The study of plant adaptation to oxygen deficiency in Saint Petersburg University

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Abstract

The first studies on plant anaerobiosis started at the Department of Plant Physiology at St. Petersburg University in the beginning of the 20th century, but interest in this subject became most intensive during the investigations of the ecological plant physiology group under the supervision of Prof. T. V. Chirkova. Their first step was focused on the mechanisms of transport of gases from the aerated aboveground part of the plant to the flooded root system. Further interest shifted towards clarifying the biochemistry of respiratory metabolism, pathways of reoxidation of the reduced cofactors, and protein and lipid metabolism of plants under anoxic conditions. The group's studies have always distinguished the comparative approach, in which the changes taking place in plants differing in resistance to oxygen deficiency were analyzed. In many ways, this research was pioneering and was recognized throughout the world. For the first time the possibility of hydrogen peroxide formation in plants under total anoxia was demonstrated. The role of cell membranes in adaptation processes was revealed. Pioneering investigations distinguished the features of photosynthesis in an oxygen-free environment and the work of an antioxidant system under conditions of anoxia and post-anoxic oxidative effects. Now, the plant ecophysiology group of the Department of Plant Physiology and Biochemistry of St. Petersburg State University concentrates on the mechanisms of anaerobic signal transduction and reveals how plant hormones regulate adaptation to anoxic and post-anoxic stresses.

Keywords: oxygen deficiency, post-anoxic stress, plant respiration, fermentation, protein and lipid metabolism, reactive oxygen species, antioxidants

Introduction

Being oxygenic photosynthetic organisms, plants are obligatory aerobes, which rely on molecular oxygen for their metabolism and survival. Nonetheless, very often they find themselves under oxygen deficiency that evolves constantly in aquatic and wetland habitats and frequently in dry lands, including agricultural, horticultural, and industrial areas. Availability of oxygen affects propagation of plant species in natural and agricultural ecosystems and has a severe economic impact. Yield losses due to lack of oxygen may reach up to 50% (Dennis et al., 2000). The oxygen shortage usually develops because of excess water during seasonal or perennial flooding and after heavy rainfalls. It also follows ice crust formation during wintertime and appears in compact soil due to the use of heavy agricultural machinery or asphalt covering. Waterlogging of the rhizosphere and partial flooding of aboveground parts of plant lead to gradual hypoxia (deficiency of oxygen), and complete submergence leads to anoxia (total absence of the gas);

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then, restoration of normal oxygen availability during desubmergence causes post-anoxic oxidative stress.

The lack of molecular oxygen leads to inhibition of aerobic respiration, which in turn ultimately results in energy starvation. After the imposition of an anaerobic condition, the ATP level in the cell is exhausted within 1–2 min (Drew, 1997). To provide ATP for cellular metabolism, glycolysis passes into fermentation at an intensity relative to the degree of oxygen deficiency. Overconsumption of reserve sugars for respiration enhances energy starvation, particularly in hypoxia-susceptible species (Chirkova, 1988a, b; Armstrong, Brändle, and Jackson, 1994; Vartapetian and Jackson, 1997). On the other hand, stimulation of lactic fermentation and lack of ATP to energize transport ATPases account for cytosol acidification (Drew, 1997). Alcoholic fermentation generates a toxic intermediate (acetic aldehyde) and end-products (ethanol) that together with acidosis self-poison the plant under oxygen deficiency (Chirkova, 1988a, b; Crawford and Braendle, 1996; Vartapetian and Jackson, 1997; Bailey-Serres and Voesenek, 2008). In natural habitats flooding leads to low soil redox potential and production of reduced substances including Fe^{2+}, Mn^{2+}, H_2S, NO_2^- along with the products of carbon metabolism such as methane, ethane, ethylene, acetylene, acetic and butyric acid, etc. (Chirkova, 1988a, 1998; Crawford, 1989; Drew, 1997). Moreover, reestablishment of normoxic conditions triggers oxidation of these substances and synthesis of reactive oxygen, nitrogen, carbonyl and sulfur species resulting in post-anoxic injury. The growth of plants is particularly sensitive to oxygen deficiency, with root elongation greater than shoot elongation (reviewed in Chirkova, 1968a, 1988a, 1988b, 1998; Crawford and Braendle, 1996; Drew, 1997; Vartapetian and Jackson, 1997; Bailey-Serres and Voesenek, 2008; Licausi and Perata, 2009; Tamang and Fukao, 2015; Voesenek and Bailey-Serres, 2015). In plants under conditions of limited aeration, the roots are shortened, thickened, and do not form a sufficient number of root hairs. Deep-lying roots die. The majority of sensitive species demonstrate depressed shoot growth, leaf chlorosis and epinasty, finally ending with the death of the aboveground part under lack of oxygen. Nonetheless, many hydrophyte species respond to submergence by accelerated shoot growth and hyponasty of petioles and leaves, facilitating escape from the hypoxic/anoxic environment; this constitutes a so-called Low-Oxygen Escape Syndrome (LOES). Other submergence tolerant species, on the contrary, limit underwater elongation growth via a Low-Oxygen Quiescence Syndrome (LOQS). These plants react to flooding mostly by metabolic switches which are particularly rigorous under strict lack of oxygen (Chirkova, 1988a,b, 1998; Armstrong, Brändle, and Jackson, 1994; Crawford and Braendle, 1996; Bailey-Serres and Voesenek, 2008; Licausi and Perata, 2009; Tamang and Fukao, 2015; Voesenek and Bailey-Serres, 2015).

The first studies on plant adaptation to lack of oxygen were carried out at the Department of Plant Physiology at St. Petersburg University in the beginning of the 20th century. The paper "Vremennyy anaerobioz vysshikh rasteniy. Chast' 1. Nablyudeniya nad protsessami rosta v beskislorodnoy srede [Temporary anaerobiosis of higher plants. Part 1. Observations on growth processes in an oxygen-free environment]" was issued in 1905 by Alexander I. Nabokikh, apprentice of Prof. Dmitri I. Ivanovski (the discoverer of tobacco mosaic virus) and Prof. Vasily V. Dokuchaev (the father of soil science) (Nabokikh, 1905). Unfortunately, the second part of this paper was never published. In 1907, Sergei P. Kostychev defended his MS thesis on "Issledovanija nad anajerobnym dyhaniem rastenij [Studies on anaerobic respiration of plants]" (Kostychev, 1907). After these episodic works, the topic did not develop for more than 50 years.

