SOIL REDOX POTENTIAL AND ITS IMPACT ON MICROORGANISMS AND PLANTS OF WETLANDS

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Abstract

Although peatlands cover only 3% of the Earth's surface, they constitute a huge reservoir of carbon. It is estimated that they accumulate one third of carbon contained in all types of soils worldwide. Therefore, knowledge of the physical, chemical, and biological properties of peat is important for prevention of peat degradation and release of carbon stored as CO_2 into the atmosphere. In organic soils, water plays a very important role as a protective factor against mineralisation of organic matter. Therefore, organic soils are characterised by high specificity and dissimilarity from mineral soils. The hydrological factor induces a variety of changes in the physical and chemical properties, e.g. low redox potential or low oxygen content in soil pores. Many soil processes are determined by the soil oxygenation status, which can be measured with various indicators as well as direct and indirect measurements. One of the indirect methods is measurement of the redox potential. The oxidation-reduction potential (redox potential or Eh) is a measure of the ratio of oxidised to reduced forms in a solution. This parameter is inextricably linked to oxygen supply and the processes of consumption thereof by microorganisms and plant roots. Therefore, the redox potential is used as an indicator of the oxygenation status and the content of biogenic forms and toxins in the soil environment and sediments. In the case of submerged soils, penetration of atmospheric oxygen into the soil is limited due to low rates of oxygen diffusion and, hence, low redox potential, which inhibits plant growth through inhibition of respiration and production of toxins in reducing conditions. The aim of this article is (1) to the show soil-plant-soil microorganism interactions taking place on peatbogs in the context of redox potential, (2) to investigate the responses of plants and soil microorganisms to the changing redox potential, and (3) to demonstrate the mechanisms of plant adaptation to the reducing conditions prevailing in peatbogs.

Keywords: redox potential, peatland, microbial communities, enzymatic activity.

INTRODUCTION

The soil oxygenation status determines many processes in the soil, e.g. the reaction of oxidation and reduction of soil mineral components, soil stability, active ion uptake by plant roots, and the composition of soil microorganism populations and their enzymatic activity. The soil oxygenation status can be assessed by direct measurements (determination of the composition of soil air, porosity and air permeability, as well as macro- and micro-diffusion) and by indirect methods (evaluation of hypoxia effects) [Gliński and Stępniewski 1985].

The indirect methods comprise redox potential, activity of oxidoreductase enzymes, soil respiration activity, and plant symptoms (yellowing of leaves, shallow roots). The oxidation-reduction potential (redox potential or Eh) is a measure of the degree of reduction of soil and the number of free electrons exchanged in redox reactions. It is expressed in millivolts or volts [Stępniewska et al. 2004, Stępniewski et al. 2005]. In practice, the redox potential is measured with a voltameter and platinum electrodes in conjunction with a reference electrode [Stępniewska et al. 2004]. The measured oxidation-reduction potential (usually

relative to a calomel electrode SCE) [Fiedler et al. 2007] corresponds to the electrochemical state of the soil/sediment and is associated with the most important soil properties and processes. These relationships were the subject of many studies. Many researchers investigated the relationship between the redox potential and the cycles of the major elements in the biosphere, such as C, H, O, N, P and trace elements [Kemmou et al. 2006]. DeLaune and Pezeshki [1991] explored the interactions between the distribution, productivity, and physiological state of bog plants and redox potential. In turn, Fenchel [2012] investigated this relationship in microorganisms and meiofauna. Researchers also studied the transport and transformation of hydrophobic pollutants, pesticides, and trace elements as well as radioisotopes in sediments in relation to the redox potential [Lindsay 1991, Gambrell 1994, Fernandez et al. 2009, Frohne et al. 2011]. The relationships between the redox potential and "chemical fossils" preserved in sediments provide information for investigations of diagenesis [Meyers and Ishiwatari 1993, Catallo et al. 1995]. The relationships between the redox potential and the functions of hydrogenic soils and taxonomy, surface water chemistry [Grenthe et al. 1992], ecotoxicology of soil microorganisms, and emission of greenhouse gases (CH_4, N_2O) [Włodarczyk 2000, Stępniewska et al. 2004, Szafranek-Nakonieczna and Stęniewska 2015] were investigated in peatbog areas.

