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ON THE MOLECULAR MECHANISMS OF ACTION OF TOCOPHEROL, PROSTAGLANDINS, ABSCISIC ACID, STEROIDS AND STRIGOLACTONES

***Aim*.** The vital functions of living systems are regulated in two ways: chemical (biologically active substances, BACs) and physical factors. Cellular "redox-status" is maintained by specialized oxidant substances (OXs; free radicals, FRs) and antioxidants (AOs). These two classes also determine the functioning and integrity of living systems. This study examines the action mechanisms of natural AOs: tocopherol, prostaglandins, abscisic acid, brassinosteroids, steroids, and strigolactones. ***Results*.** The outlined mechanisms of BACs action describe how natural antioxidants tocopherol, prostaglandins, abscisic acid, steroids, brassinosteroids and strigolactones interact into the body at the molecular level, causing specific chemical and biological effects. ***Conclusions*.** Cellular "redox status" is maintained by specialized oxidant substances and antioxidants. This article describes the mechanisms of action of natural antioxidants without the involvement of protein receptors.

Keywords: tocopherol, prostaglandins, abscisic acid, steroids, brassinosteroids, strigolactones.

I. Life activity of living systems

The vital functions of living systems are regulated in two ways: chemical (biologically active substances, BACs) and physical factors. Cellular "redox-status" is maintained by oxidants (OXs; free radicals, FRs) and antioxidants (AOs). These two classes determine redox reactions in cells and participate in the regulation of biological systems functioning. Oxidation and reduction processes are key to cellular vital functions, underpinning metabolism, respiration, photosynthesis, protective and adaptive mechanisms. For a cell to survive and function, it is necessary to maintain the certain balance of reduced and oxidized forms of molecules.

II. Chemistry of antioxidants: what properties are desirable?

Chemically, AOs are substances that also contain active hydrogen atoms (most often associated with HO-groups). By donating hydrogen atoms, they can become inert substances. Therefore, AOs act as quenchers or scavengers (neutralizers) of free radicals *in vivo*, preventing their oxidative actions. Both an increase and a decrease in the quantity of OXs or AOs relative to the steady state leads to disruption of programmed biochemical processes. Representatives of several classes of AOs are discussed here.

III. Tocopherols are a class of natural antioxidants

Among natural oxidants, α-tocopherol is an important one (Cook-Mills, 2013). Substances containing one hydroxy group in a cyclic structure can theoretically act *in vivo* as both oxidants and reductants. Possible mechanisms for the transformation of substances classified as prooxidants are illustrated using α-tocopherol as an example (Fig. 1). As can be seen from this scheme, structure I, upon loss of one hydrogen atom, is transformed into structure II (FR), which can oxidize other cellular molecules. Upon interaction with another free radical, it is transformed into the neutral molecule IV; or, as a result of intramolecular rearrangement, it is transformed into structure III (also FR). Structure III, upon interaction with another FR, can be transformed into the neutral structure VII. When structure III is restored, further transformation of α-tocopherol into structures V, VI, VIII, IX, X is possible. In this case, structure V, upon restoration, can be transformed into structure VI, which is antioxidant.

