ANAEROBIC SOILS

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Anaerobic soils occur in areas where oxygen consumption by soil biota exceeds the diffusion of oxygen into the soil profile. This condition is also termed 'soil anaerobiosis' and results in a predominantly oxygen-free environment in the soil profile. Anaerobic soils occur in a number of environments in the landscape, including: wetlands; paddy soils; organic soils; poorly drained, heavy textured soils; areas with a high water table; soils amended with heavy rates of organic materials such as animal wastes, biosolids, and composts; and soils treated with ammoniacal fertilizers.

In upland environments, anaerobic soil conditions may be temporary and may not last more than a few days; while, in wetland environments, soil anaerobic conditions last for several months. Thus anaerobic soils include: all types of wetland soils (swamps, marshes, floodplains, coastal wetlands, and bottomland hardwood forests), hydric soils, paddy soils, organic soils, and any other waterlogged or flooded soils. Because much of our knowledge of anaerobic soils has been gained through research in wetlands and rice paddies, the discussion in this paper will largely focus on the morphological and biogeochemical features of these types of soils.

Wetland soils are widely distributed throughout the world and can be found in all climates, ranging from the tropics to tundra, with the exception of Antarctica. Approximately 6% of the Earth's land surface, which equals approximately 800 million hectares (approx. 2 billion acres) is covered by wetlands. The USA alone contains approximately 12% of the world's wetlands, or approximately 111 million hectares (274 million acres). In any given landscape, wetlands are located in areas with a low elevation and a high water table. Wetlands can be broadly defined as marshes, swamps, bogs, and similar areas. These areas are poorly drained and retain water during rainy periods. Thus, the physical, chemical, and biological characteristics of anaerobic soils are important in determining the properties and functioning of wetlands.

The creation of anaerobic soil conditions is predicated in the situation where demand exceeds the supply of oxygen. Once a soil becomes saturated, the supply of oxygen is immediately reduced owing to the displacement of oxygen contained in the available pore space. Following consumption of the relatively small amount of available oxygen in the pore water, oxygen can only be supplied to respiring organisms through the process of diffusion from the nearest aerobic zone. This process is comparatively slow under saturated soil conditions as oxygen diffusion in water is approximately 10 000 times slower than through air. Under these conditions, even moderate rates of soil or root respiration can quickly deplete available oxygen and result in anaerobic soil conditions.

Depending on hydrologic conditions, wetland soils can be present: (1) flooded, with defined water depth above the soil surface; (2) under saturated soil conditions, with no excess floodwater; and (3) when the water table lies below the soil surface at a certain depth, depending on soil characteristics. Under the first two conditions, wetland soils can be classified as hydric soils, while the third group can mimic the characteristics of both wet- and upland soils, depending on soil type and hydrologic conditions. Soil taxonomy classifies soils with these characteristics into a suborder 'aquic,' which implies that soil pores are filled with water (from soil surface to a depth of 2 m), and many of the oxidized compounds are enzymatically reduced, with end products of these reductive processes accumulating in the soil. Soil taxonomists classify aquic soils according to soil color and not the accumulation of reduced products. Gray colors or low chroma (2) are used generally as indicators of soil anaerobiosis.

Physical Characteristics

Soil volume primarily comprises solid matter, water, and air. When soils are flooded, most of their pore volume is occupied by water. Upland mineral soils generally consist of about 50% by volume of solids, 25% of water, and 25% of air. In wet mineral soils, approximately 50% of the soil volume is solids, while the remaining 50% is occupied by water. In wetland organic soils, a large proportion (up to 80%) of soil volume is occupied by water, with soil organic matter and mineral matter occupying less than 20%.