The redox potential measured in peatbog areas reflects the relationships between hydrological factors (e.g. the length and frequency of waterlogging, desiccation periods), the microbial activity in soil, processes taking place in the rhizosphere, as well as the content of organic matter and biogens [Cogger and Kennedy 1992, Cogger et al. 1992]. Researchers have shown that soil desiccation and flooding and, hence, fluctuations of the redox potential are responsible for accelerated transformation of C and N, in comparison with soils characterised by static conditions (e.g. permanent waterlogging or desiccation) [Smith and Patrick 1983]. A strong correlation was also shown between the hydrology, the redox potential of biogenic sediments, and biogeochemical and ecological processes [Nyman and DeLaune 1991]. Changes in the redox potential and related changes in the properties of different types of sediments in environmental stress conditions (caused by anthropogenic and natural perturbations) have global importance for ecology [Coleman et al. 1992].

OXIDATION-REDUCTION POTENTIAL AND HYDROGENIC SOILS

Water is the main factor responsible for survival of vegetation and functioning of peatbogs. In excessively humid soils, availability of atmospheric oxygen is limited; therefore, various groups of obligatory and facultative microorganisms utilize oxidised compounds as electron acceptors in the respiratory chain transforming them into reduced forms and thereby contributing to reduction of the soil redox potential [De Mars and Wassen 1999, Fiedler and Sommer 2004, Greenway et al. 2006]. The reaction chain initiated on the surface of submerged soil involves physical, chemical, and biological processes. The physical processes are associated with limitation of diffusion of atmospheric gases into the soil, which leads to depletion of oxygen, an element required for biological and chemical processes, e.g. denitrification and reduction of iron, manganese, and sulphates, carried out by microorganisms and plant roots [Gambrell et al. 1991].

The redox potential in peat soils is used for determination of their reduction and redox capacity. The intensity of reduction is the critical Eh value at which the inorganic redox system is unstable. In turn, redox capacity is defined as the number of electrons accepted by oxidant compounds (e.g. oxygen, manganese, iron, sulphate), which accompany respiration of microorganisms responsible for organic matter decomposition [Von de Krammer 2000, Unger et al. 2008]. Oxidants can have substantial buffering capacity, therefore no sharp decline in Eh is observed in some peatbog soils, although their surface is waterlogged. The intensity of reduction determines the ease of reduction, while the redox capacity refers to the size of the redox system undergoing reduction, e.g. oxygen consumption in the root zone [DeLaune et al. 1991, Kludze and DeLaune 1995a, 1995b]. The relationship between the two parameters has been described with the equation [Mitsch and Gosselink 2007]:

$$Eh = E_0 + 2.3 \, [RT/nF] \, \log_e [Ox/Red]$$

where: E_0 – the electrode potential of the 50% oxidized system specific to that substance,
R – the gas constant,
T – the temperature (K),
n – the number of moles of electrons transferred,
F – the Faraday constant,

Ox/Red – the concentrations of the oxidized and reduced forms, respectively, of the substance under consideration,

The oxidation-reduction potential in soils oscillates in a wide range between -300 mV and 900 mV. In submerged soils, it is below 350/250 mV, while in well-oxygenated soils it reaches values exceeding 380/400 mV; different ranges have been reported by different researchers [Pezeshki 2001, Inglett et al. 2005, Yu et al. 2007]. In good oxygenation conditions, oxygen is the prime acceptor of electrons derived from organic matter decomposition and the O_2/H_2O pair determines the redox value. Soil hypoxia induced by e.g. long-term flooding or water-air imbalance results in oxygen depletion, in which case soil organisms utilise nitrogen- or manganese-bound oxygen, leading to reduction thereof. Consequently, each stage of reduction is associated with a respectively lower value of the redox potential [Stępniewska et al. 2004]. Kaurichev and Shishkova [1967] distinguished four main classes of soils in terms of oxidation-reduction conditions:

• well-aerated soils with Eh over 400 mV,
• moderately reduced soils with Eh ranging from 100 to 400 mV,
• reduced soils with Eh from -100 to 100 mV,
• highly reduced soils with Eh in the range from -100 to -300 mV.