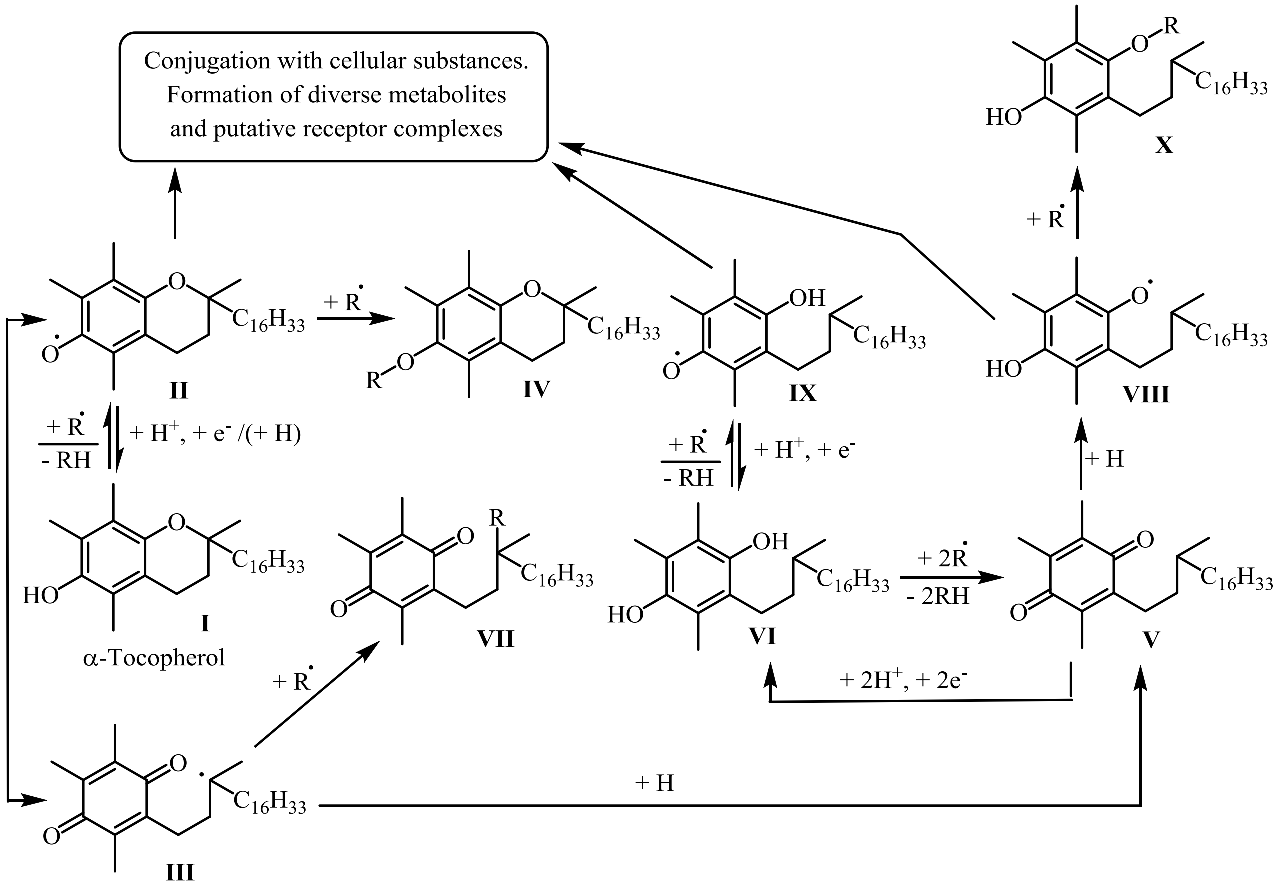

Fig. 1. Proposed mechanisms for *in vivo* α-tocopherol transformation and action. Free radicals present biologically active substances.

α-Tocopherol (structure I) is not a classic antioxidant; and *in vivo*, it can act as a free radical scavenger. By donating one hydrogen atom to neutralize intracellular free radicals, α-tocopherol is converted into a relatively stable free radical, as its free radical center is shielded by two methyl groups, which prevent it from oxidizing other substances. Structure II can be restored by oxidation of another substance, or by adding the hydrogen atom in the oxidation reaction, since the migration of the hydrogen atom from the benzene ring to an oxygen atom is difficult.

The structures of α-tocopherol in the free radical state (structures II, III, VIII and IX) can exhibit a dual action: oxidize cellular substances, being reduced in the process, or bind to cellular substances, forming various metabolites, including the so-called receptor complexes.

IV. Prostaglandins: do they act in concert with protein receptors or without them?

Prostaglandins are the broad class of biologically active substances exhibiting a variety of biological effects. Under certain conditions, prostaglandins PGE_2 ($PGF_{2\alpha}$) can act as free radical scavengers without neutralizing them, or as free radical neutralizers (Kurchii, 2019). Proposed *in vivo* mechanisms for PGE_2 transformation are presented (Fig. 2). Also, structures IV and VIII can act as free radical scavengers *in vivo*.

