



Plant protease as regulator and signaling molecule for enhancing environmental stress-tolerance

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Abstract

Proteases are ubiquitous in prokaryotes and eukaryotes. Plant proteases are key regulators of various physiological processes, including protein homeostasis, organelle development, senescence, seed germination, protein processing, environmental stress response, and programmed cell death. Proteases are involved in the breakdown of peptide bonds resulting in irreversible posttranslational modification of the protein. Proteases act as signaling molecules that specifically regulate cellular function by cleaving and triggering receptor molecules. Peptides derived from proteolysis regulate ROS signaling under oxidative stress in the plant. It degrades misfolded and abnormal proteins into amino acids to repair the cell damage and regulates the biological process in response to environmental stress. Proteases modulate the biogenesis of phytohormones which control plant growth, development, and environmental stresses. Protein homeostasis, the overall balance between protein synthesis and proteolysis, is required for plant growth and development. Abiotic and biotic stresses are major factors that negatively impact cellular survivability, biomass production, and reduced crop yield potentials. Therefore, the identification of various stress-responsive proteases and their molecular functions may elucidate valuable information for the development of stress-resilient crops with higher yield potentials. However, the understanding of molecular mechanisms of plant protease remains unexplored. This review provides an overview of proteases related to development, signaling, and growth regulation to acclimatize environmental stress in plants.

Keywords Plant protease · Environmental stress · Signaling · Protein homeostasis

Abbreviations

ROS	Reactive oxygen species
ETC	Electron transport chain
PCD	Programmed cell death
RCD	Regulated cell death
ASPG1	Aspartic protease in guard cell 1
SUMO	Small ubiquitin-like modifier
WT	Wild type
ERD1	Early response to dehydration 1
FtsH	Filamentous temperature sensitive H protease
HR	Hypersensitive response
IAA	Indoleacetic acid

Introduction

Proteases play a crucial role in plant growth, reproduction, development, photosynthesis, programmed cell death (PCD), immune response, and defense against unwanted stress. They also play an essential role in regulated cell death (RCD) and respond to environmental stimuli (Zamyatnin 2015). Protease regulates the protein quality and homeostasis in different plant organelles (Schuhmann and Adamska 2012) by degrading photodamaged proteins. Protein homeostasis is maintained by controlling the rate of protein synthesis and protein degradation by the plant's regulatory mechanism (Li et al. 2017). Plant protease is involved in development and nutrient recycling by degrading misfolded proteins (García-Lorenzo 2007). Protease degrades photoinhibition proteins and plays a crucial role in repairing plant cells (Bailey et al. 2002), and controls the protein quality by removing damaged proteins (Komenda 2006).

Plant proteases are ubiquitous enzymes that function in various processes. They play an essential role in nutrient remobilization (Van der Hoorn 2008) and controls protein

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localization in cells, and acts as a signaling molecule (Turk 2006). Proteases are substrate-specific, they are present in different subcellular compartments, and their activity is highly regulated temporally and spatially (Martins et al. 2019). Proteases cleave misfolded or damaged proteins at the N-terminal (aminopeptidases), C-terminal (carboxypeptidases), or internal peptide bonds. Different plants have different numbers of proteases. For example, *Arabidopsis thaliana* contains over 800 proteases in 60 families, and rice (*Oryza sativa*) contains 600 proteases (Van der Hoorn 2008). Cysteine protease plays an essential role in signaling, PCD, protein maturation, nutrient remobilization, hormone synthesis, and degradation of misfolded proteins (Rocha et al. 2017).

The MEROPS database provides information on plant proteases. Proteases have been divided into five classes as serine, aspartate, cysteine, threonine, and metalloproteases based on their structural properties and activities (Rawlings et al. 2018). Serine, aspartic, cysteine, and metalloproteases are the major catalytic classes of plant protease (Schaller 2004).

Plants face environmental stress such as heat, ultraviolet light, drought, cold, pesticides, pathogens, and salinity, which are the major factors that reduce crop yield potential and negatively impact their survival (Costa and Farrant 2019). Climate change decreases the productivity of crops, such as maize, rice, and wheat (Tigchelaar 2018). Plants have various strategies to adapt and acclimate to the changing environmental conditions by activating different protective mechanisms that trigger physiological, morphological, and biochemical changes (Bernstein 2019; Hirayama and Shinozaki 2010). Environmental stresses enhance the production of reactive oxygen species (ROS) such as O_2^- (superoxide), O_2 (singlet oxygen), and H_2O_2 (hydrogen peroxide) in different cellular compartments like mitochondria, chloroplasts, and peroxisomes. Production of ROS is very common in the plant during all types of stress (Jaspers and Kangasjärvi 2010). ROS triggers programmed cell death by creating adverse conditions in the organelles (Petrov et al. 2015). ROS leads to oxidative stress in different cellular compartments, which damage the proteins, lipids, metabolites, and nucleic acids, affecting multiple biological processes (Hasanuzzaman et al. 2012). Molecular chaperon refolds proteins, while protease rapidly degrades the misfolded and aggregated proteins by proteolysis. Proteolysis is necessary to remove misfolded or unwanted proteins and regulate signaling molecules.