It is necessary to emphasize that the issue of oxygen shortage in plants in those years did not attract the attention of researchers all over the world, unlike the effects of water deficiency, low and high temperature, and the action of other environmental stimuli. Therefore, scientists had a terra incognita, open to research in any direction. The biology of plant respiration had been studied at the Department of Plant Physiology of St. Petersburg University since the time of Academicians Vladimir I. Palladin and Sergei P. Kostychev. But to develop the subject of respiration precisely in the direction of oxygen deficiency was advised to Prof. Stepan V. Soldatenkov by Academician Andrei L. Kursanov, who promoted the revival of interest in this field in the USSR, both in Moscow, at the Institute of Plant Physiology, and in Leningrad (now St. Petersburg), at the Department of Plant Physiology and Biochemistry of the University. As a result, in 1960, Zhao Xian Duan came out with the theme of his PhD thesis "Rol' list'ev u fasoli i kukuruzy v dyhanii kornej, lishennyh kisloroda [The role of bean and maize leaves in the respiration of roots deprived of oxygen]". These studies were continued in the works of Tamara V. Chirkova, who defended her PhD thesis "O roli list'ev v obespechenii kislorodom kornej rastenij razlichnyh mest obitanija [On the role of leaves in providing oxygen to plant roots of various habitat conditions]" in 1964. This subject aroused great interest, which led to the start of large-scale studies of the effect of oxygen deficiency on various aspects of plant life in Leningrad/St. Petersburg University under supervision of T. V. Chirkova.

Shoot-to-root transport of oxygen as an adaptation to root hypoxia

When the oxygen access to the roots is restricted due to waterlogging or flooding, plants try to maintain oxygen normal level required for survival in all tissues. This is facilitated by the development of a variety of morphological, anatomical and physiological adaptations. Many plant species are able to tolerate periods of flooding by the formation of new adventitious roots resulting in the appearance of a shallow root system (Chirkova, 1988a,b, 1998; Crawford, 1989; Armstrong, Brändle, and Jackson, 1994; Crawford and Braendle, 1996; Vartapetian and Jackson, 1997; Bailey-Serres and Voesenek, 2008; Voesenek and Bailey-Serres, 2015). Adventitious rooting is a way to replace existing roots damaged by the lack of oxygen. Emergence of adventitious roots is controlled by auxin and ethylene, and depends on their synthesis and signaling (Yemelyanov and Shishova, 2012; Sauter and Steffens, 2014; Hu et al., 2016). Roots as well as leaves and stems develop interconnected gas-filled cavities throughout the plant that provide a pathway for movement of oxygen and other gases to/from oxygen-deficient organs. This special pneumatic tissue is called aerenchyma. Air spaces appear either by cell separation at the middle lamella (schizogenous aerenchyma) or by cell death and lysis of the cell wall (lysigenous aerenchyma). The performance of aerenchyma depends on plant tolerance to oxygen deficiency. It is less extensive in non-wetland species than in wetland ones (Armstrong, Brändle, and Jackson, 1994; Vartapetian and Jackson, 1997). Hydrophytes constitutively develop schizogenous aerenchyma in roots, internodes, petioles, and leaf sheaths (see Takahashi, Yamauchi, Colmer, and Nakazono, 2014). Lysigenous aerenchyma is predominantly formed in the cortex of roots of some wetland plants and many sensitive mesophyte species. Induction of aerenchyma development in non-wetland plants usually takes several hours after the imposition of oxygen shortage. Formation of lysigenous aerenchyma in maize and rice root cortex is triggered by ethylene (Armstrong, Brändle, and Jackson, 1994; Drew, 1997; Bailey-Serres and Voesenek, 2008; Yemelyanov and Shishova, 2012; Voesenek and Bailey-Serres, 2015; Hu et al., 2016).

Trees of tropical mangrove (*Laguncularia* sp. and *Rhizophora* sp.) and Amazon basin (*Ficus* sp.) forests have aerial prop roots that grow down from the horizontal branches, while penetrating into the soil; they are lignified and form a system of supports (Chirkova, 1988a, 1998; Voesenek and Bailey-Serres, 2015). Other mangrove trees (*Avicennia* sp.) and the swamp cypress (*Taxodium distichum*) produce specialized aerial negatively gravitropic roots called pneumatophores (Chirkova, 1968a, 1988a, 1998; Crawford, 1989). Both aerial prop roots and pneumatophores are filled with aerenchyma and covered with innumerable pores — lenticles — which admit air into the plant.

Aerenchyma facilitates ventilation and gas exchange down into submerged parts of the plant and allows the plant to avoid real lack of oxygen during waterlogging or partial flooding. The key role of leaves in providing the roots of herbaceous crops (French bean, maize, tomato and potato) and trees (poplar) with oxygen during root anoxia was first shown by Prof. S.V. Soldatenkov and T.V. Chirkova's group (Soldatenkov and Zhao, 1961; Soldatenkov and Chirkova, 1963; Chirkova and Soldatenkov, 1965). It was revealed that leaves increase consumption of oxygen from the ambient atmosphere when roots suffer from anoxia. This allows anoxic roots to sustain aerobic respiration and prevent transition of glycolysis into fermentation, thus avoiding substantial accumulation of fermentation products. Leaves of non-wetland species maintain elevated oxygen consumption only for a short term (6–7 days, Soldatenkov and Chirkova, 1963); in contrast, leaves of wetland plants *Glyceria maxima* and *Scirpus sylvaticus* consume more oxygen than mesophyte species even in a normoxic atmosphere and accelerate air uptake during waterlogging (Soldatenkov and Chirkova, 1963; Chirkova, 1968a). In woody plants of the temperate zone with leafless season lasting 6–7 months, roots are supplied with atmospheric oxygen not only through the leaves, but also through the lenticles on branches (Chirkova, 1968b).

In well-adapted species aerenchyma can extend from the leaf stomata almost to the root tip, which provides aeration throughout the plant and allows oxygenation of the rhizosphere due to radial oxygen loss (Armstrong, Brändle, and Jackson, 1994; Vartapetian and Jackson, 1997). Radial oxygen loss encourages aerobic microflora and affects oxidation of anoxic soil toxins and plant mineral uptake. On the other hand, wetland species limit oxygen loss by establishing barriers in the hypodermis/exodermis by stimulation of cell wall lignification and suberinization (Nishiuchi et al., 2012; Watanabe, Nishiushi, Kulichikhin, and Nakazono, 2013) to provide oxygen delievery directly to the root tip. Moreover, this barrier may impede the penetration of soil-derived toxins and gases into the roots (Armstrong, Brändle, and Jackson, 1994; Nishiuchi et al., 2012).

The ventilation system can include large reservoirs for gases; therefore, aerenchyma serves not only for supplying oxygen, but also for increasing the buoyancy that allows wetland plants to float on the surface of water (Chirkova, 1998). Besides the elimination of respiring cells, the formation of lysigenous aerenchyma leads to preservation of energy resources, oxygen consumption and deceleration of metabolism. One more important function of aerenchyma during flooding is disposal of volatile toxic fermentation intermediate and end products and soil-borne toxins (Chirkova and Gutman, 1972; Chirkova, 1988a, 1988b, 1998; Vartapetian and Jackson, 1997).