Generally, reduced compounds are not found in upland soils. Gaseous exchange is not restricted because of continuation of air spaces in upland soils, and oxygen dominates the respiratory and chemical environment. Gaseous composition of soil pores is approximately 10–21% O_2, 0.03–1% CO_2, and trace amounts of N_2O and NH_3. In wetland soils, there is less oxygen, because soil pores are filled with water. In the absence of oxygen, reduced

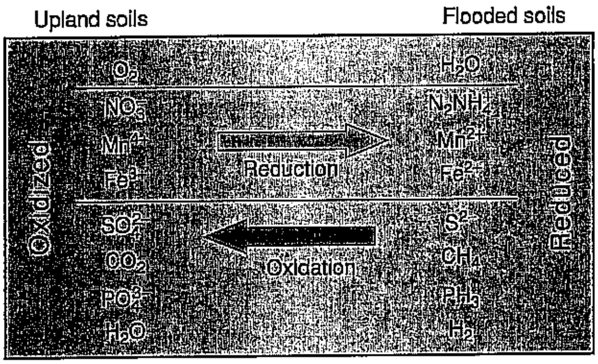

Figure 1 Various inorganic oxidized and reduced compounds in upland and wetland soils.

chemical forms predominate and are regulated by associated biogeochemical processes (**Figure 1**). In recently flooded soils, N_2O can be present as a result of denitrification of nitrate nitrogen (NO_3-N). In moderately reduced soils, H_2S can be observed, followed by CH_4 under more reducing conditions. In highly reduced soils, C_2H_4 and PH_3 (phosphine) can be observed. However, the presence and accumulation of these gases depend on respective oxidants available for reduction.

Biological Characteristics

Saturated soil conditions support microbial populations adapted to anaerobic environments. Aerobic microbial populations are restricted to zones where O_2 is available. Most of the aerobic organisms become quiescent or die, and new inhabitants, largely facultative (organisms which can function under both aerobic and anaerobic environments) and obligate anaerobic bacteria, take over.

Fungi, which are active in upland environment, are inhibited in the anaerobic wetland soil environment. This is primarily due to absence of O_2 and alteration in soil pH (acid to neutral) under anaerobic conditions. Similarly, microbial biomass decreases under saturated soil conditions. This decrease in microbial activity is primarily due to the shift from aerobic to anaerobic respiration. Thus, under wetland soil conditions, rates of many microbially mediated reactions decline, and some reactions may be eliminated and replaced by new ones.

Saturated soil conditions can support the growth of microphytic communities, including a variety of planktonic, epiphytic, and benthic algae at the soil–floodwater interface. The species composition varies with physicochemical conditions within the wetland. Many of the species in these microbial assemblages have the capacity to carry out photosynthesis. Diel fluctuations in dissolved O_2 produced as a consequence of photosynthesis often increase the O_2 levels in the floodwater beyond saturation levels during daytime and to low levels during nighttime. These large fluctuations in available oxygen have special significance in wetlands for regulating biogeochemical cycles of nutrients.

Wetland or anaerobic soil conditions also support the presence of hydrophytic vegetation, or plants that are adapted to the reducing wetland environment. These plants have unique characteristics to adapt to oxygen-deficient conditions, including physiological adaptations (such as capability to respire anaerobically), anatomical adaptations (such as development of intercellular air spaces), and morphological adaptations (such as water roots and adventitious roots). With these adaptations, hydrophytic plants are able to survive under reducing conditions considered toxic to other macrophytes. In many cases, adapted plant communities become the dominant source of organic matter in wetland systems.

Chemical Characteristics

When oxygen availability becomes limited, bacteria must utilize other compounds as electron acceptors to maintain their metabolism. These compounds, many of which are nutrient elements, can exist in both dissolved and solid phases, and include oxidized forms of elements such as N, Fe, Mn, and S. As they are utilized during respiration, these elements gain electrons and thus become chemically reduced. The result of microbial metabolism therefore is the conversion of oxidized elements to the corresponding reduced form under anaerobic conditions. When wetland soils are drained, many of the reduced compounds are oxidized either by chemical or biochemical reactions. Therefore, in upland and/or drained soils, oxidized forms of chemical species dominate the system, while reduced forms dominate the wet soil system (**Figure 1**).