The mechanisms of prostaglandin PGE_2 transformation presented in Fig. 2 suggest the following conclusion: depending on the nature of the biological tissue and experimental conditions, these substances will act as either oxidizing agents or as antioxidants. Consequently, the physiological responses of biological systems to these substances may be opposite. Moreover, prostaglandins do not require protein receptors to carry out primary chemical reactions *in vivo*.

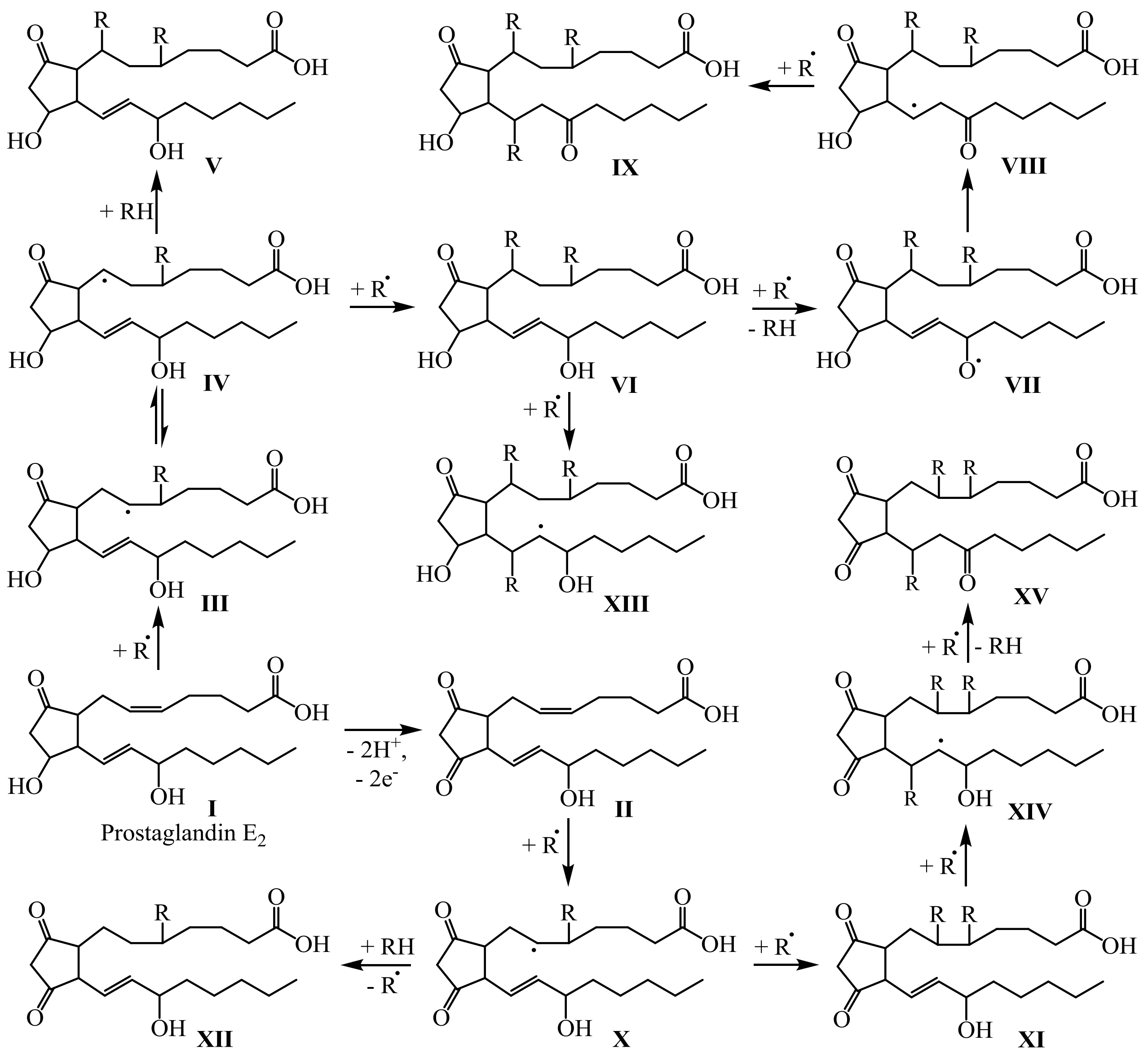

Fig. 2. Proposed mechanisms for *in vivo* prostaglandin E_2 (PGE_2) transformation. Oxidation of PGE_2 can be performed by free radicals or enzymatic redox systems.