Cultivated soils characterised by good aerobic conditions have a redox potential in the range from +300 to +500 mV [Bennicelli et al. 2006, Macías, Camps-Arbestain 2010].

Soil is a heterogeneous formation, in which aerobic conditions are accompanied by anaerobic conditions. The importance of the heterogeneity of soil aggregates in the context of the redox potential has long been investigated. For instance, the redox potential inside aggregates (with a 6–7 mm diameter) of wet soil may be by 100–200 mV lower than that on the surface of the aggregates [Sexstone et al. 1985].

EH-PH RELATIONSHIPS

The soil pH and redox potential are characterised by considerable temporal variability in a diurnal and seasonal cycle [Snakin et al. 2001, Mansfeldt 2003]. Sabiene and collaborators [2010] also reported interannual changes associated with climate change and soil moisture levels. Soil flooding dramatically changes both pH and the redox potential [Kashem and Singh 2001]. Balakhnina and co-workers [2010] reported a rapid decline in the redox potential from 542 mV to 70 mV taking place within a few hours after flooding.

The soil redox potential and pH determine soil carbon persistence, particularly in organic soil. The Eh-pH relationship can be graphically illustrated by diagrams introduced by Pourbaix. They are widely used in metallurgy, and Krumbein and Garrels [Chesworth 2004] were the first
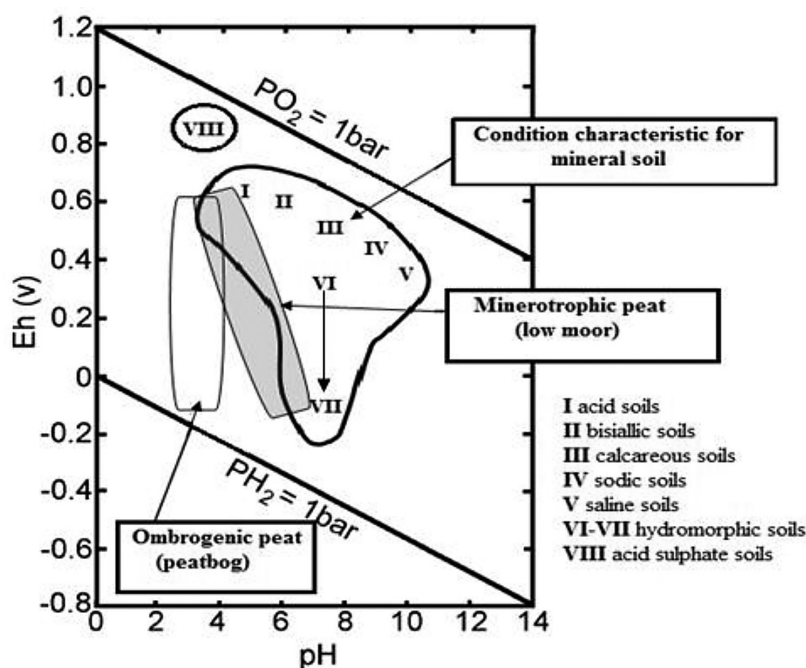

Figure 1. pH and Eh ranges in different types of soils and peats [modified after Chesworth 2004]

to apply them in Earth sciences. Figure 1 presents pH-Eh ranges that can be expected to characterise various soils and peats on the Earth's surface.