Reduction–oxidation, or redox potential (E_h), reflects the intensity of reduction *or* a measure of electron (e^-) activity analogous to pH (which measures H^+ activity). Depending on soil characteristics, E_h generally decreases with time and approaches a steady value after flooding. Redox potential is the most common parameter used to measure degree of soil wetness or intensity of soil anaerobic conditions. The range of E_h values observed in wetland soils is from +700 to −300 mV (**Figure 2**). Negative values represent high electron activity and intense anaerobic conditions typical of permanently waterlogged soils. Positive values represent low electron activity and aerobic to moderately anaerobic conditions typical of wetlands in transition zone. Soils with

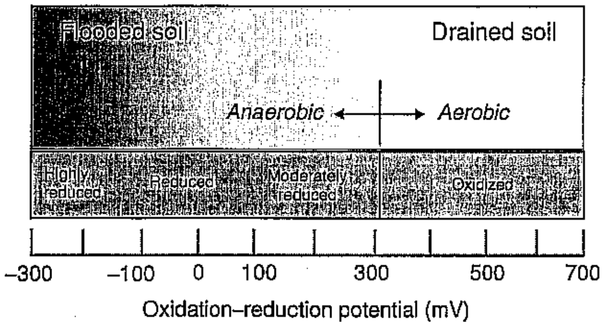

Figure 2 Schematic showing relationship between oxidation–reduction potential and oxidized and reduced conditions in wetland soils.

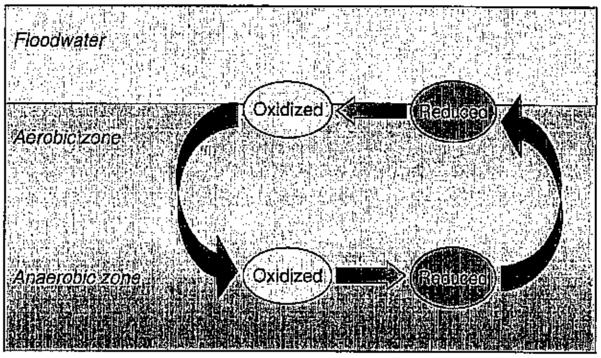

Figure 3 Diffusional patterns of reduced and oxidized compounds in response to anaerobic gradients in flooded soils.

$E_h > 300$ mV are considered aerobic or upland. Under these conditions, oxygen is used as the dominant electron acceptor. Soils with $E_h < 300$ mV are considered anaerobic or wetland.

The chemical nature of the reduction process also affects soil pH, electrical conductivity, cation exchange capacity, and sorption and desorption processes. In general, saturated soil conditions result in an increase in pH, electrical conductivity, and ionic strength, but a decrease in soil redox potential. The pH of most soils tends to approach the neutral point under flooded conditions, with acid soils increasing and alkaline soils decreasing in pH. Increase in pH of acid soils depends on the activities of oxidants (such as NO_3^-, Fe^{3+}, Mn^{2+}, and SO_4^{2-}) and proton consumption during reduction of these oxidants under flooded conditions. In alkaline soils, pH is controlled (and generally lowered) by the accumulation of dissolved CO_2 and organic acids.

Accumulation of reduced compounds in the anaerobic soil layer results in the establishment of concentration gradients across the aerobic–anaerobic interface. The concentration of reduced compounds is usually higher in the anaerobic layer, which results in upward diffusion into aerobic soil or floodwater, where they are oxidized (Figure 3). Similarly, some of the dissolved, oxidized compounds diffuse downward, i.e., from floodwater or aerobic soil layer into underlying anaerobic soil layer, where they will be reduced. The exchange rates between soil and overlying water determine whether the wetlands soils or sediments are functioning as a sink or source for nutrients. The rate of exchange of dissolved species depends upon: (1) concentration of dissolved species in soil pore water; (2) soil type and other related physicochemical properties (pH, cation exchange capacity, organic matter content, and bulk density); (3) concentration of dissolved species in the floodwater; and (4) kinetics of related biogeochemical processes in soil and floodwater.