This review demonstrates the role of plant protease as a growth regulator and signaling molecule in response to environmental stress in crops. It also provides a comprehensive assessment of plant protease to identify various proteases in crop plants for a better understanding of the biological processes for improving crop yield and upcoming applications.

Relationship of proteases with reactive oxygen species

ROS is produced in response to abiotic and biotic stresses. ROS triggers oxidative stress involving various biological processes, such as autophagy, apoptosis, and necrosis. Under environmental stress conditions, plants generate ROS, which affects the different biochemical and physiological reactions. ROS is an important signal molecule of a plant for controlling growth and development (Cappetta et al. 2020). Several studies have been demonstrated the relations between ROS and protease in the plant. The peptide molecule is involved in the ROS signaling process. The Peptides derived from proteolysis regulate ROS signaling under oxidative stress in the plant (Møller and Sweetlove 2010). Photosystem II (PSII) of chloroplast produces ROS, which accelerates the damage of the D1 protein of PSII. The FtsH protease has been involved in removing the damaged D1 protein in the plant (Nixon et al. 2010). In addition, Deg protease, an ATP-dependent serine protease, has been linked in the degradation of D1 protein with the cooperative action of FtsH protease (Kato and Sakamoto 2018). MtbHLH2 and MtCP77 in *Medicago truncatula* showed a crucial role in ROS accumulation, PCD, and nodule senescence (Deng et al. 2019). OsNAC2 induces the expression of caspase-like protease OsAP37 and leads to PCD producing ROS (Mao et al. 2018). The cysteine protease HopN1 reduces the production of ROS in the chloroplast (Rodríguez-Herva et al. 2012). Therefore, protease has an essential role in the regulation of ROS in the plant.

Proteases in response to abiotic and biotic stresses

Plants encounter various stress during their growth phase. Environmental stress includes drought, salinity, cold, temperature, UV- B radiation, pathogen, pesticides, and metal toxicity, which delays plant growth and yield potentials. Plants acclimatize the environmental stress at physiological, molecular, and biochemical levels, primarily via proteolysis machinery (Table 1).

Drought

Drought is often considered a major environmental factor that reduces crop yield and negatively impacts plant survival. The effects have particularly been accentuated with global warming, especially in crop plants such as maize, rice, and wheat (Furlan et al. 2016). Nevertheless, plants have developed various strategies to minimize the damage

Table 1 Effect of the abiotic and biotic stress on the plant

Stress	Effects	References
Drought	Chlorophyll loss, leaf water potential decrease Effect on root length density ABA biosynthesis Flowering, carbohydrate accumulation Denatured floral buds	Nayyar et al. (2005); Kashiwagi et al. (2005); Tan et al. (1997) Pingping et al. (2017) Shi et al. (2019)
Temperature	Sugars, amino acids Reduced flowering, increase leaf Synthesis of heat shock proteins	Went (1953); Menzel and Simpson (1988); Belanger et al. (1986)
Salinity	Reduction shoot growth Reduced photosynthetic pigments Osmotic potential Damage leaf area Protein content	Munns and Tester (2008); Taffouo et al. (2010); Rodriguez et al. (1997); Yilmaz and Kina (2008); Sultana et al. (1999)
Cold	Delay in flowering Seedlings	Suzuki et al. (2008) Turk et al. (2020)
UV radiation	Nucleic acids, proteins, amino acids, hormone, lipids, membrane, photosynthesis Seed germination	Hollósy (2002); Popp and Brown (1933)
Pathogen	Induced oxidative stress Metabolism and morphology of chloroplast	Mithöfer et al. (2004); Goodman et al. (1986)

due to drought (Shah et al. 2017). Plants commonly respond to drought stress by producing ROS, which causes oxidative stress in different cellular compartments. Oxidative stress damages proteins, nucleic acids, metabolites, and lipids. Dehydration stress increases the number of misfolded, aggregated, and post-translationally modified proteins, which, in turn, activate the chaperone system. Chaperones refold the proteins damaged by oxidation, and proteases degrade the misfolded and aggregated proteins (Pulido et al. 2017). Plant protease significantly contributes to a drought stress response. Protein homeostasis and nutrient remobilization are essential for plant responses to drought stress. Protease plays an essential role in many events, including removal of damaged, denatured, and aggregated proteins, remobilization of amino acids, and signal transduction (Van der Hoorn 2008).