Apart from aerenchyma, the formation of aerial films on non-wettable leaf/stem surface also facilitates gas flow between the air and the flooded part of the plant (Pedersen, Rich, and Colmer, 2009; Voesenek and

Bailey-Serres, 2015). In wetland monocots hydrophobic wax cuticle on the leaf surface enlarges the gas–water interface and allows fast O_2 and CO_2 diffusion, which is important not only for respiration, but also for underwater photosynthesis (Pedersen, Colmer, and Sand-Jensen, 2013). During partial and complete submergence, internal aeration of wetland species relies on underwater photosynthesis during the day and entry of oxygen from the floodwater during the night (Winkel, Colmer, Ismail, and Pedersen, 2013). Submergence-tolerant landraces of rice sustain underwater photosynthesis over a 12-d submergence period (Winkel et al., 2014) and Amazonian palm *Astrocaryum jauri* — for 300 days (Armstrong, Brändle, and Jackson, 1994). Rice chloroplasts showed a complete recovery of photochemical activity after 72 h of oxygen deficiency, whereas wheat chloroplasts remained inactive even after shorter treatment (Chirkova, Walter, Leffer, and Novitskaya, 1995). The impairment of activity of Photosystem II appeared earlier than in Photosystem I, especially in sensitive mesophytes (wheat), indicating that non-wetland species are incapable of implementation of effective underwater photosynthesis (Chirkova, Walter, Leffer, and Novitskaya, 1995). Thus, the leaves of resistant plants, in contrast to those of non-resistant ones, not only ensure their ventilation by enhancing the absorption of oxygen from the ambient atmosphere during hypoxia, but also are able to keep its supply for a long time through the process of underwater photosynthesis.

The mechanisms listed above (adventitious shallow rooting, aerenchyma formation, gas films and underwater photosynthesis) represent a strategy to avoid root hypoxia/anoxia during soil waterlogging and partial flooding. But these adaptations become ineffective when the plant is totally submerged.

Acceleration of shoot growth as an adaptation to complete submergence

Fast underwater growth of shoot axial organs like coleoptiles, stem internodes, and petioles has been demonstrated in a wide variety of wetland species of different taxonomical origin displaying low-oxygen escape syndrome (LOES). The growth is stimulated either by cell elongation with little or no change in their division, e.g., in *Callitriche platycarpa*, *Hydrocharis morsus-ranae*, *Ranunculus sceleratus*, *Rumex crispus* and *R. palustris* (reviewed in Peeters et al., 2002; Yemelyanov and Shishova, 2012), or by cell proliferation and subsequent elongation, like in deepwater rice (Kende, van der Knaap, and Cho, 1998), *Nymphoides peltata*, *Ranunculus repens* and *R. pygmaeus* (Yemelyanov and Shishova, 2012).

LOES is strictly regulated by the plant hormonal system. Submergence induces synthesis and physical entrapment of ethylene inside plant tissues (reviewed in Armstrong, Brändle, and Jackson, 1994; Vartapetian and Jackson, 1997; Kende, van der Knaap, and Cho, 1998; Bailey-Serres and Voesenek, 2008; Yemelyanov and Shishova, 2012; Voesenek and Bailey-Serres, 2015; Hu et al., 2016). In well-adapted wetland species, ethylene accumulation occurs only within the first hours of submergence and never reaches a high concentration like in non-tolerant mesophyte species. This plant hormone is thought to be the master signal for rearrangement of hormone crosstalk during flooding stress. Ethylene stimulates a decrease in ABA levels in deepwater rice coleoptiles, internodes and petioles of *Rumex palustris* by repressing ABA biosynthesis and enhancing ABA catabolism. Plants which are more susceptible to oxygen deprivation accumulate a higher amount of ABA during submergence or total anoxia (Yemelyanov and Chirkova, 1996; Yemelyanov, 1998; Emel'yanov, Kirchikhina, Lastochkin, and Chirkova, 2003; Hu et al., 2016). The ethylene-induced drop in ABA concentration in LOES species relieves the inhibition from synthesis of bioactive GAs, which mediates the majority of ethylene effects on fast underwater shoot growth. This interaction between ethylene, ABA, and GA accelerates the growth of stems and leaf petioles by stimulating cell elongation and division. Promotion of shoot extension by hormone rearrangement during submergence is linked with cell wall loosening provided by stimulation of pectinase, xylanase, xyloglucan endotransglucosylase/hydrolase, and expansins (Bailey-Serres and Voesenek, 2008; Yemelyanov and Shishova, 2012; Voesenek and Bailey-Serres, 2015; Hu et al., 2016). These proteins are also involved in aerenchyma formation. In some plants, underwater growth is supported by accumulation of auxin, caused by submergence either in an ethylene-dependent or -independent manner (Yemelyanov and Shishova, 2012; Voesenek and Bailey-Serres, 2015; Hu et al., 2016). Ethylene–auxin interaction regulates epi- or hyponastic response of leaves and formation of adventitious root system depending on plant tolerance (Yemelyanov and Shishova, 2012; Hu et al., 2016). Carbohydrates required for new cell wall synthesis and fast growth are provided by underwater photosynthesis and by the mobilization of starch reserves via an increase in α-amylase activity (Bailey-Serres and Voesenek, 2008; Voesenek and Bailey-Serres, 2015). These responses allow plants to reach water surface with the shoot tips extending above the water surface, escaping from the oxygen-deficient environment; they exchange gases for respiration and photosynthesis, which finally results in plant adaptation and survival. Non-tolerant mesophyte species accumulate relatively high amounts of ethylene and ABA and decrease the levels of growth stimulators (GA and auxin) under lack of oxygen, leading to stimulation of senescence, epinasty, leaf abscission, and finally plant death (Yemelyanov and Shishova, 2012).

Furthermore, ethylene is supposed to be not only the master signal for regulation of hormone crosstalk during flooding stress, but also for choice of adaptation strategy and sensing of oxygen level. Interestingly, the largest group constituting about 20% of all transcription factors up-regulated by oxygen deficiency in *Arabidopsis thaliana* belongs to Apetala 2-like Ethylene Responsive Factors group VII (ERF-VIIs, Licausi and Perata, 2009; Licausi et al., 2011). There are five genes encoding ERF-VIIs in *A. thaliana*. Three of these are constitutively expressed *Related to AP2 12* (*RAP2.12*), *RAP2.2* and *RAP2.3* and up-regulated by ethylene, and the other two *HYPOXIA RESPONSIVE ERF1/2* (*HRE1/2)* are highly induced by oxygen deprivation (Voesenek and Bailey-Serres, 2015). These ERF-VIIs bear a conserved Met-Cys N-terminal motif that is targeted to constitutive proteasomal degradation through the N-end rule pathway under normoxia and due to interaction with reactive oxygen and nitrogen species (Banti et al., 2013). Oxygen deprivation leads to stabilization of the ERF-VIIs, RAP2.12 migrates into the nucleus and activates transcription of hypoxia-responsive genes, including *HRE1/2* and *PDC* encoding pyruvate decarboxylase (Voesenek and Bailey-Serres, 2015).

