2015). Some of these proteases also have importance in plant acclimatization to low temperatures. Under low-temperature conditions, a decrease in the content of polypeptides of the main energy antenna of PSII (LHCII), namely Lhcb1 and Lhcb2, has been observed. The degradation of these proteins in low-temperature conditions is attributed to the heterocomplex AtFtsH, located in the thylakoid membranes (Luciński and Jackowski, 2013). It is also possible that the inner membrane protease S2P2, located within chloroplasts, plays a role in shaping cold resistance in *A. thaliana* (Wang et al., 2016). S2P2 is a metalloprotease belonging to the class of site-2-proteases (S2P), which are known as enzymes that release transcription factors from membranes. Therefore, it can be imagined that the involvement of S2P2 in shaping cold resistance is more related to shaping the expression profiles of certain genes rather than the direct degradation of proteins damaged by the action of a stress factor.

High temperature

High temperature has a significant impact on the development, growth, flowering, and productivity of plants. It also alters the rate

and efficiency of metabolic pathways. Throughout evolution, plants have developed various mechanisms that allow them to rapidly respond to temperature changes in their environment and, consequently, adapt quickly to changing temperatures. Therefore, the temperature values that are harmful to plants are largely species-specific (Sharma and Gayen, 2021). Plants often respond to the presence of temperature stress factors through changes in the composition of membrane lipids, increased activity of stress-related transcription factors, alterations in the course and regulation of metabolic pathways, and various detoxification pathways (Kai and Iba, 2014). Proteins are molecules that undergo significant changes due to temperature stress. Dangerous phenomena for plants include protein denaturation, improper folding, and, consequently, changes in spatial structure. Protein denaturation itself is an irreversible process in which proteins lose their biological activity. Improper folding can lead to the formation of aggregates, preventing proper cell function. The consequences of such a state can be equally severe. In plant cells, protein aggregates can cause endoplasmic reticulum dysfunction, known as ER stress (Li and Sun, 2021). To prevent such situations or mitigate their consequences, cells have a range of structures and mechanisms. Firstly, lysosomes and proteasomes should be mentioned, whose primary role is the degradation of damaged proteins. Additionally, plant cells contain special chaperone proteins, known as heat shock proteins (HSP; Burgos et al., 2020).

Proteases also play a significant role in the response of plant cells to temperature stress. In the green tissues of leaves with constitutive expression, Clp proteases are involved (Sharma and Gayen, 2021). These serine proteases, ATP-dependent, play a crucial role in the functioning and development of plastids by removing improperly folded, aggregated, or otherwise unwanted proteins. The plant Clp system consists of a tetradecameric proteolytic core with catalytically active ClpP subunits and inactive ClpR subunits, hexameric ATP-dependent chaperone proteins, and adaptor proteins (Nishimura and van Wijk, 2015). ClpB, ClpC, and ClpD subunits function as chaperone proteins (Lee et al., 2007). In *A. thaliana* cells, these proteins are essential for plant acclimatization to high temperatures. ClpB is constitutively expressed in chloroplasts and mitochondria in *A. thaliana* (Lee et al., 2007) and *P. lunatus* (Keeler et al., 2000). On the other hand, strong upregulation of the ClpB gene was observed in *O. sativa* cells in response to high temperatures. Moreover, *A. thaliana* mutants lacking the ClpB protein grew significantly slower than the wild-type form, and under high-temperature conditions, the absence of this protein in mutants led to premature plant death (Lee et al., 2007).

The FtsH metalloproteases are crucial for the functioning of chloroplasts and mitochondria under high-temperature conditions. These proteases are a fundamental component that determines a plant's ability to survive in high-temperature conditions (Langer, 2000). In chloroplasts, the FtsH11 protease is essential for the functioning of photosystem I (PSI) and PSII under high-temperature conditions. *A. thaliana* mutants lacking FtsH11 showed significantly reduced efficiency in PSI and PSII reactions (Chen et al., 2018). Chlorophyll a fluorescence analyses indicate that

the presence of FtsH11 is necessary for regulating the response of photosystems to high-temperature stress (Chen et al., 2018).