Figure 2 shows that organic matter is a component of the soil ecosystem with the highest susceptibility to reduction; it is also the largest source of electrons derived from the organic matter decomposition process and, hence, it can be regarded as an electron pump supplying parts of soil characterised by better aeration [Lovley et al.
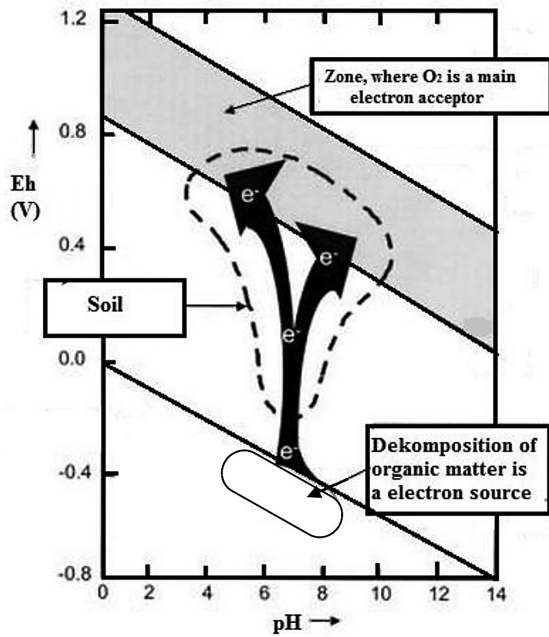

Figure 2. Organic matter as an electron source [modified after Chesworth 2004]

1998, Chadwick and Chorover 2001]. An increase in the content of soil organic matter causes a decrease in the oxidation-reduction potential in soil that is rich in easily degradable organic matter, degradation of which requires high oxygen levels [Lovley et al. 1998, Stottmeister et al. 2003]. However, Miller et al. [1991] reported that addition of fresh straw during the process of composting caused an increase in the oxidation-reduction potential from 0 mV (pH 7.7) at the beginning of the process to 300–400 mV at the end. This allows a conclusion that organic matter (its quality and quantity) has a substantial impact on soil Eh and exhibits buffering properties. Organic matter also buffers soil reaction [Reddy and DeLaune 2008]. At high pH values noted in bogs, organic matter takes part in acidification through formation of soluble complexes with such cations as Ca^{2+} or Mg^{2+}, thereby eliminating alkaline cations from soil [Brady and Weil 2010]. The soil oxidation-reduction potential and pH are the main factors that influence the rate and intensity of the humification process [Rusanov and Anilova 2009], which proceeds more slowly in anaerobic conditions. The decomposition rate is also determined by the metabolism of soil microorganisms and its efficiency and by the capacity of soil to provide electron acceptors.

Figure 3 presented above shows electron flow in the soil environment together with electron acceptors. It was drawn on the basis of redox reac-
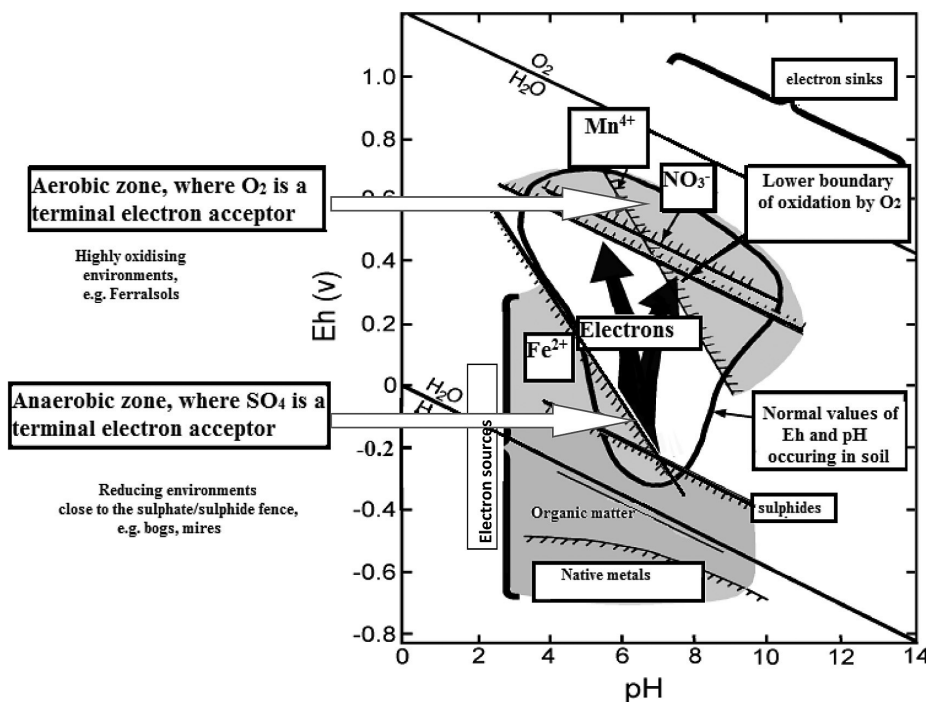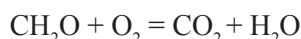

