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Oxidative stress response in plants to combined abiotic and biotic stress factors

Abstract: Reactive oxygen species were considered to be toxic by-products of aerobic metabolism, which were disposed of using antioxidants. However, it has become apparent that plants actively produce reactive oxygen species as signalling molecules to control processes such as programmed cell death, abiotic stress responses and pathogen defense. Oxidative stress, accompanied by increased generation of reactive oxygen species, occurs under the influence of both abiotic and biotic factors. Despite extensive studies of oxidative stress caused by temperature and various pathogens, there is a little understanding about cross-interaction between these factors. This review attempts to focus on influence of a combined action of abiotic and biotic factors on oxidative stress responses in plants. This knowledge might help to provide an insight into mechanisms of molecular interactions in response to multiple stress factors.

Keywords: oxidative stress, abiotic factors, biotic factors, reactive oxygen species, viral infection.

Reactive oxygen species (ROS) are derivatives of O₂ produced during normal cellular aerobic metabolism. They are free radicals such as superoxide, hydroxyl radicals, hydrogen peroxide and singlet oxygen. However, high concentrations of ROS are also generated by the action of environmental stresses such as UV and ionizing radiation, xenobiotics and pathogen infection. Each of these abiotic and biotic stress factors lead to the disruption of cellular homeostasis resulting in an enhanced generation of ROS that can pose a threat to organisms. Cells in this condition are known to be in a state of oxidative stress. Oxidative stress, defined as a shift of the balance between prooxidative and antioxidative reactions in favor of the former seems to be a common denominator of the action of various agents on living organisms[1].

An oxidative stress triggered by all environmental and biotic stresses can damage cell components and cause their dysfunction. The oxidative stress is caused by the following: (a) an imbalance between ROS generation and detoxification due to disturbance of 'normal' cell physiology; (b) ROS biosynthesis de novo as a constituent part of stress signaling and immunity response needed for defense and adaptation [2]. In humans and animals, oxidative stress is thought to underlie many diseases and contribute to the process of aging. Studies with plants in this field are less abundant but oxidative stress does not seem to be less important than in the animal world [3].

Plant oxidative stress is a complex physiological phenomenon. As for all organisms, plant ROS also play a dual role depending on their concentration. They were initially thought to be toxic byproducts of aerobic metabolism, but have now been acknowledged as central players in the complex signaling network of cells [4]. In the plant cell, ROS can directly cause strengthening of cell walls via cross-linking of glycoproteins, or lipid peroxidation and membrane damage. An increased level of ROS causes damage to cells, whereas at acceptable concentration they have additional signaling roles in plant adaptation to the stress. ROS are important signals mediating defense gene activation. Additional regulatory functions for ROS in defense occur in conjunction with other plant signaling molecules [5-7]. However, ROS also regulate additional plant responses in relation to other signals. Reactive oxygen species play a major role in plant defense against pathogens. Because of the duality of ROS, it is important for the cells to tightly control the level of ROS to not cause an oxidative stress and at the same time not to eliminate them completely. A balance is achieved by an antioxidative system that involves several antioxidant molecules. Some well known enzymatic antioxidants are superoxide dismutase (SOD), catalase (CAT) and some peroxidases and reductases [2].

Unlike other organisms, due to their sessile lifestyle, plants are continuously exposed to a wide range of environmental stimuli and stresses. Several abiotic stress factors such as temperature, drought, salinity and radiation alter physiological processes in plants and negatively affect yield of agricultural crops. Moreover, plants have to face attacks by various pests and pathogens, including

bacteria, fungi, viruses, nematodes, and herbivores. At the same time, some environmental factors have an effect on plant-pathogen interactions. Particularly high and low temperature conditions might suppress an immunity of plants against viral pathogens. These observations have a tremendous significance because temperature stress is becoming the major concern for plant scientists worldwide due to the changing climate. Current climate prediction models indicate a gradual increase in ambient temperature. The difficulty of climate change is further added considering its precisely projecting potential agricultural impacts. For example, global warming will be accompanied by heat waves that drastically affect the conditions under which crop plants are grown [8].