Two major adaptive responses, LOES and LOQS, are primarily governed by the multigenic *SNORKEL* (*SK*) and *SUBMERGENCE-1* (*SUB1)* loci, respectively, both of which encode ERFVIIs (Bailey-Serres and Voesenek, 2008; Nishiuchi et al., 2012; Banti et al., 2013; Tamang and Fukao, 2015; Voesenek and Bailey-Serres, 2015; Hu et al., 2016). The *SNORKEL* locus encodes the two ERF-VII genes. Ethylene-triggered induction of *SK1* and *SK2* during submergence upregulates expression of the GA20 oxidase gene responsible for GA biosynthesis, and promotes fast underwater growth. The *SUBMERGENCE-1* locus encodes two ERF-VII genes, *Sub1B* and *Sub1C* in all *japonica* and some submergence-intolerant *indica* rice cultivars. In the tolerant *indica* cultivars using LOQS, like FR13A and Kurkaruppan, which the *Sub1* locus was first isolated from, three ERF-VII genes are present, with addition of *Sub1A*. *Sub1A* and *Sub1C* transcripts levels are upregulated by submergence and ethylene (Fukao, Xu, Ronald, and Bailey-Serres, 2006) and downregulated by ABA (Fukao and Bailey-Serres, 2008). *Sub1A* confers tolerance to prolonged complete submergence in lowland rice. It dampens ethylene production and represses ethylene- and GA-mediated responses in cell elongation and carbohydrate breakdown, including expansin and amylase genes expression. On the other hand, the *Sub1C* gene is upregulated by submergence, ethylene and GA, and it stimulates shoot elongation in LOES rice. In quiescent-tolerant rice cultivars, *Sub1C* is repressed by Sub1A (Fukao, Xu, Ronald, and Bailey-Serres, 2006; Tamang and Fukao, 2015). Sub1A was reported to increase the accumulation of the signaling proteins Slender Rice-1 (SLR1) and SLR1 Like-1 (SLRL1), which repress GA signaling (Fukao and Bailey-Serres 2008), possibly via stimulation of brassinosteroid signaling pathway and with transcriptional activation of GA2ox7, which catabolizes GA, thus reducing the levels of endogenous active GAs (Schmitz et al., 2013). At the same time, Sub1A induces metabolic adaptation by upregulation of genes, encoding pyruvate decarboxylase and alcohol dehydrogenase (ADH) involved in alcoholic fermentation (Fukao, Xu, Ronald, and Bailey-Serres, 2006). Thus, Sub1A blocks LOES and stimulates LOQS, transiently limiting growth, which allows the plant to keep its energy and capacity for regrowth upon desubmergence. The same LOQS based primarily in metabolic adaptation is used by dormant rhizomes of wetland species. The study of metabolic adaptations of plants to hypoxia and anoxia was the main subject of study of Prof. T.V. Chirkova's group in Leningrad/St. Petersburg University.

Alteration of metabolism as an adaptation to total hypoxia and anoxia

The metabolic adaptations of plants to oxygen deficiency affect various aspects of cellular metabolism, but due to the nature of the stressor, they involve mainly respiration adjustments. When the oxygen level drops, it results in inhibition of cytochrome c oxidase (COX, complex IV) activity and suppression of aerobic respiration. Disturbance of aerobic respiration takes place after a more prolonged period of oxygen deprivation, and recovery of respiration rate after anoxia occurs earlier in seedlings of a tolerant plant (rice) than of a non-resistant one (wheat, Chirkova and Nastinova, 1975a). This corresponds to the less injury and better maintenance of cell structures involved in respiration in well-adapted species. Low respiration rate is characteristic for wetland species even under normoxic conditions (Chirkova, 1988a, b, 1998). It is specific for floating and underwater leaves of hydrophytes compared to aerated abovewater ones, for rhizomes of aquatic plants, for the roots of resistant plants (*Salix alba*, *Glyceria maxima*) in contrast to sensitive ones (*Populus petrowskiana*, *Phaseolus vulgaris*) (Chirkova and Petrova, 1971; Chirkova and Khazova, 1974). Low respiration rate indicates moderate consumption of oxygen, which allows the plant to maintain the intensity of respiration almost unaltered even under mild oxygen deficiency.

The inhibition of aerobic respiration by oxygen deficiency leads to a depleted ATP level, and providing ATP becomes the major problem for respiratory metabolism. Solution of this problem is mainly accounted for by acceleration of glycolysis, subsequently turning into lactic and ethanolic fermentation, which was shown in our work (Chirkova, 1988a,b, 1998). However, the rate of transition from aerobic metabolism, as well as the dynamics of glycolysis, differs significantly in plants

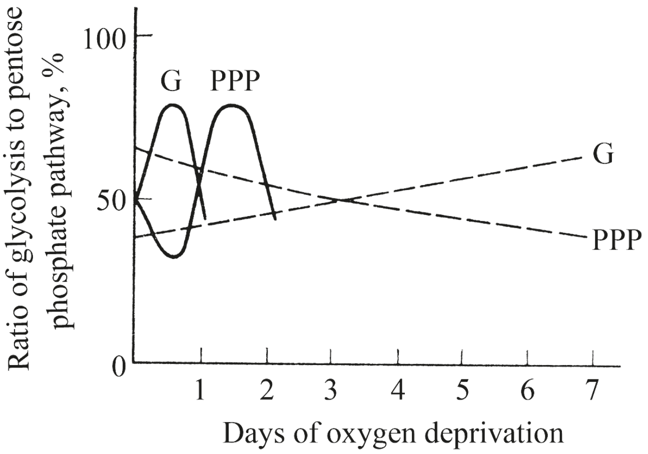

Fig. 1. Scheme of alteration of respiratory pathways ratio under oxygen deprivation in non-resistant (solid lines) and resistant (dashed lines) plant species. G — glycolysis, PPP — pentose phosphate pathway (Chirkova, 1988a).

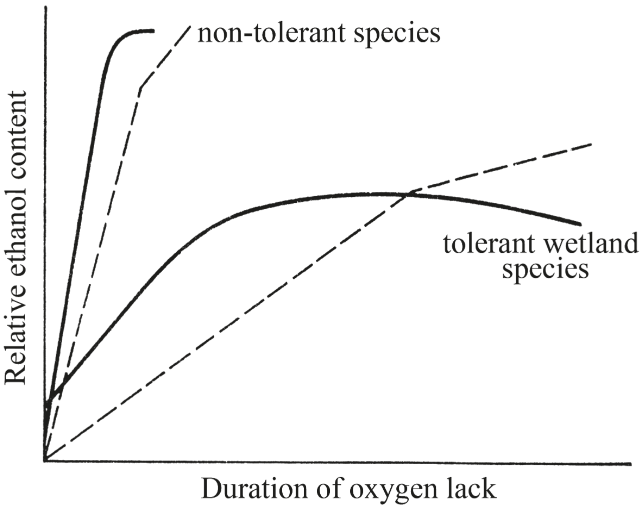

Fig. 2. Scheme of ethanol accumulation in plant tissues (solid lines) and ambient medium (dashed lines) under oxygen deprivation (Chirkova, 1988a).

contrasting in resistance to hypoxia. A fast short-term increase of glycolytic activity was observed in non-resistant plants (wheat, *Phaseolus vulgaris*, poplar) already in the first hours of anaerobic exposure (Fig. 1). In adapted species (rice, *Glyceria maxima*, willow) activation of this process was less intensive and took a longer time, which determined a more reliable supply of energy (Chirkova and Petrova, 1971; Chirkova and Nastinova, 1975b; Chirkova and Zhukova, 1987; Crawford, 1989).