V. Abscisic acid is a product of carotenoid breakdown under oxidative stress

The natural plant growth regulator abscisic acid (ABA) has attracted particular attention from plant biology researchers. However, despite the large number of publications and hypotheses, the mechanisms of ABA formation and action at the level of primary elementary chemical reactions are presented fragmentarily. Analysis of ABA metabolites suggests that they are one of the stable breakdown products of the carotene molecule destruction under the influence of oxidative stress (Kurchii, 2019).

VI. Is the function of ABA in the regulating stomatal size unique?

Currently, knowledge about how biochemical and physiological processes are initiated and regulated by ABA is limited. ABA is believed to be involved in the regulation of plant stomatal aperture (Samarah, 2016). However, other plant growth regulators, such as strigolactones (Lv et al., 2018), hydrogen peroxide (H_2O_2), and nitric oxide (NO) also regulate stomatal aperture (Daszkowska-Golec and Szarejko, 2013). Thus, in the context of the above information, it can be concluded that ABA does not have a unique function in regulating stomatal aperture.

VII. Abscisic acid: being present does not mean participating

The literature notes opposite effects of exogenous ABA: stimulation (Humplík et al., 2017) or inhibition of biochemical processes in plants (Liu et al., 2010). These contradictory data can be explained in terms of the transformation of ABA into a free radical state, or its reduction to 1´,4´-diol ABA, which is antioxidant from the steric structure. Therefore, depending on the transformation, ABA will act as the stimulator or the inhibitor of growth processes as presented in Fig. 3.

VIII. Steroid substances act as antioxidants or oxidants in living systems

An important component of biological membranes is cholesterol (CL) (Mason and Jacob, 2017), which is involved in many biochemical and physiological processes, including membrane stability and permeability, stimulation or inhibition of membrane protein function (Yeagle, 2016). However, the primary mechanisms of these functions are presented fragmentarily in the literature. Based on its steric structure, CL is a natural antioxidant. However, by transforming *in vivo* into the free radical state, it can also act as an oxidant. A simplified description of the possible mechanism of CL transformation *in vivo* is shown in Fig. 4. Estradiol, testosterone, progesterone, and other steroids also act as redox agents.

IX. Brassinosteroids are a class of natural antioxidants

Brassinosteroids (BRs) are steroid-structured substances involved in the regulation of metabolism and defense mechanisms against biotic and abiotic factors (Lopez-Gomez et al., 2016). Depending on the chemical reactions and the number of BRs molecules in the cell *in vivo*, they can act as oxidants or as antioxidants. Unlike phenolic compounds, the oxidized HO-groups of BRs can be reduced due to intramolecular rearrangements (Kurchii, 2019). This is due to the fact that hydrogen migration from the benzene ring to the oxygen atom is difficult, but can easily migrate from the cyclopentane or cyclohexane rings.

X. Strigolactones are a class of natural antioxidants

Strigolactones, as natural plant growth regulators, have been the subject of intensive research in the past decade (Zwanenburg and Blanco-Ania, 2018). However, the mechanisms of their function and *in vivo* action described in the literature are contradictory.

Figure 5 shows the mechanism of transformation and action of strigol as the scavenger of free radicals or as the antioxidants (neutralizers of free radicals). Here, structures (A) and (B) can act as scavengers of FRs, while structure (C) can act as the oxidant. Having unsaturated bonds protected by methyl groups, diverse strigol structures can also act as scavengers of FRs. Therefore, the initial reactions will prevail as scavengers of FRs. Compound (C), by oxidizing other compounds, can be reduced to neutral compounds (A), or due to conjugation with other FRs can be transformed to structure (D)