Drought induces aspartic protease activity, mainly in beans (*Phaseolus vulgaris* and *Vigna unguiculata*) (de Carvalho et al. 2001). ASPG1 (Aspartic protease in guard cell 1) plays an essential role in drought avoidance in *A. thaliana* (Yao et al. 2012). Overexpression of APA1 in *A. thaliana* ensures drought tolerance compared to the Wild-type (WT) plant. Overexpressing APA1 causes lower stomatal density and smaller stomatal aperture compared to that in WT plants (Sebastián et al. 2020). Lon protease is an ATP-dependent, nuclear-encoded, mitochondrial protease that belongs to the serine protease family (Pinti et al. 2016). Lon protease is necessary for cellular homeostasis and many developmental changes that have been induced by stress (Pinti et al. 2016). Lon protease has been involved in mitochondrial homeostasis. Lon protease (Atlon4) in modified *A. thaliana* makes

the plant more tolerant to drought stress than the wild-type plant (Li et al. 2010). SUMO (small ubiquitin-like modifier) protease belongs to the cysteine protease family, found in plants, eukaryotes, and yeast, and is crucial for stress tolerance. SUMO protease influences drought tolerance in wheat (*T. aestivum*) (Le Roux et al. 2019) by SUMOylation, which is also crucial for plant development. The ERD1 (Early response to dehydration 1) of *A. thaliana* induces the expression of the ClpA and ClpB protein levels during dehydration stress (Kiyosue et al. 1993). In addition, it has been reported that ASPG1 protease plays an essential role in drought avoidance in *A. thaliana* (Yao et al. 2012).

Salinity

Soil salinity is a critical environmental stress factor that reduces the quality and yield of crops worldwide. Hyper-salinity has multiple impacts on plants, such as genotoxicity, nutrition deficiency, oxidative stress, osmotic stress, and ionic imbalance (Shah et al. 2017). Consequently, this decreases photosynthesis rate, generates an excessive amount of ROS, and affects the electron transport chain. Nevertheless, plants adopt various strategies, like exclusion and salt compartmentalization (Wang et al. 2016). In plant cells, both enzymatic and non-enzymatic systems operate to minimize salinity stress. Many proteins and genes are involved in these resistance mechanisms for increasing tolerance to salinity, which includes H⁺-pyrophosphate, OsMYB3R-2, and AtSOS1 (Dai et al. 2007). Plant protease activity significantly increases in response to high salinity stress. Salt stress reduces the synthesis of proteins,

carbohydrates, lipids, DNA, and RNA and increases the degradation of damaged or harmful proteins by proteases (Parida et al. 2004). Salt stress affects various physiological and metabolic processes such as ion transport, synthesis and accumulation of osmotic solute, protein turnover, osmotic adjustment, nitrogen metabolism, and compartmentation.

Plant protease significantly contributes to the salt stress response. Cysteine protease, also called thiol protease, is an essential family of plant protease. Plant Protease plays a vital role in plant growth and development by degradation of endogenous proteins through proteolysis (Van Wyk et al. 2014). Salt stress enhances the level of ROS and oxidized proteins in different cell compartments. Degradation of oxidized proteins is necessary for recycling, which ensures plant growth and development under salt stress. Cysteine protease often plays a crucial role in the degradation of oxidized proteins and regulates ROS levels (Van der Hoorn 2008). RD21a and RD19a are cysteine proteases that belong to the papain-like family, and these two genes are induced by dehydration and salinity stress (Koizumi et al. 1993). The Cyp15a gene in peas (*Pisum sativum*) is a cysteine protease that induces and modulates mRNA levels in plants in response to high salt stress (Jones and Mullet 1995). The SPCP2 gene demonstrated tolerance during salinity and drought stress (Chen et al. 2010). Many of the cysteine protease genes are involved in altering physiological responses during salinity stress. Therefore, cysteine protease plays an essential role in the signaling pathway and the coping mechanism against salt stress. The serine protease gene HtrA in *Halothece* sp. PCC7418 is highly upregulated in response to salt stress (Patipong et al. 2020). The ClpD1 protein expression in *A. thaliana* has been increased in response to high salinity stress compared to the wild-type (Mishra and Grover 2016). Cyp15a gene of pea (*Pisum sativum*) is a cysteine protease induced and modulates mRNA levels in the plant in response to high salt stress (Jones and Mullet 1995).

Cold

One-third of the global land area is used for agriculture, and 42% of the land temperature is less than -20°C (Miura and Furumoto 2013). There are two types of cold stress like chilling (0 to -15°C) and freezing ($<0^{\circ}\text{C}$). Plants in cold areas are constantly exposed to chilling and freezing temperatures. So, they require specialized mechanisms to survive in such low temperatures. Cold stress restricts crop production, development, and growth. The harmful impact of cold stress on photosynthesis and metabolic function further affects the production, metabolism, and growth of the plants. Phenotypic symptoms in cold stress response include wilting, chlorosis, necrosis, stunted seedlings, poor germination, and reduced leaf expansion. Therefore, the development of cold stress tolerance in crops is vital to increase crop

production. Light is converted to chemical energy by photosynthesis to form carbohydrates, and this process is sensitive to cold stress. The PSII efficiency and photosynthetic rate are altered at low temperatures. RuBisCo is the most crucial protein for carbon assimilation during photosynthesis.