Therefore, it is important to focus on complex cross-talks between plant responses to both abiotic and biotic stress factors in order to enhance plant immunity and crop productivity. Until now, little has been known about plants exposed to simultaneously occurring abiotic and biotic stresses [8]. An implementation of a versatile multifactorial test system, allowing simultaneous application of heat, chilling (low non-freezing temperatures) and virus stress to plants might shed some light on molecular plant responses to multiple stress factors.

Oxidative DNA damage, unless repaired, may have detrimental consequences and increase genetic instability. Therefore, it is important to determine the role of heat-shock or chilling induced oxidative stress on induction and repair of DNA damage in relation to oxidative stress tolerance in virus infected plants. It seems that heat-stress or chilling-stress factors influence on the interactions between plants and virus pathogens and act on pathogenicity and host defense responses.

It is possible that an abiotic stress can weaken or strengthen the plant protection against pathogens. Earlier we have shown that heat as a constant factor of the environment leads to increased generation of ROS in water and aqueous solutions [1].

Chilling stress is another major environmental factor that often affects plant growth and crop productivity and leads to significant crop losses. Heat and chilling oxidative stresses include responses that lead to the excess accumulation of toxic compounds, especially reactive oxygen species. The end result of ROS accumulation is oxidative stress [9]. It is also known that many mammals are sensitive to the action of viruses under the influence of low temperatures. We also found that low temperatures lead to an increase in aldehyde oxidase (AO) activity in barley plants.

It is well known that reactive oxygen species signaling network is involved in the regulation of numerous biological processes, including resistance to pathogens [10]. One of the earliest plant responses to pathogen invasion is a significant increase of ROS production, called oxidative (respiratory) burst [11, 12]. Recently we showed an involvement of plant AO in defense mechanisms against viral infection. In addition, the infection caused an increased accumulation of hydrogen peroxide, compared to mock-inoculated plants [13]. The virus infection resulted in increased activity of catalase (CAT) and superoxide dismutase (SOD) in roots and leaves of *N. benthamiana*. Moreover, activation of two additional CAT isoforms was observed in the leaves of plants after virus inoculation. Our findings indicated that the virus infection significantly affects enzymes responsible for the balance of ROS accumulation in plant tissue in response to pathogen attack [13].

Interestingly, it has been recently shown, that the increased content of hydrogen peroxide in virus infected plants promote the spread of silencing signal between different cells, contributing to the activation of RNA interference (RNAi) in the whole organism [14]. Nevertheless, many aspects of the interaction of the type as a temperature-plant-virus are open to investigation. For example, we know that an attack by pathogens leads to an increased generation of ROS, but we also know that because of the ROS the mammalian organism resists infection [11]. Therefore, can temperature-induced oxidative stress increase plant resistance to infection? This study is poorly understood in relation to the plants. In certain cases, such crosstalk can lead to a cross-tolerance and enhancement of a plant's resistance against pathogens. An investigation is needed to give an insight into cross-tolerance between abiotic and biotic stress, focusing on the molecular level and regulatory pathways.

The very early response of plant cells to infection or elicitors, the oxidative burst, which is fast stimulated, may hold a key for triggering the cascade reactions which are involved in the hypersensitive resistance response. Some organisms, for example, the pathogenic *Phytophthora* fungi seem to acquire the potential factors, suppressors, to overcome the system of the oxidative burst of host plant cells for the establishment of a compatible host-parasite relationship. In this sense, the oxidative

burst in plant cells may be an emergency signal for the expression of the active defence response in plants [11, 16]. Unfortunately, published data on this crosslinks are scarce, there is only a very limited number of studies which shed light on interaction between the viral intervention, temperature induced oxidative burst and plant response. Therefore, more research is needed.

It is clear plants potentially carry a self-defence system with or without resistance-encoding genes to certain pathogens. An incompatible recognition by plant cells may automatically trigger the oxidative burst through a signal transduction system, and then construct the chemical and/or physical defence barrier. The switching-on for the oxidative burst may be responsible for the successful resistance even in susceptible host cultivars. Plant cultivars without major resistance genes to their pathogens also carry the system for the oxidative burst and expression of the defence genes and metabolism. From this viewpoint, there is no need to introduce resistance-encoding genes or genes associated with the expression of resistance [8, 11]. In connection with the above, it is necessary to understand: 1) does the temperature affect the "aggressiveness" of the virus attack against the plant; 2) can plants use a temperature-induced oxidative "explosion" against a viral infection; 3) what will be the response of the plant to the "combined" (temperature and viral infection) oxidative stress.