Sufficient substrate availability is required for efficient glycolysis operation. Since glycolysis provides only 2 moles of ATP per 1 mole of glucose, it leads to an overconsumption of sugars, especially in non-wetland species (Chirkova, 1973; Zhukova, 1987). Many resistant plants of aquatic and semiaquatic habitat accumulate a significant amount of carbohydrates in the rhizomes (up to 50% of their dry weight, Armstrong, Brändle, and Jackson, 1994; Vartapetian and Jackson, 1997; Bailey-Serres and Voesenek, 2008; Licausi and Perata, 2009). Moreover, carbohydrate supply is important for both adaptive strategies, LOES and LOQS (Bailey-Serres and Voesenek, 2008; Voesenek and Bailey-Serres, 2015). In experiments with excised organs (coleptiles, stem sections, roots), exogenously applied sugars is absolutely required for anoxic tolerance (Chirkova, 1988a; Vartapetian and Jackson, 1997). However, the availability of carbohydrate reserves is not sufficient for the survival of non-resistant plants. Many of them are incapable of mobilizing polysaccharides due to the absence of expression of genes encoding starch phosphorylase and α-amylase during anoxia action. However, seeds and rhizomes of hydrophytes do mobilize reserves during hypoxic/anoxic germination (see Licausi and Perata, 2009).

Another "bottleneck" of metabolism during oxygen shortage is reoxidation of NADH reduced in glycolysis, since its oxidation in the mitochondrion is blocked. This is generally achieved through fermentation pathways. Both fermentations are stimulated by an increase of activity of their enzymes (lactate dehydrogenase, pyruvate decarboxylase and alcohol dehydrogenase) at the steric, transcriptional and translational level (Chirkova and Petrova, 1971; Chirkova, 1973, 1988b; Chirkova, Khazova, and Astafurova, 1974; Nastinova and Chirkova, 1978; Chirkova, Nastinova, and Zhukova, 1978). Activation of fermentation as well as glycolysis occurs earlier and more intensely in non-resistant mesophyte species compared to in adapted hydrophytes (Chirkova, 1988a,b, 1998; Crawford, 1989), resulting in the synthesis of intermediate and end-products that contribute to toxicity (acetic aldehyde, ethanol) and cytosolic acidification (lactate) under lack of oxygen. Moreover, glycolytic flux to lactate is minor compared with that to ethanol, especially in wetland species, while non-resistant plants stimulate lactic fermentation during oxygen deficiency to a higher extent (Chirkova, 1973). Nonetheless, ethanolic fermentation is the major pathway throughout the plant kingdom. Non-tolerant plants accumulate a higher amount of ethanol followed by disposal of ethanol into the rhizosphere and flooded water within the first hours–days of oxygen deprivation (Fig. 2). Well-adapted species produce less alcohol and lactate for a longer period of oxygen shortage due to limiting of metabolism, and they remove more end products into the environment — both into the ambient solution and via aerenchyma into the air during root hypoxia (Chirkova and Gutman, 1972; Chirkova, 1978; Chirkova, Nastinova, and Semenova, 1978). Besides deceleration of metabolic rate and disposal of toxic products, toxic metabolite accumulation may be avoided by alteration of metabolic pathways leading to substances other than ethanol or

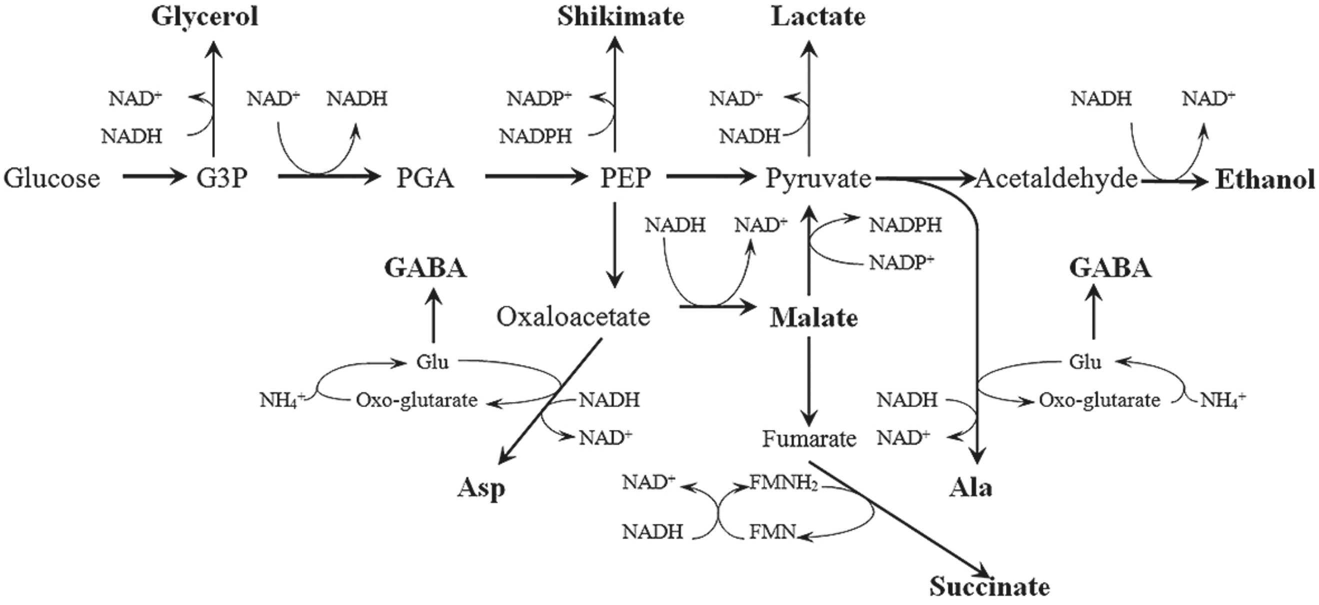

Fig. 3. Scheme of NADH reoxidation pathways involved in plant metabolic adaptation under partial or total oxygen deficiency (Crawford, 1978; Chirkova, 1988b, 1998, with modifications). Bold arrows indicate the major glycolytic pathway passing into ethanolic fermentation. Compounds indicated in bold correspond to the main metabolites of resistant wetland plants during hypoxia. G3P — glyceraldehyde 3-phosphate, GABA — γ-aminobutyric acid, PEP — 2-phosphoenolpyruvate, PGA — 3-phosphoglyceric acid.