The mitochondrial protease FtsH4 and OMA1 are crucial for *A. thaliana*'s acclimatization to moderate, prolonged temperature stress (Maziak et al., 2021). Mutants lacking FtsH4 or OMA1 displayed a range of phenotypic changes when grown at 30°C, although their phenotype remained unchanged compared to wild-type plants when grown at 22°C (Smakowska et al., 2016; Migdal et al., 2017). Phenotypic changes observed in *ftsH4* mutants included delayed germination, reduced rosette size, and shorter root length. Similar changes in rosette size and root length were observed in *oma1* mutants (Smakowska et al., 2016; Migdal et al., 2017; Maziak et al., 2021). These phenotypic effects are associated with the accumulation of protein aggregates composed of small heat shock proteins (sHSPs). The protease and chaperone activities of FtsH4 and the protease activity of OMA1 are crucial for protecting mitochondria from the formation of these aggregates (Maziak et al., 2021). Additionally, the FtsH4 protease plays a significant role in regulating the developmental processes of *A. thaliana* by mediating a peroxidase-dependent interplay between hydrogen peroxide and auxin homeostasis (Zhang et al., 2014).

For the proper functioning of plants under elevated temperature conditions, another mitochondrial protease, Deg10, is also essential. The absence of this protein in *A. thaliana* mutants was associated with disruptions in root elongation, reduced seed production, and changes in the content of proteins that build components of the mitochondrial respiratory chain (Huber et al., 2019).

Deg proteases also play a significant role in the functioning of chloroplasts and their photosynthetic apparatus. Under high-temperature conditions, damage can occur to, among others, the polypeptide Lhcb6, which is subsequently intensively degraded. Experiments conducted using *deg2* mutants have determined that the degradation of Lhcb6 under temperature stress, as well as under salt stress, is carried out by the Deg2 protease (Luciński et al., 2011).

Light

Light is a crucial factor that determines the functioning of plants and the existence of life on our planet. Light energy is converted into chemical energy, which is used in biochemical reactions in the process of photosynthesis. Simultaneously, photosynthesis is the primary source of oxygen in the Earth's atmosphere. Excessive light intensity can lead to the phenomenon of photoinhibition, and prolonged light stress can result in damage to key proteins that make up the photosynthetic complexes in thylakoid membranes (i.e., Haußühl et al., 2001; Luciński and Jackowski, 2006; Sharma and Gayen, 2021). As a result, there is a limitation or inhibition of the light reactions of photosynthesis and a decrease in the efficiency of CO₂ assimilation. Chloroplast proteases play a role in plant acclimatization to high light intensities. They are responsible for the degradation of light-damaged proteins, thereby enabling the regeneration of entire photosynthetic complexes.

The protein most susceptible to photodamage, especially, is the polypeptide PsbA (D1), which, along with PsbD (D2), forms the core

of the PSII reaction center (Baena-Gonzales and Aro, 2002; Luciński and Jackowski, 2006; Sun et al., 2007). Damage to PsbA leads to the inactivation of the entire PSII complex and necessitates its repair by replacing the damaged PsbA with a new, functional copy (Baena-Gonzales and Aro, 2002). The degradation of photodamaged PsbA is a multi-step process involving proteases from different classes. It is believed that proteases Deg and FtsH play a crucial role in this process. Deg1 and Deg2 proteases perform the initial proteolytic cleavage within the hydrophilic loops connecting the individual transmembrane domains of the PsbA protein (Chassin et al., 2002; Kapri-Perdes et al., 2007). There are also reports in the literature suggesting that the Deg5/Deg8 protease complex is also involved in this process (Sun et al., 2007). Likely, the protease Deg1 cleaves the CD loop, while the Deg5/Deg8 complex cleaves the CD loop of photodamaged PsbA (Kapri-Perdes et al., 2007). Furthermore, high light intensity stimulates the activation of the Deg1 protease by inducing the transformation of an inactive monomer into an active proteolytic hexamer (Kley et al., 2011). All Deg proteases perform peptide bond hydrolysis in an ATP-independent manner. The degradation products generated by Deg proteases are subsequently digested in an ATP-dependent manner by the FtsH protease (Sakamoto et al., 2002; Sakamoto et al., 2003; Kato and Sakamoto, 2018). It has been shown that the degradation of the 23 kDa fragment of PsbA is mediated by the FtsH1 protease (Lindahl et al., 2000), although other experiments indicate the involvement of FtsH2 and FtsH5 proteases, which are part of the FtsH heterocomplex (Sakamoto et al., 2002, 2003; Kato and Sakamoto, 2018). In the case of *Synechocystis* spp. cells, the degradation of D1 is attributed to the FtsH2/FtsH3 heterocomplex (Krynicka et al., 2015).