Moreover knowing how to control the oxidative burst system will be much more effective to protect plants depending on their own latent potential of resistance. Therefore a better understanding of the oxidative burst and its associated signal transduction in plants may provide some reagents which can induce the acquired immunity depending on their own latent defence systems, and contribute to the sustainable development of crop production by reduction of the use of chemicals for the control of pathogens.

The need to study a biological complex relationship between abiotic stress-plant-pathogen is because a plant disease control is largely based on the use of fungicides, bactericides, and insecticides - chemical compounds toxic to plant invaders, causative agents, or vectors of plant diseases. However, the hazardous effect of these chemicals or their degradation products on the environment and human health strongly necessitates the search for new, harmless means of disease control [16]. There must be some natural phenomenon of induced resistance to protect plants from disease. A study is required that investigates molecular responses of combined stress, where the elevated level of ROS in plants formed as a result of temperature-induced oxidative stress will be directed by a host-plants against viral invasion. Thus understanding of molecular mechanisms of natural regulation in plant "fights" against pathogen attack could minimize the scope of chemical control, thus contributing to the development of sustainable agriculture. A successful research in this field will determine the role of temperature-induced ROS in the plant combating the pathogen action and, accordingly, will identify novel ways of defending plants against infection.

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Реакция окислительного взрыва у растений к одновременным абиотическим и биотическим стрессовым факторам

Аннотация: активные формы кислорода считаются токсичными побочными продуктами аэробного метаболизма, в дальнейшем устранимые антиоксидантами. Однако было установлено, что растения активно производят активные формы кислорода в качестве сигнальных молекул для контроля некоторых клеточных процессов как апоптоз, реакции к абиотическим стрессовым факторам и защита от патогенов.

Окислительный взрыв, сопровождающийся увеличением концентраций активных форм кислорода, происходит как ответ к абиотическим и биотическим факторам. Несмотря на достаточное количество исследований окислительного взрыва, возникающего из-за температуры и различных патогенов, взаимосвязанное влияние этих факторов все еще остается мало изученным.

Данный обзор рассматривает эффект комбинированного действия абиотических и биотических факторов на окислительный взрыв у растений, который поможет раскрыть механизмы молекулярных взаимодействий в ответ к нескольким стрессовым факторам одновременно.

Ключевые слова: окислительный взрыв, абиотические факторы, биотические факторы, активные формы кислорода, вирусная инфекция.

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Бір мезгілдегі абиотикалық және биотикалық стресстік факторларға жауап ретіндегі өсімдіктегі тотығу жарылысы

Аннотация: оттегінің белсенді формалары антиоксиданттар көмегімен жойылатын аэробты метаболизмнің зиянды қосымша өнімдері болып саналады. Алайда өсімдіктер оттегінің белсенді формаларын сонымен қатар апоптоз, абиотикалық стресске жауап және патогендерден қорғаныс секілді процестерді бақылауға қажетті сигнал молекулалары ретінде де белсенді түрде түзеді. Оттегінің белсенді формалары мөлшерінің артуымен жүретін тотығу жарылысы абиотикалық және биотикалық факторларға жауап ретінде орын алады. Температура және патогендер себебінен туындайтын тотығу жарылысына арналған зерттеу жұмыстары жеткілікті болғанымен, аталған факторлардың біріккен әсері әлі де белгісіз болып отыр. Бұл шолу абиотикалық және биотикалық факторлардың біріккен эффектісінің

өсімдіктегі тотығу жарылысына әсерін қарастырады және бірнеше стресстік факторларға жауап ретіндегі молекулалық өзара әрекеттердің механизмін ашуға көмек береді.

Түйін сөздер: тотығу жарылысы, абиотикалық факторлар, биотикалық факторлар, оттегінің белсенді формалары, вирустық инфекция.

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