lactate. Many tolerant plants are capable of rerouting glycolytic intermediates to alternate end products such as malate, succinate, glycerol, Ala and GABA (Fig. 3). Production of these alternative hypoxic metabolites allows the plant to reoxidize NADH into NAD$^+$, which is required for glycolysis and prevents cell toxicity during hypoxia. Importantly, accumulation of Ala and GABA copes with cytosolic acidosis during oxygen deprivation (Bailey-Serres and Voesenek, 2008; Licausi and Perata, 2009). The first step in the pathway is reversal of the dicarbonic part of the Krebs cycle converting oxaloacetate into malate (Crawford, 1978; Chirkova, 1988a, 1998) due to activation of NAD-dependent malate dehydrogenase (Chirkova, Barzhinkova, Barkova, and Magomedov, 1984) and then into fumarate and succinate (Chirkova and Nastinova, 1977; Chirkova, Barkova, Barzhinkova, and Magomedov, 1985). Succinate accumulation is not related to the glyoxylate cycle, since isocitrate lyase is inhibited by oxygen deprivation in plant tissues irrespectively of their tolerance (Chirkova and Grevnina, 1982). Later research demonstrated that reversal of the Krebs cycle occurs in resistant plants only during hypoxia, and severe anoxia provokes mostly activation of fermentation (Kulichikhin, Kurchakova, and Chirkova, 2000; Kulichikhin, Chirkova, and Fagerstedt, 2009). Nonetheless, hypoxia-resistant plants (rice, willow) may tolerate rather high concentrations of ethanol (Chirkova and Semenova, 1979; Chirkova, Barzhinkova, and Hoang, 1980) and incorporate it into metabolism during hypoxia, and especially post-hypo/anoxia (Chirkova, 1975, 1978). Plants also may prevent formation of toxic end-products by using other respiratory pathways such as oxidative pentose phosphate pathway (PPP). The pattern of its stimulation depends on plant tolerance to oxygen deprivation. Short-term supression of PPP activity occurs with simultaneous acceleration of glycolysis in non-resistant plants during the first hours of oxygen deficiency (Fig. 1). Later, when the glycolytic pathway slows down, PPP transiently activates. Wetland species are characterized by gradual long-term activation of glycolysis and the same stopping of PPP under hypoxia (Chirkova and Nastinova, 1975b; Chirkova, 1988a,b, 1998). PPP generates reduced NADPH and requires its reoxidation, which may be performed via condensation of erythrose 4-phosphate with phosphoenolpyruvate to produce shikimate (Fig. 3, Crawford, 1978).

As previously discussed, oxygen shortage affects the electron transfer chain in the mitochondria, which is determined by the high sensitivity to oxygen of the energy and transport processes in the mitochondria. Oxygen deprivation causes blockage of the electron transport chain in plants grown under normal aeration. However, its components retain some potential activity, which is renewed after the return of oxygen into the environment. The ability to restore respiration in resistant plants remains even after a longer period of anaerobiosis in comparison with non-resistant ones (Chirkova, Dragunova, and Burgova, 1977; Chirkova and Karpenko, 1981). Moreover, involvement of alternative cyanide-resistant oxidase in plant adaptation to oxygen deprivation was revealed (Chirkova and Kovalenko, 1982); this was confirmed later by analysis of *AOX* gene expression (see Bailey-Serres and Voesenek, 2008). High capacity of reparation of aerobic respiration of adapted species is determined by stability of cell membranes (Chirkova, 1983) and mitochondrial proteins (Hoang et al., 1979; Chirkova and Hoang, 1981; Chirkova, Saakov, Semenova, and Avdeeva, 1993), and adenylate kinase activity (Chirkova, Zhukova, and Ivanova, 1984). All together these processes provide sufficient ATP synthesis (Zhukova, Chirkova, and Tretyakov, 1984; Chirkova, 1988b; Kulichikhin, Aitio, Chirkova, and Fagerstedt, 2007) and effective maintainence of intracellular pH (Chirkova, Verzilin, Barzhinkova, and Petryaevskaya, 1981; Kulichikhin, Aitio, Chirkova, and Fagerstedt, 2007) in wetland plants during oxygen deprivation in comparison to non-resistant plants.

During submergence oxygen availability is limited and plants have to use other acceptors of electrons and protons; this is generally called "anoxic endogenous oxidation" and "nitrate respiration" in the case of nitrate. Treatment of plants with nitrates favors anoxic metabolism and adaptation of poplar, willow, cereals (Chirkova, 1971; Chirkova and Benko, 1973; Belonogova and Chirkova, 1995), *Amaranthus caudatus*, *A. cruentus* and *A. edulus* (Belonogova and Chirkova, 1994; Belonogova, Chirkova, and Zabruskov, 1995). Higher uptake of nitrate, activation of nitrate reductase, accumulation of ammonium and amino acids (mostly Ala, Glu and GABA, Licausi and Perata, 2009) occurs predominantly in resistant plants (Chirkova, 1971, 1988b; Belonogova and Chirkova, 1994, 1995). Importantly, the nitrate reductase in the cytosol reduces nitrate into nitrite while simultaneously oxidizing NAD(P)H. Then nitrite enters the mitochondrion and serves as an alternative terminal electron acceptor at sites of cytochrome bc1 complex (III) and cytochrome c oxidase (COX, complex IV), producing nitrogen oxide that is involved in anoxic signaling and can be converted in the cytosol by hypoxically induced non-symbiotic haemoglobin back to nitrate. The latter is again reduced to nitrite by nitrate reductase, forming the so-called haemoglobin/nitric oxide cycle (Igamberdiev and Hill, 2009). This cycle not only reoxidizes NAD(P)H but also provides proton pumping at the COX site sufficient for ATP synthesis. Therefore, in case of nitrate we may truly call this metabolic pathway "nitrate respiration". Anoxic endogenous oxidation also includes the hydrogenation of double and triple bonds of unsaturated compounds, for example, of carotenes, terpenoids and polyunsaturated fatty acid residues in cell lipids (Chirkova, 1988a,b, 1998).

All of the above mentioned changes in plant growth and respiratory pathways during oxygen deficiency are due to alterations of protein metabolism. Like any other stressor, oxygen shortage negatively affects protein content, since its synthesis is inhibited and degradation is stimulated (Chirkova, 1988a,b, 1998; Chirkova and Voitsekovskaya, 1999b). However, there are significant differences between proteolysis and protein synthesis in plants depending on their resistance to submergence. Decrease of protein content occurs in resistant plants much more slowly and after a stronger and more prolonged oxygen deprivation than in non-resistant ones (Chirkova, Nastinova, and Zhukova, 1978; Chirkova and Hoang, 1981). Moreover, proteins from energy-producing organoids (mitochondria and chloroplasts) of tolerant species manifest higher stability (Chirkova and Hoang, 1981; Chirkova, Saakov, Semenova, and Avdeeva, 1993; Chirkova, Novitskaya, Walter, and Leffer, 1995; Chirkova, Walter, Leffer, and Novitskaya, 1995). At the same time, the number of molecular forms of cytosolic and organellar proteins increases (Chirkova and Hoang, 1981), which may indicate both the degradation of more complex proteins and the synthesis of new proteins during oxygen deficiency. The idea of the possibility of protein synthesis in an oxygen-free environment was developed and experimentally confirmed only in the mid-1970s. We were among the first who demonstrated the crucial role of protein synthesis in activation of peroxidase (Chirkova and Sokolovskaya, 1976), LDH and ADH (Chirkova, Nastinova, and Zhukova, 1978; Nastinova and Chirkova, 1978), malate dehydrogenase (Chirkova, Barzhinkova, Barkova, and Magomedov, 1984), nitrate reductase (Chirkova, 1988b) and non-histone chromatin proteins (Chirkova, Surodeeva, and Semenova, 1986; Voitsekovskaya and Chirkova, 1992; Voitsekovskaya, Badyina, and Chirkova, 1993; Chirkova and Voitsekovskaya, 1999a) in rice, *Glyceria maxima*, and other wetland species during hypo/anoxia. It is now generally accepted that lack of oxygen induces synthesis of anaerobic stress proteins belonging to the signal transduction network, to enzymes of the respiratory pathways, carbohydrate mobilization, nitrogen metabolism, cell wall loosening, and antioxidant defence (Vartapetian and Jackson, 1997; Chirkova and Voitsekovskaya, 1999b). Proteomic studies revealed from about 30 to 70 upregulated proteins in different plants under oxygen shortage (Chen et al., 2014; Yin, Sakata, Nanjo, and Komatsu, 2014).