The production of the large subunit of RuBisCo is reduced during cold treatment. It indicates that cold stress reduces the photosynthetic efficiency mainly by degrading the large subunit of RuBisCo. Several novel proteins such as GroEL, FtsH-like protein, the 26S proteasome unit, and legumin play a crucial role in response to cold stress (Susin et al. 2006). Transcription factor ZmFtsH2B has been upregulated in leaves, whereas ZmFtsH2A has been constitutively expressed in the roots and leaves under cold stress (Yue et al. 2010). FtsH, Clp, and DegP are the prominent protease families located in the chloroplast. These proteases display constitutive gene expression and are involved in protein quality control and maintenance of homeostasis, rather than degrading proteins (van Wijk 2015). Under low temperature, Clp protease expression has been increased in rice (*Oryza Sativa*) (Cui et al. 2005).

Temperature

The ambient temperature has a significant impact on growth, development, and plant productivity. Consequently, plants can acclimate rapidly and evolve various mechanisms to detect their environment and respond with physiological, developmental, and cellular changes for efficient reproduction and optimal growth. High temperatures affect the physiological, metabolic, molecular, and biochemical changes in plants. In addition, high temperature induces cellular homeostasis and alters multiple genes of plants.

The Clp protease is constitutively expressed in plant tissues, primarily in the chloroplasts of green leaves. Many proteases function as molecular chaperones, such as the ClpB, ClpC, and ClpD protein subunits. The ClpB gene in *A. thaliana* has been constitutively expressed in chloroplasts and mitochondria during high-temperature stress response (Lee et al. 2007). In addition, the ClpB gene in *O. sativa* has been upregulated in response to heat stress (Singh et al., 2010). The ClpB gene in lima beans (*Phaseolus lunatus*) has been constitutively expressed in chloroplasts during high-temperature stress (Keeler et al. 2000).

The metalloprotease FtsH (Filamentous temperature-sensitive H protease) is essential for photosynthesis at high ambient temperatures. Mutant FtsH causes a filamentous temperature-sensitive phenotype in *E. coli* (Begg et al. 1992). FtsH is crucial for plant survival during high-temperature stress (Langer 2000). The mutant FtsH11 gene reduces the photosynthetic efficiency of PSI and PSII at high temperatures. FtsH11 in *A. thaliana* plays a vital role in thermotolerance (Chen et al. 2018). The matrix metalloproteinase

(MMP) Gm1-MMP has been found in the plasma membrane and is highly expressed in mature leaves, mature seeds, and old leaves associated with seed development. Gm1-MMP is essential for high-temperature tolerance and has been over-expressed during the development of leaves and roots in *A. thaliana* at high temperatures (Liu et al. 2017). Hence, it is well established that protease is essential for thermotolerance in many organisms.

Pathogen

Pathogen infection, which accounts for many harmful diseases, reduces crop yield and affects food security globally. Pathogens affect plant physiology, including respiration, pathogenesis, cell membrane permeability, transcription and translation, and translocation of water and nutrients. Plants have developed several conserved and sophisticated strategies to protect from pathogens. Plants create many antimicrobial compounds and physical barriers to deal with most of the pathogens. When plants perceive PAMPs (pathogen-associated molecular patterns), such as chitin, by membrane-localized PRRs, multiple immune responses are triggered within a cell. The success of the defense response depends on how soon the plant detects the invasion signals, which leads to the initiation of the defense response.

Protease is an integral part of the immune system of plants. These processes are influenced by proteases in different cellular compartments. Apoplastic serine protease SBT3.3 (Subtilase 3.3) in *A. thaliana* regulates the defense response. The mutant protease *sbt3.3* gene in *A. thaliana* is hyper susceptible to bacterial pathogen *Hyaloperonospora arabidopsidis* and *Pseudomonas syringae* (Ramírez et al. 2013).

Cathepsin-B is a papain-like cysteine protease that generates a hypersensitive response (HR). CathB is necessary for the hypersensitive response activated by co-expression of the potato gene R3a and the *Phytophthora infestans* gene Avr3a (Gilroy et al. 2007). Aspartic protease OsCDR1 (*Oryza sativa*) expressed in *A. thaliana* enhanced resistance against fungal and bacterial pathogens (Prasad et al. 2009). The papain-like proteases Rcr3 and Pip1 are both inhibited by Avr2 secreted by the fungal pathogen *Cladosporium fulvum* (Shabab et al. 2008). In plants, deletion of Pip1 causes hypersusceptibility to *Pseudomonas syringae*, *Cladosporium fulvum*, and *Phytophthora infestans* (Ilyas et al. 2015). AtMC1 and AtMC2 are cytosolic metacaspase protease in *A. thaliana*, regulating hypersensitive response in an antagonistic manner. AtMC1 acts as a positive regulator of the HR during cell death caused by *Pseudomonas*

syringae, and AtMC2 acts as a negative regulator (Coll et al. 2010).

Threonine protease PBA1 is an essential protease that is triggered by *Pseudomonas syringae* (Hatsugai et al. 2009). Vacuolar processing enzymes (VPEs) have caspase-1-like activity and are crucial for virus-induced HR upon infection by TMV (Tobacco mosaic virus) in *Nicotiana benthamiana* (Hatsugai et al. 2004). C14 and RD21 are both orthologous papain-like cysteine proteases found in *Arabidopsis thaliana* and *Solanum lycopersicum*, respectively (Thomas and Van der Hoorn 2018).