Photodamaged PsbA is not the sole proteolytic target of chloroplast proteases under high light stress conditions. Polypeptides Lhcb1 and Lhcb2, damaged under light stress conditions, can be degraded by the chloroplast heterocomplex FtsH (Luciński and Jackowski, 2013). Protease Deg1 is also suspected of degrading other PSII polypeptides, specifically PsbS and PsbO. Furthermore, based on *in vitro* experimental results, it is attributed the ability to degrade the polypeptide Lhcb4 and Lhcb5, which constitute the polypeptide moiety of CP29 and CP24, respectively (Chassin et al., 2002; Kapri-Perdes et al., 2007; Zienkiewicz et al., 2011).

On the other hand, protease Deg2 is responsible for the degradation of polypeptide Lhcb6, similarly under temperature and salt stress conditions (Luciński et al., 2011).

The chloroplast subunit of the Clp complex with chaperone activity, ClpB3, is also upregulated under high light stress conditions (Adamiec et al., 2011). It has been demonstrated that the gene encoding ClpB3 contains specific cis-regulatory elements to which transcription factor PAPI can bind. It is suggested that PAPI acts as an intermediary in the induction of CLPB3 gene expression under stress conditions (Adamiec et al., 2011).

High light intensity also enhances the expression of the gene encoding the pseudo-protease EGY3 (similar to what occurs under temperature stress) and the protease EGY2. However, despite demonstrated proteolytic activity of EGY2 (Chen et al., 2012), its

substrates are generally not known. However, there are speculations that such a substrate may be the chloroplast transcription factor pTAC16, which is able to interact with chloroplast RNA polymerase (Adamiec et al., 2018 and unpublished data). It is known that its absence significantly alters the levels of PsbA, PsbD, and PsbC polypeptides by affecting the expression of the genes that encode them (Adamiec et al., 2018). Therefore, EGY2 may be another protein with protease activity that plays a significant role in a plant's response to light stress.

Intramembrane proteases and their role in plant response to stress factors

Intramembrane proteases are a relatively recently discovered, remarkable group of proteases. What distinguishes these enzymes from other proteases is their ability to hydrolyze the peptide bond within the lipid bilayer of the biological membrane (Chen et al., 2012; Adam, 2013; Adamiec et al., 2017). Despite the uniqueness of this process, it occurs widely in practically all living organisms. Intramembrane proteases are classified into several different families, including site-2-proteases, rhomboid proteases, presenilins, and signal peptide peptidases. These enzymes play a significant role in plant developmental processes and in the course of many metabolic pathways, being involved in protein quality control, cell adhesion, membrane remodeling, and cell signaling (Adam, 2013; Schneider and Glickman, 2013; Adamiec et al., 2017).

It is often believed that the primary function of these proteases is to cleave the polypeptide chain, releasing membrane-anchored transcription factors. This activity ultimately leads to changes in the expression profile of certain genes, a process referred to as regulated intramembrane proteolysis (RIP) (Figure 1) (Adam, 2013; Schneider and Glickman, 2013; Adamiec et al., 2018; Adamiec et al., 2021). The first substrate described within the RIP framework was the endoplasmic reticulum (ER)-associated transcription factor bZIP28 (Liu et al., 2007a; Tajima et al., 2008; Adam, 2013; Sun et al., 2015; De Backer et al., 2022). It has been demonstrated that the release of bZIP28 from the ER membrane to the cytoplasm allows it to migrate to the cell nucleus, where it induces the expression of genes related to the plant's response to salt stress (Liu et al., 2007b; Tajima et al., 2008). It is possible that the protease directly responsible for releasing bZIP28 from the ER is S1P or S2P (Liu et al., 2007a; Tajima et al., 2008). Another transcription factor, whose release from the ER membrane is associated with the response to stress is bZIP60 (Iwata and Koizumi, 2005). Accumulation in the cell nucleus of the soluble domain of this protein is linked to increased transcription of BIP proteins, which belong to the HSP70 family and are typical representatives of the plant's ER stress response (Iwata et al., 2008). S1P and S2P proteases are once again involved in the release of the bZIP60 factor from ER membranes. Intramembrane proteases are also suspected of releasing the transcription factors belonging to the NAC family: NTL1, NTL7 and NTL8 from endoplasmic reticulum membranes and NTL6 from the plasma membrane. NTL8 is associated with the