Stability of lipids also plays an important role in providing plant resistance to oxygen deficiency. Phospholipids and other constituents of cell membranes are of particular interest. Oxygen deficiency lowers the content of total lipids and phospholipids, dampens lipid biosynthesis (Hoang, Sinyutina, and Chirkova, 1979; Sinyutina, Hoang, and Chirkova, 1979; Chirkova et al., 1989; Chirkova, Sinyutina, Smetannikova, and Krynkina, 1989) and stimulates lipid degradation, leading to accumulation of free fatty acids (Valyavskaya, Sinyutina, and Chirkova, 2000, 2002). Degradation of lipids and free fatty acids is facilitated by lipid peroxidation

(LPX). LPX usually occurs in normal unstressed conditions and drastically increases upon stress action. LPX is activated mainly after reoxygenation, when the plant returns to aeration. But we demonstrated LPX even in an oxygen-free environment (Chirkova and Blokhina, 1991). The anoxia-induced lipid loss is less intense in resistant plants than in non-resistant ones (Hoang, Sinyutina, and Chirkova, 1979; Valyavskaya, Sinyutina, and Chirkova, 2000) even after treatment with ethanol (Chirkova, Hoang, and Sinyutina, 1980). Sterol content increases upon oxygen deficiency (Valyavskaya, Sinyutina, and Chirkova, 2000), particularly in mitochondria of non-resistant plants (Valyavskaya, Sinyutina, and Chirkova, 2002). In contrast, mitochondrial membranes accumulate less sterols and maintain phospholipid level in wetland species during oxygen deficiency. Lipids of photosynthetic membranes demonstrated even higer stability, again in well-adapted plants. Imposition of anoxia with light results in sustaining of chloroplast phospholidid (Chirkova, Gobedzhishvili, Hakala and Sinyutina, 1991a) and galactolipid (Chirkova, Gobedzhishvili, Hakala, and Sinyutina, 1991b) biosynthesis in the shoots of rice seedlings. Surprisingly, the effect of darkness on the chloroplast lipids was more dramatic than the effect of anoxia. If anoxic treatment is accompanied by illumination, this permits photosynthesis and diminishes the negative aftermath of oxygen deficiency. Besides the effect on lipid synthesis and degradation, the saturation of the fatty acid component of phospholipids undergoes significant changes, since it is responsible for the physico-chemical characteristics and function of the membranes. Oxygen deprivation leads to a gradual increase of the fraction of saturated and monounsaturated fatty acid residues, while the fraction of polyunsaturated fatty acid residues is exhausted (Blyudzin, Hoang, and Chirkova, 1980; Chirkova, Hoang, and Blyudzin, 1981; Blyuzdin, Barskiy, Chirkova, and Sokolova, 1986). This process takes part in anoxic endogenous oxidation for NAD(P)H recycling. In wetland species, saturation of membrane lipids occurs under stronger oxygen deficiency than in non-resistant ones, especially in mitochondria (Chirkova, Hoang, and Blyudzin, 1981).

Thus, the rearrangements of both protein and lipid metabolism are related to the needs to cope with the requirements of plant respiratory pathways under oxygen deficiency. They are interconnected to the integral role of cell membranes in plant resistance to adverse impacts. The integrity and functional activity of the plasma membrane, tonoplast, mitochondrial and chloroplast membranes of adapted plants maintain longer in an oxygen-deficient environment (Chirkova, 1983, 1998). Therefore, tolerant plants are able to generate a sufficient amount of energy, maintain membrane permeability and mineral uptake, and even grow in total absence of oxygen (Chirkova, Zhukova, and Goncharova, 1991a; 1992). Moreover, assessment of membrane permeability in an electrolyte leakage test makes it possible to evaluate the degree of plant resistance to oxygen deprivation and other environmental stimuli (Chirkova, Zhukova, and Goncharova, 1991b; Chirkova, Zhukova, Goncharova, and Belonogova, 1991).

Adaptation to post-hypoxic/post-anoxic reoxygenation

Under reestablishment of a normal oxygen level after hypoxia or anoxia, plants face multiple external challenges affecting plant growth and survival. Fast reentry of oxygen results in oxidation of reduced intermediate and end-products that accumulated during preceding anoxia, soil toxins (Cu^+, Fe^{2+}, Mn^{2+}), overproduction of reactive oxygen species (ROS) and toxic oxidative products (Crawford, 1989; Vartapetian and Jackson, 1997), leading finally to large-scale oxidative post-anoxic stress. Unexpected exposure to higher light may induce photooxidative damage to the photosynthetic apparatus (Tamang and Fukao, 2015). Desiccation of the aboveground part of the plant following reoxygenation is also observed. Weakening of the plant due to the effect of anoxia and post-anoxia may increase the probability of pathogen infection or herbivore attack, since high humidity favors pathogen and phytophage propagation (Tamang and Fukao, 2015).

Nonetheless, oxidative stress is the major challenge during desubmergence or post-anoxic action. We were the first to demonstrate production of hydrogen peroxide (long-living ROS) in plant cells during anoxia and subsequent reoxygenation (Blokhina, Chirkova, and Fagerstedt, 2001). Lipid peroxidation (LPX) begins even under anaerobic conditions and is significantly enhanced upon the return of oxygen to the environment (Chirkova and Blokhina, 1991). Wetland species (*Iris pseudacorus*, rice) produce a smaller amount of ROS and products of LPX under anoxic and post-anoxic stress than non-resistant ones (*I. germanica*, oats, wheat, Chirkova, Novitskay, and Blokhina, 1998; Blokhina, Fagerstedt, and Chirkova, 1999). Suppression of oxidative damage in hypoxia-resistant plants correlates with activation of antioxidant enzymes: peroxidase (Chirkova, Sokolovskaya, and Khazova, 1973; Chirkova and Sokolovskaya, 1976; Lastochkin, Yemelyanov, and Chirkova, 2000) and superoxide dismutase (Chirkova, Novitskaya, and Blokhina, 1998), accumulation of tocopherols (Chirkova and Gobedzhishvili, 1993; Chirkova, Novitskaya, and Blokhina, 1998; Blokhina et al., 2000), and turnover of ascorbic acid and glutathione (Blokhina et al., 2000). Thus, hypoxia-resistant plants demonstrate resistance to oxidative stress, too.