Morphological Characteristics of Wetland Soils

Wetland protection now requires identification of the boundaries between uplands and wetlands. Criteria based on hydrology, vegetation, and soils are individually or together used to determine these boundaries. Among these three components, soils assessment is particularly critical because, while vegetation and hydrology are temporally affected by climatic fluctuations, soils are the most stable and respond only to long-term inundation. The term 'hydric soils' is now commonly used in jurisdictional language synonymous with wetland soils. Hydric soils are defined as soils formed under conditions of saturation, flooding, or ponding long enough during the growing season to develop anaerobic conditions in the upper part of the soil profile.

Saturated soils develop several unique morphological characteristics as a result of several oxidation–reduction reactions. These features are now used as soil indicators to evaluate independently wetland boundaries. Some of the key hydric soil indicators are formed by the accumulation or loss of iron and manganese, hydrogen sulfide, or accumulation of organic matter. In many cases, soil color is used to assess both the accumulation of organic matter (dark horizons) and the reduction of iron species (formation of gray or gley colors).

Biogeochemical Characteristics

Microbial communities in anaerobic soils play a key role in regulating a number of essential biogeochemical cycles such as carbon, nitrogen, phosphorus, and sulfur. Organic matter released by the primary producers is degraded by microbial communities, releasing nutrients back into the environment. Degradation of organic materials allows heterotrophic microbial groups to obtain energy and nutrients

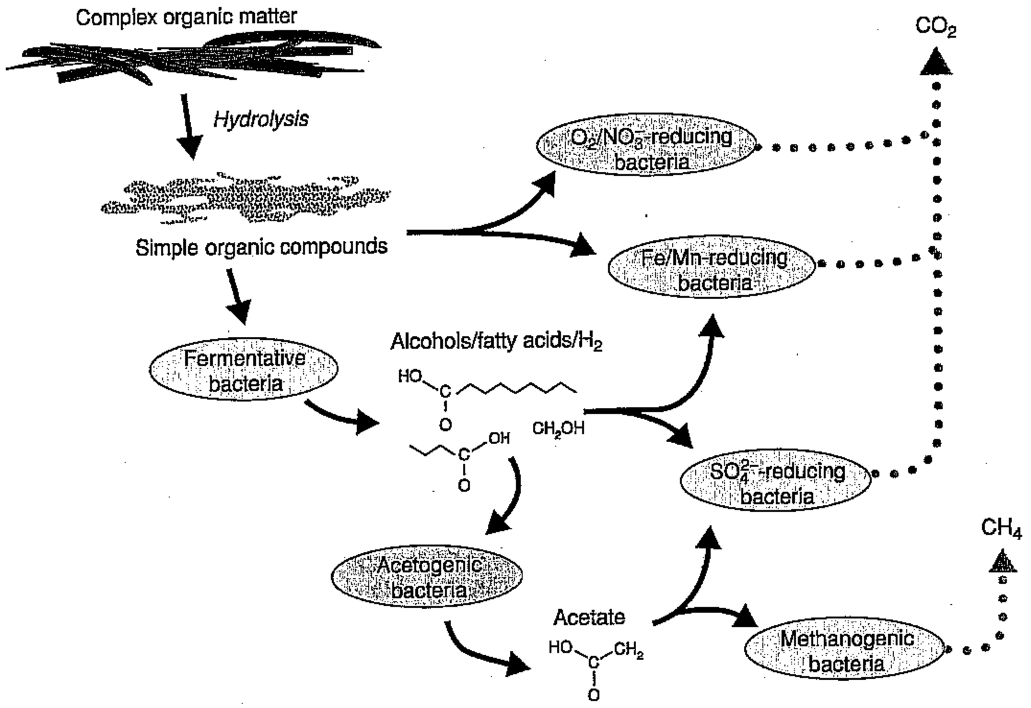

Figure 4 Pathways of organic matter decomposition in wetland soils.

for growth. Enzymatic hydrolysis of organic matter produces several monomers, including glucose, xylose, fatty acids, and amino acids. These simple reduced compounds then serve as substrates for microbial metabolism as chemical energy is released during their oxidation.