Light

Light plays a vital role in the growth and development of plants. It is required for photosynthesis, whereby plants convert energy from sunlight to chemical energy. Two proteins, D1 and D2, are found at the core of the PSII subunit (Hankamer et al. 2001). Deg2 is a serine protease that primarily cleaves photodamaged D1 proteins of PSII at high light intensity (Haußühl et al. 2001). The metalloprotease FtsH1 is responsible for the degradation of the D1 protein (Andersson and Aro 2001; Adam et al. 2005).

Nevertheless, it is not yet clear how FtsH functions in regulation. Prohibitin-like proteins form a large complex with FtsH homohexamers and modulate its proteolytic activity in *E. coli* (Kihara et al. 1996). Prohibitin-like proteins probably form a 2MD complex with the mitochondrial FtsH in *A. thaliana* (Piechota et al. 2010). Besides, the RC47 complex interacts with the FtsH protease, and this interaction is essential for the degradation of the D1 protein by the FtsH protease (Komenda et al. 2006; Kato et al. 2009; Krynická et al. 2015). EngA is a unique family of GTPase protease (Verstraeten et al. 2011) located on the thylakoid membrane. EngA interacts with the ATPase domain of the FtsH protease and affects its turnover. This interaction is essential for the degradation of the D1 protein. FtsH turnover is accelerated under high light stress in *Chlamydomonas reinhardtii* (Wang et al. 2017). It is well established that Deg and FtsH proteases are essential for tolerance to light-induced stress.

Protease in signaling and phytohormone mediated regulations during stress

The *Arabidopsis* mitochondrial FtsH3, FtsH4, and FtsH10 are involved in the biogenesis of oxidative phosphorylation (Marta et al. 2007). Loss of AtFtsH4 gene showed morphological and physiological abnormality of *Arabidopsis*

during short-day conditions (Gibala et al. 2009). It has been found that FtsH protease acts through the production of ROS to change the leaf morphology (Kato et al. 2009). Protease rapidly degrades misfolded and aggregated proteins by proteolysis under stress. ROS acts as a signaling molecule to manage numerous biological processes, including PCD, pathogen defense, and stomatal development; thus, controlling the growth and development of the plant in response to environmental stress (Apel and Hirt 2004). Under stress, a close association occurs between ROS and plant hormones, such as ABA, salicylic acid, jasmonic acid, GA, and ethylene (Bright et al. 2006; Gudesblat et al. 2007). The homeostasis and signaling of auxin have been induced by the apoplastic reactive oxygen species (Blomster et al. 2011). ROS negatively affects the auxin response in *Arabidopsis thaliana*. The expression of the auxin-inducible genes has been downregulated due to the mutation of mekk1 and mpk4 (Nakagami et al. 2006). The morphology of the plant aggravates due to the production of ROS and its impact on auxin signaling (Potters et al. 2007). ROS mediates the interaction between auxin and ABA signaling (He et al. 2012). Auxin homeostasis alters by hydrogen peroxide and promotes change in the gene expression of PINOID, which disturbs the polar transport of auxin (Pasternak et al. 2005). It has been suggested through various morphological studies that ROS interacts with auxin to control growth and development in the plant. Therefore, comprehensive studies are required to elucidate the interaction between ROS and auxin to dissect the molecular mechanism.

FtsH4 is an ATP-dependent AAA-protease having proteolytic activity. FtsH4 is associated with plant dwarfism, and mutation of FtsH4-4 shows numerous axillary branches due to a decrease of IAA concentration. It has been hypothesized that the FtsH4 is involved in auxin synthesis to regulate plant growth and development (Zhang et al. 2014a, b). FtsH4-dependent assembly of various proteins inhibits hydrogen peroxide (H₂O₂) production, which affects the regulation of Indole-3-acetic acid (IAA) metabolism, signaling, and transport of auxin.

Aspartic protease plays a crucial role in response to stress (Guo et al. 2013). It is a large family of proteolytic enzyme involved in programmed cell death, senescence, and reproduction. Overexpression of aspartic protease induces the expression of various genes, which promote ABA synthesis and signaling (Fig. 1). Additionally, the overexpression of APA1 in *A. thaliana* confers drought tolerance (Sebastian et al. 2020).

There is a close relation between ROS, signaling molecule, and phytohormones such as abscisic acid (ABA), salicylic acid (SA), gibberellic acid (GA), jasmonic acid (JA), nitric oxide, and ethylene (Bright et al. 2006; Desikan et al. 2008; Galvez-Valdivieso et al. 2009; Gudesblat et al. 2007). Mitochondrial FtsH4 in *Arabidopsis thaliana* regulates the expression of WRKY gene through modifying the ROS level, and WRKY genes control the salicylic acid synthesis and signaling (Zhang et al. 2017).