Conclusions

The study of plant adaptation to oxygen deficiency has been carried out at the Department of Plant Physiology and Biochemistry in Leningrad/Saint Petersburg State University for more than 50 years. Data obtained have been published in more than 100 publications, including 3 textbooks (Chirkova, 1988b; Semikhatova and Chirkova, 2001; Chirkova, 2002). In the course of this research work, more than 80 M. S., 11 Ph.D. and 3 Doctor of Science Theses have been defended. Long-term investigations were summarized in Doctor of Science Theses of T. V. Chirkova (1984), where the scheme of pathways of plant adaptation to oxygen deprivation (Fig. 4) was first suggested. Later it was modified and updated (Chirkova, 1988a,b, 1998); this scheme continues to be developed according to the results of further research.

The pathways of adaptation to oxygen deprivation reflect the general strategy in organism reaction to the effects of various damaging agents (Chirkova, 2002). This strategy consists of, first of all, attempts to avoid an adverse effect; in the case of hypoxia — to avoid oxygen deficiency by the facilitated transport of oxygen into the roots (physiological adaptation) and the formation of associated anatomic-morphologic and developmental adaptations (aerenchyma, superficial adventitious root system, etc.). Avoidance strategy may be realized in both non-tolerant mesophytes and well-adapted wetland plants during soil waterlogging or root flooding. When a plant becomes partially or totally submerged, the avoidance strategy is complemented by growth response. The majority of hydrophyte species respond to submergence by accelerated shoot growth, which facilitates escape from the hypoxic/anoxic environment and constitutes LOES (low-oxygen escape syndrome). Rearrangement of the hormonal network, respiratory metabolism and photosynthesis provide fast underwater growth. Other submergence-tolerant species limit underwater elongation growth and demonstrate quiescent LOQS (low-oxygen quiescence syndrome). These plants react to flooding mostly by metabolic alterations (biochemical adaptation) that become dominant with an increase of the strength of anoxic exposure. Quiescent syndrome involves general decceleration of metabolic rate, providing sufficient carbohydrate supply; compensatory alterations of respiratory, protein and lipid metabolism; anoxic endogenous oxidation; removal and metabolization

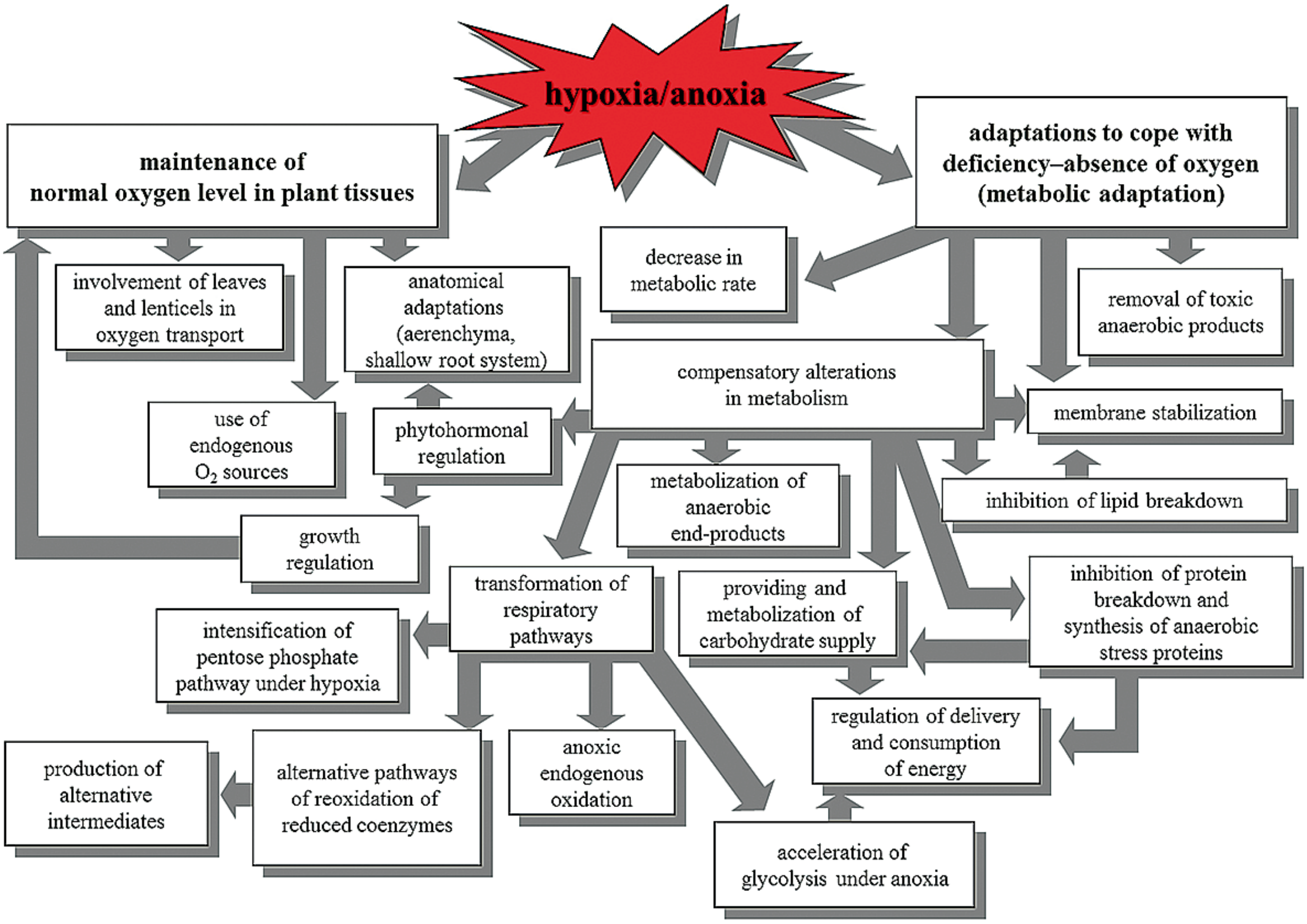

Fig. 4. Scheme of pathways of plant adaptation to oxygen deprivation (Chirkova, 1988a, b, 1998, with modification).

of toxic anaerobic products; antioxidative defence, etc. The choice of growth responses LOES or LOQS depends on the plant genotype and ambient circumstances, and is governed by ethylene interaction with other plant hormones. LOES is used as an adaptation to long-term flooding in aquatic and semiaquatic habitats by wetland species. LOQS is deployed to survive short-term complete submergence by other hypoxia-resistant plants. Quiescent syndrome ensures preservation of homeostasis and repair of changes upon return to normal aeration conditions. Switching from LOES to LOQS takes place when LOES is incapable of providing successive adaptation due to severe oxygen deficiency or depletion of adaptive capabilities (for non-resistant plants). The combination of different adaptation strategies ensures long-term plant survival in their flood-prone habitat. Non-resistant plants also have a certain set of protective reactions, which are poorly regulated and effective only for short-term adaptation to mild hypoxia. For resistant species the transition from one adaptive strategy to another occurs gradually and provides a longer-term maintenance of metabolism and survival.

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