Figure 3. Electron flow between the donor and acceptor in soil [modified after Chesworth 2004]

tions that can take place in soil. The lower part of the diagram represents a portion of soil that is rich in organic matter, which is decomposed by microorganisms; this in turn ensures a wide range of Eh, even reaching the lower limit, where oxygen is an oxidant. In the absence of free oxygen, other electron acceptors will carry out decomposition of organic matter and production of CO_2. Below, we present the sequence of some redox reactions that may take place in the soil environment [Manahan 2001, Chesworth 2004].
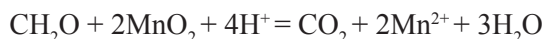
- Aerobic oxidation

$$CH_2O + O_2 = CO_2 + H_2O$$

- Denitrification

$$CH_2O + 0.8NO_3^- = CO_2 + 0.4N_2 + 1.4H_2O$$

- Manganese reduction

$$CH_2O + 2MnO_2 + 4H^+ = CO_2 + 2Mn^{2+} + 3H_2O$$

- Iron reduction

$$CH_2O + 2FeOOH + H^+ = CO_2 + 2Fe^{2+} + H_2O$$

- Sulphate reduction

$$CH_2O + 0.5SO_4^{2-} + 0.5H^+ = CO_2 + 0.5HS^- + H_2O$$

- Methane formation

$$CH_2O + 0.5CO_2 = CO_2 + 0.5CH_4$$
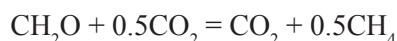
Under deficiency of molecular oxygen at Eh of ca. 400 mV, nitrates are reduced in the denitrification process. It occurs in the presence of oxygen bound in nitrates (V) and (III) at simultaneous maximum reduction of the molecular oxygen concentration and abundance of organic matter, which is an electron donor. The process is carried out by various heterotrophic bacteria characterised by varied denitrification capacity. Persistent reducing conditions are unfavourable due to the absence of sorption and leaching of NO_3^- from soil as well as loss of gaseous nitrogen (N_2, N_2O) [Bohrerova et al. 2004, Stępniewska et al. 2004].

Eh of 380 mV corresponds to reduction of manganese oxides to Mn^{2+}. The process of reduction of manganese oxides is performed by anaerobic microorganisms. The Eh value below 300 mV is related to reduction of iron oxides, which maintain the reduction processes for the longest time, i.e. to an Eh value of ca. 100 mV. An arbitrary limit of Eh = 300 mV between oxidised and reduced soils has been assumed. Iron oxides delay reduction of sulphates, which takes place at Eh of ca. -100 mV and leads to formation of H_2S. Hydrogen sulphide binds to heavy metals, forming insoluble sulphides (FeS, CuS, PbS, CdS) [Kogel-Knabner et al. 2010].

The redox potential below -150 mV indicates the appearance of gaseous hydrogen. Stępniewska and collaborators [2004] report that the Eh range from -150 mV to -220 mV is characteristic for methane formation as a result of methane fermentation. Also, N_2O emission is associated with the oxidation-reduction potential and soil reaction, as they have an impact on three important processes of N_2O and N_2 generation, i.e. nitrification, denitrification, and dissimilatory NO_3^- reduction to NH_4^+ [White and Reddy 2001, Simek and Cooper 2002].