Therefore, the identification of various stress-responsive protease and their phytohormone function may elucidate valuable information for the preparation of crops with higher stress tolerance and increase yield potentials (Table 2).

Protease in plant development

Protease, Proteolytic enzyme, Proteinase, and Peptidase are the enzymes that hydrolyze the peptide bond of stress-damaged proteins (Mótyán et al. 2013). Protease is a crucial component of plants, distributed in the different subcellular compartments, such as vacuole, chloroplast, endoplasmic reticulum, cytoplasm, nucleus, mitochondria. Protease plays a significant role in stress responses, pathogen recognition, systematic defense response, stomata development, and plastid development (Fig. 2). Protease participates in the various cellular process, including the signaling pathway, which moderates multiple biological functions such as PCD (Thomas and Van der Hoorn 2018; Moschou et al. 2016).

Papain-like cysteine proteases (PLCP) are involved in proteolysis and various physiological process. The HvPap-1, a GA-induced PLCP, is involved in protein remobilization during barley seed germination (Cambra et al. 2012). Other PLCPs proteolytic enzymes like CEP1 play an essential role in tapetal programmed cell death and pollen development in *Arabidopsis thaliana* (Zhang et al. 2014a, b). In addition, PLCPs play a crucial role in protein degradation via proteolysis during leaf senescence, such as SAG12, AtRD19A, RD21A (Gepstein, et al. 2003; Lohman et al. 1994; Yamada et al. 2001). PLCPs such as ATRD21A and ATRD19A are two essential protein-marker that plays a vital role in the adaptation of dehydration, salt, and drought stresses (Koizumi et al. 1993). The malfunctioning of protease leads to various pleiotropic effects in the plant, such as reduced plant growth, impaired chloroplast development, leaf variegation, and photosynthesis (Sjögren et al. 2006).

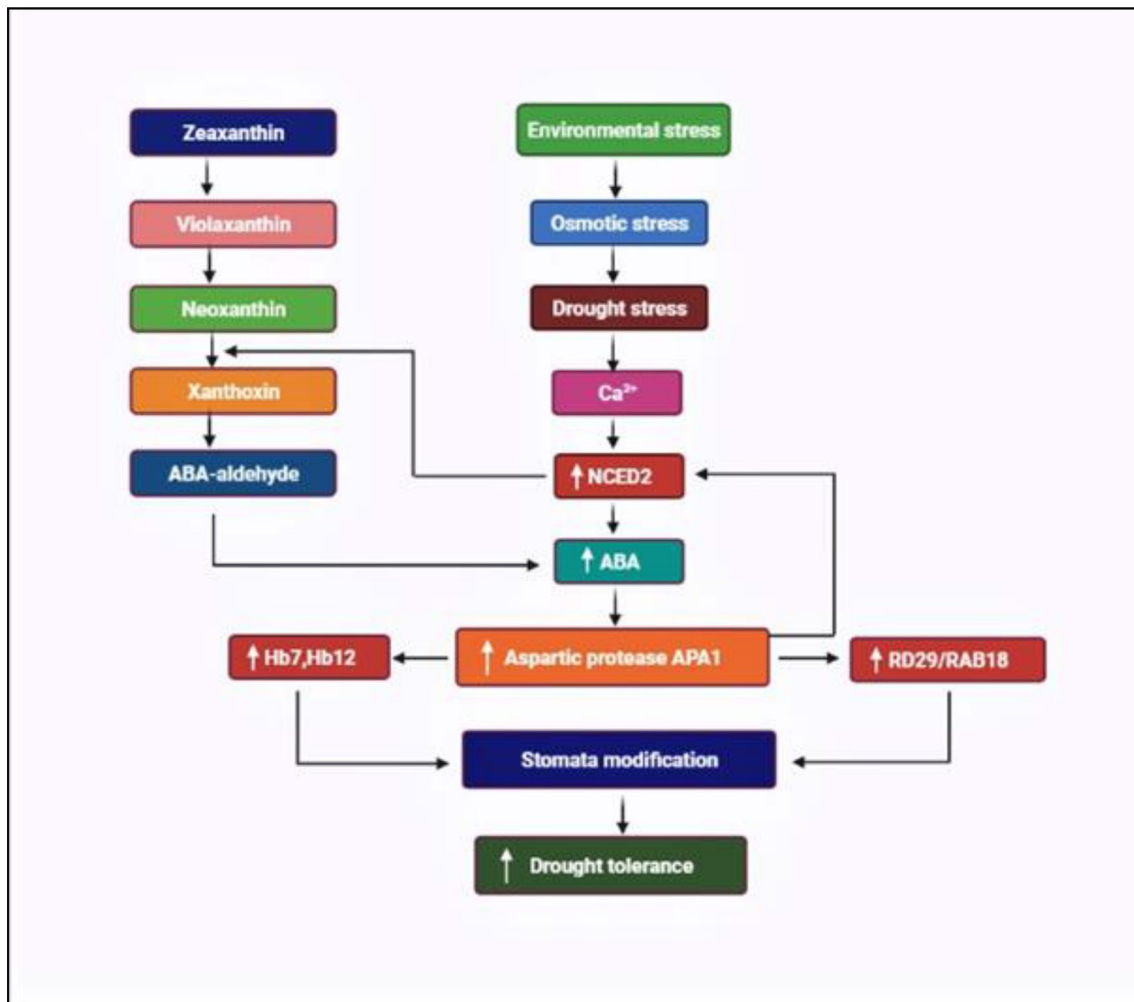


Fig. 1 Correlation between the Aspartic protease (APA1) and Abscisic acid (ABA) signaling in response to environmental stress. Environmental stress induces ABA production that triggers the expres-