regulation of flowering processes in *A. thaliana* under saline and low temperature conditions (Kim et al., 2007). NTL1 and NTL7 is activated under oxidative stress conditions (De Backer et al., 2022), while NTL6 and NTL8 are related to salinity and low temperature (Kim et al., 2007; Seo, 2008, 2010) (Table 2).

Despite the still limited knowledge about the role of intramembrane proteases, some of them are suspected to be involved in the response of plant cells to various stress factors. In this context, examples include the chloroplasts' rhomboid protease RBL10, which may be involved in photoprotective mechanisms in response to low temperatures (Thompson et al., 2012). On the other hand, the plasma membrane-localized RBL14 seems to be involved in the response to elevated temperature (Lee et al., 2015). Rhomboid proteases are also suspected to be involved in the response to H₂O₂-mediated stress signaling by releasing the ANAC017 transcription factor from ER membranes (Ng et al., 2013) (Table 2).

Within chloroplasts, intramembrane proteases belonging to the S2P family, namely EGY1 and EGY2, may also influence the functioning of these organelles under light stress conditions. Both proteins are located within the thylakoid membranes (Chen et al., 2005; Chen et al., 2012). It has been shown that *Arabidopsis thaliana* mutants lacking EGY1 or EGY2 exhibit changes in the stoichiometry of proteins building the PSII core and LHCII antennas, resulting in increased sensitivity to photoinhibition (Adamiec et al., 2018; Adamiec et al., 2022). There are also suggestions that EGY2 may affect the expression of chloroplast genes PSBA, PSBC, and PSBD by releasing the protein factor pTAC16 from the thylakoid membranes. On the other hand, the protein EGY3, considered a pseudoprotease due to the lack of proteolytic activity, seems to play a significant role under salt stress conditions, influencing the amount of H₂O₂ produced in chloroplasts by stabilizing copper/zinc superoxide dismutase 2 (CSD2; Zhuang et al., 2021).

Programmed Cell Death

Programmed Cell Death (PCD) is an essential part of the plant life cycle, occurring throughout the development of a plant, from embryogenesis to the death of the entire plant (Stael et al., 2019). PCD in plants can be executed through various pathways, including autophagy, apoptosis, hypersensitive reactions, and autolytic (vacuolar) PCD. Inducing PCD is required for many growth and development processes, such as the development of aleurone cells and grain in cereals, tissues that store seeds, the differentiation of female gametophytes, leaf abscission, pollen separation, the aging of the entire plant, and many more (Mondal et al., 2021; Basak and Kundu, 2022).

Several groups of proteolytic enzymes are involved in the process of PCD, including metacaspases (Fagundes et al., 2015). Metacaspases are structural homologs of caspases, which are enzymes found in animals. Unlike caspases, metacaspases do not show substrate specificity for aspartate (Asp); instead, they cleave substrates just after arginine (Arg) or lysine (Lys) residues (Vercammen et al., 2004). Two main types of metacaspases are recognized (Fagundes et al., 2015). Type I metacaspases have a proline-rich N-terminal prodomain and a C-terminal metacaspase domain with a zinc finger motif. Type II metacaspases lack a prodomain at the N-terminus but have a connecting region between the large (p20) and small (p10) caspase-like catalytic domains. Most metacaspases feature a catalytic dyad His-Cys in their active site, with the Cys residue acting as a nucleophile for peptide bond hydrolysis of substrates (Vercammen et al., 2004). In *Arabidopsis thaliana*, there are nine metacaspases, with AtMC1, AtMC2, and AtMC3 exhibiting characteristics of type I metacaspases, while enzymes from AtMC4 to AtMC9 display type II metacaspase features.

TABLE 2 Membrane bound transcription factors that are substrates for intramembrane proteases in different stress conditions.