OXIDATION-REDUCTION POTENTIAL AND SOIL MICROORGANISMS

The kinetics of the redox potential is regulated by catalytic enzymes produced by soil microorganisms [Fenchel et al. 2012]. The microbial activity is dependent on the soil reaction and oxidation-reduction potential [Falkowski et al. 2008] with an important role of the clay mineral content. Minerals serve a function of surface catalysts [Theng and Orchard 1995], as they retain organic matter [Wardle 1992] and contribute to emergence of microhabitats suitable for growth and development of soil microorganisms [Heijnen and van Veen 1991]. As early as in 1934, Heintze suggested including the variation of the redox potential for characterisation of microbial groups, since each type adapted to specific oxido-reducing conditions in either a wide or narrow Eh range. The role of the oxidation-reduction potential in determination of the availability of substrates in the soil environment and its essential role in regulation of the abundance and species diversity of microbial communities have been explored by many other authors [Lüdemann et al. 2000, Pett-Ridge and Firestone 2005, Hines 2006, Song et al. 2008]. For instance, aerobic bacteria such as *Actinomyces* sp. or *Azotobacter* sp. require high redox potential values for their growth [Rabotnova and Schwartz 1962]. In turn, fungi prefer weakly reducing conditions and exhibit the best development at Eh > 250 mV, whereas bacteria prevail in high strongly reducing conditions (Eh < 0 mV) [Seo and DeLaune 2010]. Considerable fluctuations of the redox potential can be the major factor determining the phylogeny and physiology of soil microorganisms, and changes in Eh can favour metabolism flexibility or mechanisms promoting growth in a wide range of Eh. Native soil bacteria (e.g. *Acti-*

nobacteria sp., *Micrococcus* sp., *Streptomycetes* sp., *Clostridium* sp.), which are highly specialised in the response to changing redox conditions, are a good example [Pett-Ridge and Firestone 2005]. Song et al. [2008] investigated the diversity of soil organisms associated with changes in the oxidation-reduction potential and found that the highest abundance (16% of the abundance of all soil microorganisms) in anaerobic conditions was shown by Gram-positive bacteria, which indicates their low sensitivity to oxygen, compared with other microbial groups. Furthermore, the researchers found a growing tendency (33%) in the abundance of these bacteria with increasing depth and a decline in the oxidation-reduction potential. Soil reaction has a substantial effect on the growth and composition of soil microorganisms. A majority of soil bacteria grow in the pH range of 4.5–10. The greatest microbial diversity is observed in soils with a neutral pH and the lowest in acidic soils [Hinsinger et al. 2009, Lauber et al. 2009].

Compared with other organisms, soil microorganisms exhibit greater capability of modifying the redox potential and pH of their environment to meet their requirements [Fierer and Jackson 2006]. Potter [1911] was probably the first researcher who emphasised the fact that soil microorganisms reduced the redox potential by utilising oxygen as an electron acceptor in the respiratory chain. It was also reported that an increase in soil moisture content led to a decrease in the redox potential through rapid consumption of oxygen by microorganisms, which created anaerobic conditions.

PLANT RESPONSE TO CHANGES IN EH

The redox potential is a factor that limits occurrence of plants that are able to grow at Eh in the range from 300 mV to 700 mV [Volk 1993]. Since normal root growth and function requires appropriate oxygen content (10% volume), root respiration at oxygen deficiency resembles alcohol fermentation [Dessaux et al. 2009]. Ethanol is accumulated in root tissues and ethylene, organic acids, and other metabolism-disrupting compounds are accumulated in the entire plant. In consequence, changes affecting roots (retarded growth and development) and the aerial plant organs (yellowing and wilting of leaves, drooping flowers) occur [Drew 1990, 1997].

Plants can change the oxido-reducing conditions and reaction in the root zone [Hartmann et al. 2009]. The plant adaptation mechanisms comprise morphological and functional adaptations as well as production of shallow roots [Lambers et al. 2008]. Morphological adaptations of roots involve adapting to strong reducing conditions by accumulation of air and oxygen in intracellular spaces [Flessa and Fischer 1992]. Mire plants are capable of raising the redox potential in their rhizosphere through transport of oxygen from the atmosphere along the entire plant to the aerenchyma [Gliński and Stępniewski 1985; Evans 2004]. This protects them against high concentrations of such toxins as reduced iron and manganese forms, ethanol, lactic acid, acetaldehyde, formic acid, acetic acid, butyric acid, and cyanide compounds [Vartapetian and Jackson 1997, Chestworth 2004,].