sion of APA1, Hb7, and Hb12. Besides, RD29/RAB18 activates the expression of NCED2, involving ABA biosynthesis

Conclusion and future perspectives

Protease plays a crucial role in all living organisms. Protein turnover requires for the growth and differentiation facilitated by the specific proteolytic enzymes. Protease plays other essential functions, including amino acids recycling by the degradation of non-functional proteins and regulation of regulatory proteins and essential enzymes. Most of the previous studies have been accomplished in the model plant. However, the role of the protease of crop plants is mostly unexplored. Therefore,

exploration of the underlying molecular mechanism of crop plant protease is very crucial to adapt the environmental stress. Plant productivity decreases severely with increasing environmental stresses, which must be a significant concern in the present scenario. With the increasing world population, crop production needs to be increased several folds in the near future. Therefore, the identification of novel protease would contribute a significant role in plant science. The plant protease would facilitate the development of stress tolerance crop plants for improving growth and yield potentials during environmental stress

Table 2 Proteases reported in plant and their function

Name of Protease	Function of protease	References
FtsH	Proteolysis	Wagner et al. (2012)
GGTs	Degradation of glutathione	Martin et al. (2007)
DEK1	Early embryogenesis	Tran et al. (2017)
Rcr3	Fungal pathogen	Krüger et al. (2002)
Lon	Proteolysis	Tsitsekian et al. (2019)
AraSP	Development of chloroplast	Bölter et al. (2006)
IAR3	Decreased sensitivity to IAA-Ala	Dixon et al. (2000)
VAR1/ VAR2	Degrade photodamaged protein in PSII	Sakamoto et al. (2002)
ILR1	Insensitive for indole acetic acid-Leu	Bartel and Fink (1995)
At2MMP	Early senescence, late flowering	Gollmack et al. (2002)
MPA1	Meiotic chromosome segregation	Sánchez-Morán et al. (2004)
Clp1	Shoot development	Kuroda and Maliga (2003)
Clp4	Leaves development	Shen et al. (2007)
Clp6	Chlorotic rosette leaves	Sjögren et al. (2006)
SNG1	Secondary metabolites	Lehfeldt et al. (2000)
SNG2	Decreased activity sinapoylglucose:choline sinapoyltransferase	Shirley et al. (2001)
AtSPP	Pollen function	Han et al. (2009)
ESD4	Pleiotropic effect and the early flowering	Sun et al. (2007)
SUMO	Decreased Stomatal pore aperture	Castro et al. (2016)
DEG5/ DEG8	PhotosystemII repairing	Sun et al. (2007)
BRS1	Enhanced brassinosteroids sensitivity	Li et al. (2001)
NbVPE	Programmed cell death	Hatsugai et al. (2006)
AtPARL	Plant development	Kmiec-Wisniewska et al. (2008)
SASP	ABA signaling	Wang et al. (2018)
UBP1/2	Resistance to canavanine	Yan, et al. (2000)
UBP3/4	Pollen development and transmission	Doelling, et al. (2007)
UBP15	Leaf development	Liu, et al. (2008)
AtDEK1	Alter epidermal cell interdigitation	Johnson et al. (2008)
UCH1/2	Shoot development and inflorescence architecture	Yang et al. (2007)
NbDEK1	Cell proliferation and differentiation	Ahn, et al. (2004)
DEK1	Cell division and elongation	Perroud et al. (2020)
CRSP	Negative regulate of stomata development	Hunt and Gray (2009)
NbCathB	Hypersensitive response	McLellan et al. (2009)
EGY1	Chloroplast development	Barry et al. (2012)
EGY2	Hypocotyl elongation	Chen, et al. (2012)
AtRBL1	Cleave EGFR	Kanaoka, et al. (2005)
AtRBL2	Proteolytic activity	Kanaoka, et al. (2005)
AtRBL8	Flower development	Thompson et al. (2012)
MciPa	During embryogenesis, reduced cell death	Bozhkov et al. (2005)
SDD1	Negative regulation of stomata development	Liu et al. (2015)
EPF1/ EPF2	Negative regulation of stomata development	Shimada et al. (2011)
EPFL9	Positive regulation of stomata development	Shimada et al. (2011)
Mir1	Defend against insect herbivores	Lopez et al. (2007)
ALE1/ PASPA3	Programmed cell death	Fourquin et al. (2016)
VPE3	Vacuole rupture	Lu et al. (2016)
Plsp1	Protein folding	McKinnon et al. (2019)
ASPG1	ABA signaling	Yao et al. (2012)
RLR1/2	Primary root development and lateral root formation	Soares (2017)
Gm1-MMP	Growth and development of leaf and seed	Liu et al. (2017)
Cs1-MMP	Involved in PCD and senescence	Delorme et al. (2000)