Anaerobic decomposition of organic matter is more complex and less energetically favorable than aerobic decomposition. It is mediated by a complex group of physiologically different microorganisms which participate in the decomposition pathways (**Figure 4**). Often, the end product of one metabolism is substrate for the next until the decomposition is complete. Initially, fermenting bacteria mediate the extracellular hydrolysis of high-molecular-weight polymers (i.e., proteins, polysaccharides, lipids, and nucleic acids) and ferment their respective monomers (e.g., amino acids, sugars, fatty acids, and nucleotides) to CO_2, H_2, acetate, propionate, butyrate, and other fatty acids and alcohols.

Microbial Respiration

Oxygen, if present in wetland soils, provides an electron acceptor (oxidant) for supporting microbial oxidation of reduced carbon compounds (respiration). Thermodynamically, oxygen is the most preferred electron acceptor by microorganisms (Table 1), and as a result, aerobic microorganisms maintain a competitive advantage while oxygen is present. Oxygen is used preferentially because it receives electrons from the reductant material (organic matter) more readily than do other oxidants. The greater energy yield during the aerobic process is due to: (1) complete oxidation of carbon atoms in the organic substrates to CO_2, and (2) the oxygen redox couple having a relatively high, positive reduction potential. This leads to a large net difference in electrical potentials between electron donor (organic substrate) and terminal electron acceptor (oxygen).

Once oxygen is depleted in the soil, bacteria must respire anaerobically. Under these conditions, bacteria capable of utilizing the electron acceptor with the next-highest thermodynamic potential dominate. Thus, the microbial use of electron acceptors proceeds in a sequential manner dependent on their electron affinity, energy yield, and related enzyme systems in the bacteria. In this manner, the order of electron acceptor use following oxygen depletion is: NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-} and finally CO_2 (**Figure 5**, Table 2). Anaerobic respiration is typically reflected in vertical profiles of these electron acceptors, with soil and/or sediment depth, as the most favorable electron acceptors are utilized first. However, the exclusion of less-favorable respiration pathways is not complete, resulting in considerable overlap between the different forms of organic carbon mineralization. The rate at which electron acceptors are consumed in soil systems depends on their concentration, the availability of organic compounds, and the activity of the microbial population involved in the reductive processes.

Table 1 Microbial groups involved in various redox reactions in wetland soils

Redox potential (mV)	*Electron acceptor*	*Decomposition end products*	*Microbial groups*
Aerobic			
>300	O_2	CO_2, H_2O	Aerobic fungi and bacteria
Fermenting			
less than −100 to +300	Organics	Organic acids, CO_2, H_2, alcohols, amino acids	Fermenting bacteria
Facultative anaerobic			
100–300	NO_3^- Mn^{4+} Fe^{3+}	N_2O, N_2, CO_2, H_2O Mn^{2+}, CO_2, H_2O Fe^{2+}, CO_2, H_2O	Denitrifying bacteria Mn(IV) reducers Fe(III) reducers
Obligate anaerobic			
less than −100	SO_4^{2-} CO_2 and acetate Organic acids	HS^-, CO_2, H_2O CH_4, CO_2, H_2O Acetate, CO_2, H_2	Sulfate reducers Methanogens H_2-producing bacteria