The aerenchyma plays a key role in methane transport from the plant to the atmosphere [Thomas et al. 1996, Kuzyakov and Domanski 2000]. The mean rate of methane emission by bog plants is estimated at approximately 940 mg CH_4/m^2/day [Yavitt and Knapp 1995, Yu 2012] and 826 mg in the case of paddy fields. Banker et al. [1995] estimated that over 95% of methane emitted from paddy fields was released into the atmosphere through plants. In turn, Thomas et al. [1996] found that helophytes were responsible for 50-90% of total methane emissions from peatlands. Investigations conducted by Stottmeister et al. [2003] showed that the rate of oxygen transport from the plant into the atmosphere was the greatest in the range -250 mV < Eh < -150 mV, and *Typha latifolia* was considerably more efficient in oxygen transport into the rhizosphere than *Juncus effusus*. Both species provide the rhizosphere with oxygen even when the oxidation-reduction potential has positive values. It has long been known that gas exchange occurs in a small part of the root system, primarily through the root tip and lateral roots.

Functional adaptation involves adaptation of the activity of released enzymes to anaerobiosis and activation of alternative metabolic pathways leading to production of less toxic products (e.g. malic acid, lactic acid) in order to remove the accumulated ethanol [McKersie and Leshem 1994]. Adaptation to oxygen deficiency is reflected in production of shallow roots of plants, which makes the route of oxygen to plant roots shorter and easier [Gliński and Stępniewski 1985].

Peatland vegetation growing in anaerobic conditions has also evolved metabolic adaptations, which facilitate survival in the adverse reducing conditions. The roots of mire plants have a limited supply of oxygen, as they are covered by a thin layer of water, which is characterised by a 30 000-fold lower diffusion coefficient than that of the air and serves as a barrier to gas transport [Stępniewska et al. 2004]. In oxidative stress conditions, roots replace aerobic (mitochondrial) respiration with fermentation processes, which involve conversion of pyruvate to ethanol (through the activity of alcohol dehydrogenase ADH) or to lactate through the activity of lactate dehydrogenase (LDH) [Hopkins and Huner 2009].

Increased ADH activity implies oxygen deficit [Crawford 1992] in both flooding-tolerant and -sensitive plants [Kennedy et al. 1992, Kogawara et al. 2006]. In flooding-tolerant plants, the role of ADH involves changing the pH inside cells by acidification of the cytoplasm by the products of anaerobic respiration (e.g. lactate), which has an impact on cell metabolism by reducing the activity of enzymes whose optimum activity is noted at pH close to 7. Due to anaerobic respiration, ADH activity is inversely proportional to the soil oxidation-reduction potential [Reddy and DeLaune 2008].

Anaerobic respiration is an inefficient method for energy production, since only two moles of ATP are produced by one molecule of glucose, whereas in aerobic respiration each molecule of glucose yields 36-38 moles of ATP. Hence, in flooding conditions, many plants exhibit energy deficiency resulting in impaired water and nutrient uptake, disturbed transport inside the plant and, hence, insufficient CO_2 uptake for photosynthesis. Changes in metabolism lead to inhibition of plant growth. However, many plants grow in anaerobic conditions. They utilise stored carbohydrates for production of ATP; therefore, carbohydrates contribute to plant survival in the condition of low redox potential of soil [MacDonald and Kimmerer 1993].

In reducing conditions, nutrient uptake is impaired due to dysfunction of roots and even their death [DeLaune et al. 1998, 1999, Kogawara 2006], phytohormonal imbalance caused by a decline in the levels of gibberellins and cytokinins and an increase in the abscisic acid and ethylene levels [Jackson 2002, Dat et al. 2004, Hattori et al. 2009]. During prolonged waterlogging when the redox potential and pH further decrease, the availability of zinc increases, leading to elevated levels of this element in plant tissues; this is accompanied by reduction of iron and manganese. The concentration of these elements is higher in plants growing in anaerobic rather than aerobic conditions [Gries et al. 1990].