Table 2 (continued)

Name of Protease	Function of protease	References
Pta1-MMP	Seed germination and seedling elongation	Delorme et al. (2000)

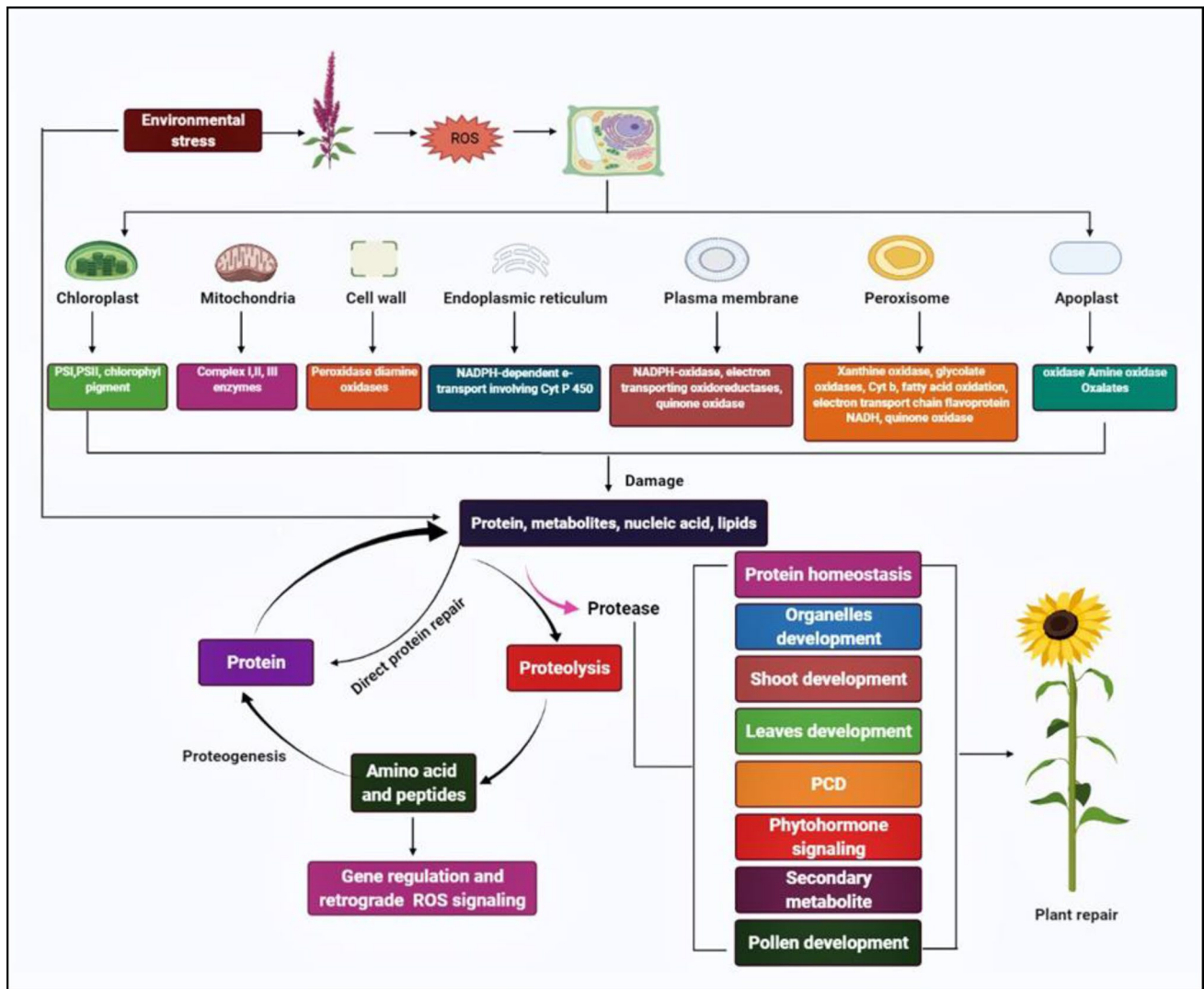


Fig. 2 Plant protease in promoting growth, development, and degradation of misfolded protein in the different organelle. Misfolded protein is mainly cleaved by proteases and repairs cell damage during

stress. Proteolysis plays a crucial role in removing toxic proteins and provides amino acids for the synthesis of new protein

conditions. Understanding plant protease in response to stress will provide a vast field to develop climate-resilient crop plants.

Author contribution statement DG conceived the idea and designed the concept. The manuscript was prepared with the potential contribution of PS and DG. All authors have read and approved the manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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