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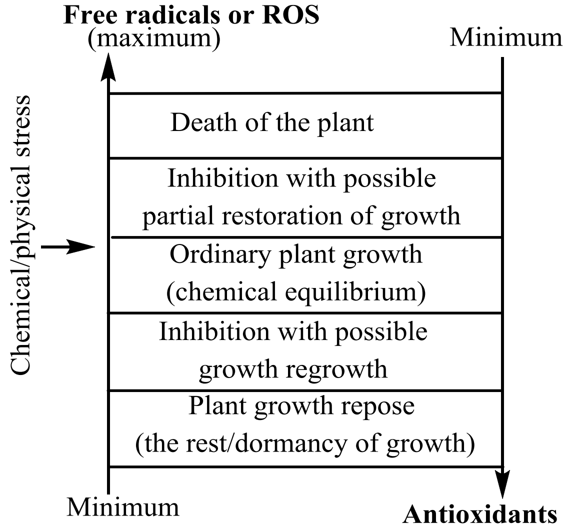

Fig. 3. Schematic representation of the interaction between oxidants and antioxidants in living systems.

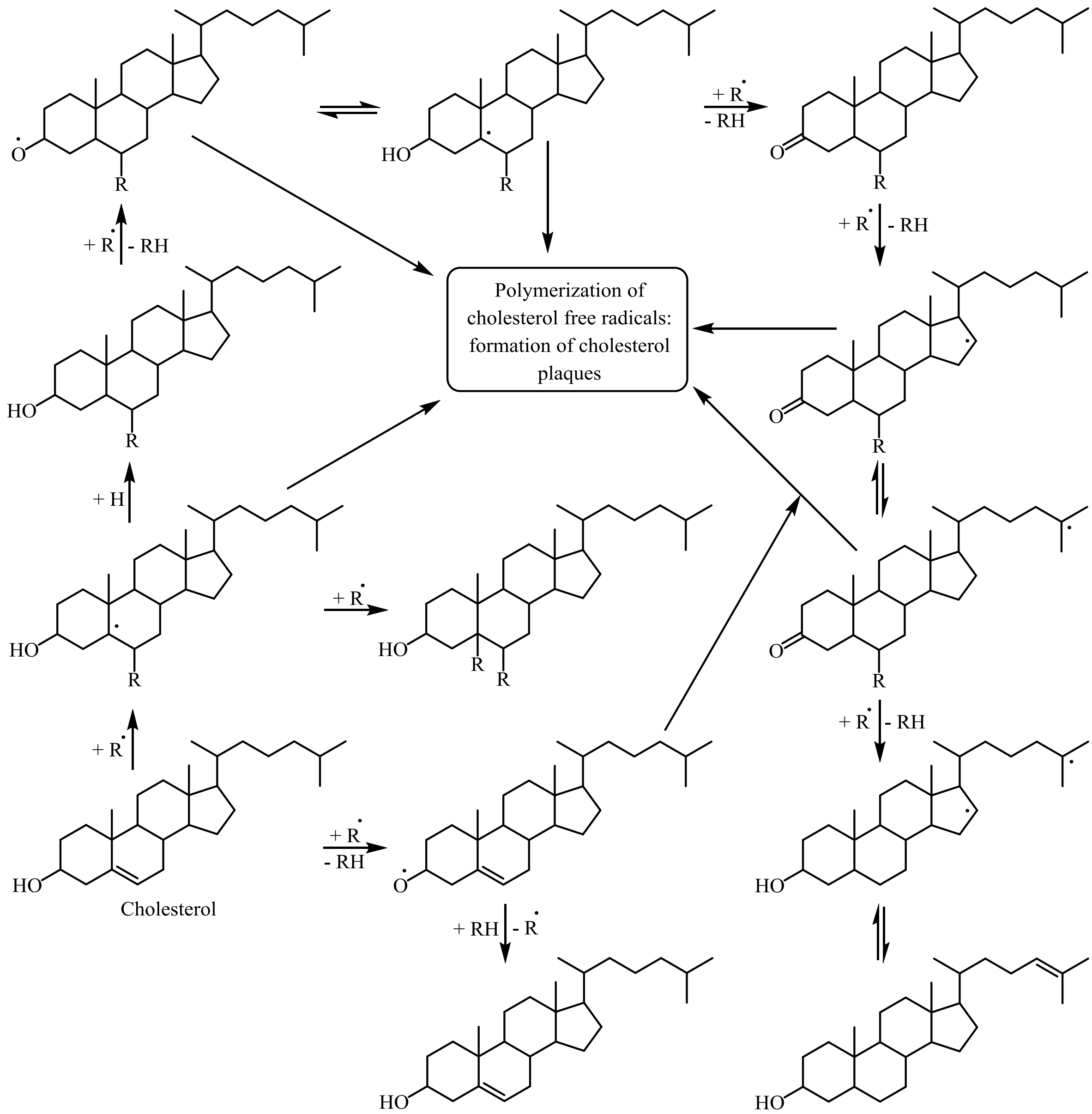

Fig. 4. Proposed mechanism for oxido-reductive transformation of cholesterol *in vivo* and formation of cholesterol plaques.

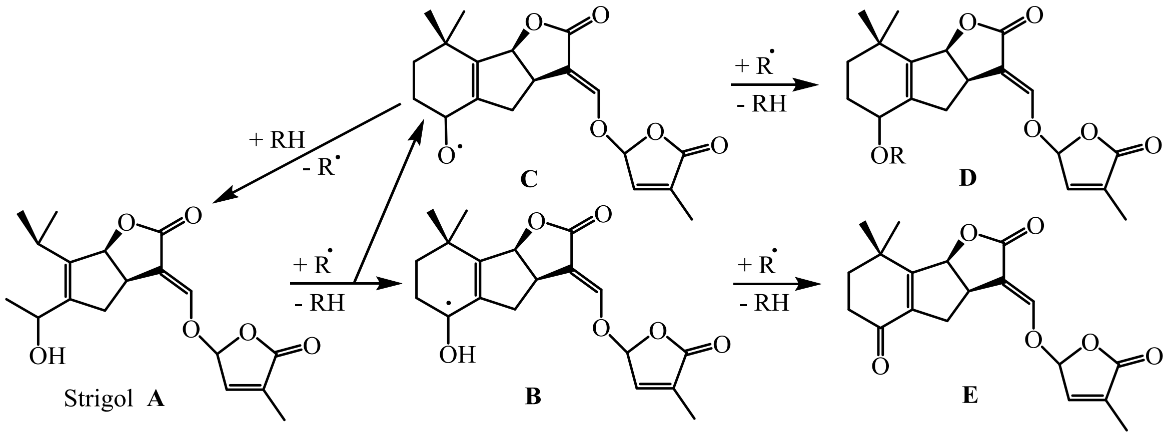

Fig. 5. Possible mechanisms of activation and mode of action for strigol.

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ПРО МОЛЕКУЛЯРНІ МЕХАНІЗМИ ДІЇ ТОКОФЕРОЛУ, ПРОСТАГЛАНДИНІВ, АБСЦИЗОВОЇ КИСЛОТИ, СТЕРОЇДІВ І СТРИГОЛАКТОНІВ

Мета. Життєдіяльність живих систем регулюється двома факторами: хімічними (біологічно активними речовинами, БАР) і фізичними. При цьому клітинний «редокс-статус» підтримується спеціальними речовинами оксидантами (OXs; вільними радикалами, FRs) і антиоксидантами (AOs). Ці два класи також визначають функціонування і цілість живих систем. У даній роботі розглянуті механізми дії природних AOs токоферолу, простагландинів, абсцизової кислоти, брасиностероїдів, стероїдів і стриголактонів. ***Результати***. Викладені механізми дії БАР описують як природні антиоксиданти токоферол, простагландини, абсцизова кислота, стероїди, брасиностероїди та стриголактони взаємодіють в організмі на молекулярному рівні, викликаючи певний хіміко-біологічний ефект. ***Висновки***. Клітинний «редокс-статус» підтримується спеціалізованими речовини оксидантами і антиоксидантами. У даній статті викладені механізми дії природних антиоксидантів без участі білкових рецепторів. *Ключові слова*: токоферол, простагландини, абсцизова кислота, стероїди, брасиностероїди, стриголактони.

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