MB-TF	Cellular localization	Stress or other TF biological function	Processing protease	Reference
bZIP17	ER	ER stress response	Site-1 protease (S1P); site-2 protease (S2P)	Liu et al. 2007a; Tajima et al., 2008; Adam, 2013; De Backer et al., 2022
bZIP28	ER	ER stress response	Site-1 protease (S1P); site-2 protease (S2P)	Liu et al. 2007a; Tajima et al., 2008; Adam, 2013; Sun et al., 2015; De Backer et al., 2022
bZIP60	ER	ER stress response	Site-1 protease (S1P); site-2 protease (S2P)	Iwata et al., 2008; Adam, 2013; Seo, 2014
NTM1	ER, NM	Salinity	Calpain protease	Kim et al. 2007; Seo et al., 2008; Seo, 2014
NTL1	ER	Oxidative stress	Rhomboid protease	De Backer et al., 2022
NTL6	PM	Cold, drought, salinity	metaloproteases	Kim et al. 2007; Seo et al., 2008; Seo et al., 2010; Seo, 2014
NTL7	ER	Oxidative stress	Rhomboid protease	De Backer et al., 2022
NTL8	ER	Cold, salinity	metaloproteases	Kim et al. 2007; Seo et al., 2008; Seo, 2014
PTM	ChE	Chloroplast-nucleus signalling	Serine-type protease	Sun et al., 2011; Adam, 2013
ANAC013	ER	Hypoxia	Rhomboid-like 2 (Rbl2)	Eysholdt-Derzso et al., 2023
ANAC017	ER	Oxidative stress	Rhomboidlike proteases	Ng et al., 2013

Proteolytic cleavage allows the release of a soluble protein fragment from membranes, which, are able to changes the expression level of related genes. MB-TF, membrane bound transcription factor; ER, endoplasmic reticulum; NM, nucleus membrane; PM, plasma membrane; ChE, chloroplast envelope.

AtMC1 and AtMC2 antagonistically regulate the PCD process in *A. thaliana*. AtMC1 promotes programmed cell death, while AtMC2 acts as an inhibitor of AtMC1-dependent PCD (Coll et al., 2014). Vacuolar processing enzymes (VPEs) are activated in the acidic environment provided by the vacuole, as well as during the hypersensitive response (HR) and abiotic stresses. Thus, AtMC1 activates hydrogen peroxide-dependent cell death and initiates the hypersensitivity response (Coll et al., 2010; Coll et al., 2014).

The CEP proteases are another group involved in PCD in plants. CEP1 is a protease responsible for PCD in the tapetum of anthers, which is essential for pollen grain development in angiosperms (Zhang et al., 2014). Premature or interrupted cell death of tapetal cells disrupts the nutrient supply to pollen microspores, leading to plant infertility (Ku et al., 2003). CEP1 initially appears as a proenzyme in precursor vesicles of the protease and is then transported to the vacuole, where it matures into an active enzyme. CEP1 influences nuclear degeneration, the formation of tapetal secretory structures, and pollen development (Zhang et al., 2014). Additionally, CEP1 is involved in xylem maturation in *A. thaliana*, regulating secondary wall thickening (Han et al., 2019).

Conclusion

Proteases in plant cells are a crucial part of the enzymatic machinery, contributing to a plant's ability to acclimatize to changing environmental conditions. These enzymes are responsible not only for the degradation of damaged or unnecessary proteins within the cell but also for preventing the formation of non-functional protein aggregates or breaking them down. A well-functioning cellular proteolytic system is a condition that enables the cell to change its protein composition and redirect its metabolism to new pathways that are better suited to the altered environmental conditions. Additionally, proteases can play a significant role in processes aimed at removing unfavorable metabolites from the cell. Proteolytic enzymes are also essential components of many signaling pathways and can influence changes in the gene expression profile.

Despite many years of research into various aspects of proteolysis in plant cells, many aspects remain unclear. In

particular, intramembrane proteases, commonly believed to be involved in intramembrane regulatory proteolysis processes, appear to be poorly understood. This process leads to the release of transcription factors from membranes, resulting in changes in gene expression. Intramembrane proteases are enzymes that operate in the extremely hydrophobic environment of the lipid bilayer of biological membranes. This characteristic alone makes them extraordinary enzymes, the full significance of which is not yet completely understood. A thorough understanding of the mechanisms of protease action and the processes they are involved in will undoubtedly bring us many tangible benefits in the future.

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