Plants exhibit varied tolerance to changing oxidation-reduction conditions and soil reaction. Investigations carried out by Dwire and collaborators [2006] indicate that plant biodiversity is closely related to the hydrological gradient and the soil redox potential of bog areas. A similar close correlation was observed between various plant communities and Eh in renaturalised wetlands. Five-year-old trees growing at an Eh range from 400 to 450 mV were characterised by higher survival rates and were higher than trees from areas with an Eh ranging from 250 to 380 mV. These investigations suggest that natural plant communities can be used for characterisation of oxygen conditions in wetland soils [Pennington and Walters 2006].

The redox potential is of fundamental importance for agriculture, as it exerts an impact on crop yields. Annual yields of sugarcane were reported to decrease by 0.2–0.3 t/ha per day at Eh decreasing below 332 mV [Carter 1980]. The highest rice yields in acidic sulphate soils were noted when jarosite (aqueous ferrous or potassium sulphate) increasing local Eh to ca. 400 mV formed around rice roots.
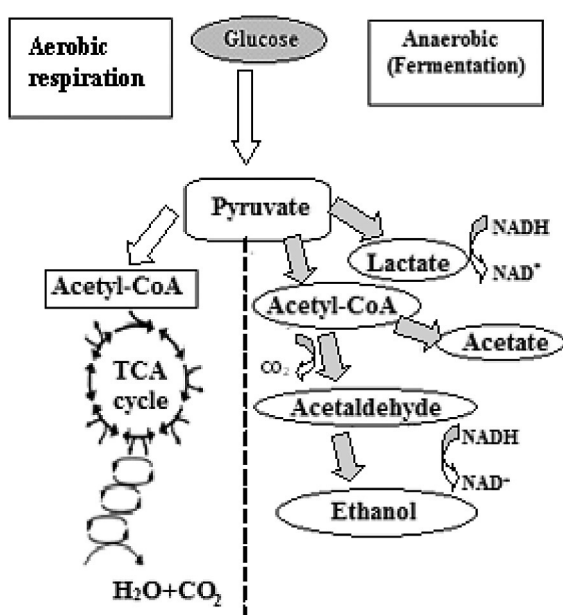

Figure 4. Metabolic pathways in aerobic and anaerobic conditions [modified after Reddy and DeLaune 2008]

CONCLUSIONS

Still, the relationship between soil Eh and plant response to changing redox conditions in peatland areas is poorly known. From the physiological and environmental point of view, the redox potential provides information about the presence and form of chemical compounds that are important for plant growth. For example, soil Eh of 0 mV indicates depletion of oxygen and nitrates as well as availability of iron and manganese forms as electron acceptors. The redox potential of +400 mV shows that in these conditions oxygen is still present in the environment despite the strong hydration of soil [DeLaune et al. 1998].

Plants inhabiting wetlands have adapted to the low Eh level by evolving a number of metabolic, physiological, and functional adaptation traits. The response of these plants depends on a number of factors such as plant species, the duration and frequency of flooding, the degree of soil reduction, and its buffering capacity. Reducing conditions of sediment/soil are the major factor in the peatland ecosystem responsible for plant survival, growth, development, and productivity. Plant survival in reducing conditions largely depends on the efficiency of the mechanisms of adaptation to low Eh. However, many plants with considerable tolerance to flooding are not able to survive in such conditions, because oxygen deficiency is not the only effect of low Eh; a greater threat is posed by highly phytotoxic compounds produced in the fermentation process. Therefore, reducing conditions affect the most fundamental plant processes such as gas exchange, water relations, photosynthesis, phytohormonal balance, nutrient uptake, growth, and biomass production.

Therefore, the knowledge of the nature of peatlands and wetlands requires understanding of the processes that take place in aerobic and anaerobic conditions, and the redox potential is a good indicator of the sediment/soil condition.

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