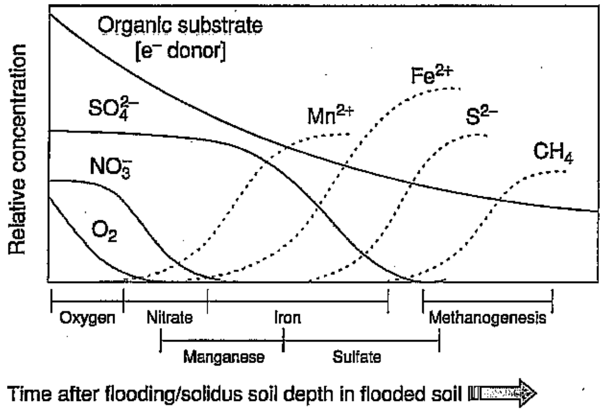

Figure 5 Sequential reduction of oxidants (oxidized compounds) and accumulation of reductants (reduced compounds) in wetland soils.

Nitrate reduction can occur in wetlands according to two major pathways:

- Dissimilatory nitrate reduction to ammonia (DNRA):

$$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+$$

- Denitrification:

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$$

Dissimilatory reduction of NO_3^- is performed by a variety of facultative anaerobic bacteria. During this process, NO_3^- is first converted to nitrite NO_2^-, which may be further reduced to NH_4^+. Reduced NH_4^+ produced through dissimilatory NO_3^- reduction results in high NH_4^+ levels characteristic of wetland soils and sediments. Denitrifiers are heterotrophic bacteria (most of them facultative anaerobic) that couple the oxidation of organic substrates to the reduction of NO_3^- to either N_2O or N_2. This reaction occurs in moderately reduced conditions in the absence of oxygen and is one of the dominant mechanisms for removal of nitrogen from aquatic systems.

The oxidation and reduction of iron in many soils is possibly one of the main components of soil formation. Its relatively ubiquitous presence in soils and sediments makes this respiratory pathway a major contributor of organic-matter mineralization. A large variety of microorganisms are capable of reducing iron, including fungi. When Fe(III) is reduced, Fe(II) is the reduced end product. For Mn, Mn(II) is generally accepted as the end product of Mn(IV) reduction; however, Mn(III) may also be encountered as an intermediate species.

In the general Fe(III) and Mn(IV) reduction model, complex organic matter is hydrolyzed to smaller components (i.e., sugars, amino acids, fatty acids). The sugars and amino acids are metabolized by fermentative microorganisms, which may reduce a small amount of Fe(III) or Mn(IV) in the process. The majority of the primary products from this first stage of the metabolism of sugars and amino acids are short-chain fatty acids and possibly hydrogen. This hydrogen can then be oxidized by Fe(III) and Mn(IV) reducers (e.g., *Pseudomonas* sp.), while other fermentation products are oxidized through Fe(III) or Mn(IV) reduction by species such as *Shewanella putrefaciens*. Alternatively, *Thiobacillus thiooxidans* or *T. ferrooxidans* can reduce Fe(III) or Mn(IV), with elemental sulfur S^0 as the electron donor.

Sulfate reducers are obligate anaerobes that couple oxidation of organic substrates to CO_2 with the reduction of terminal electron acceptor SO_4^{2-} to sulfides ($-S^{2-}$). Gram-negative bacteria such as *Desulfobacterium*, *Desulfobulbus*, and *Desulfotomaculum* are the most common types of sulfate-reducing bacteria in freshwater sediments. Sulfate-reducing bacteria cannot

Table 2 Summary reactions for microbial respiration pathways in wetland soils

Electron acceptor	*Reaction coupled to glucose oxidation*	ΔG_f^o *(kJ mol^{-1})*
O_2	$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$	−2879
NO_3^-	$5C_6H_{12}O_6 + 24NO_3^- + 24H^+ \rightarrow 30CO_2 + 12N_2 + 42H_2O$	−2713
MnO_2	$C_6H_{12}O_6 + 12MnO_2 = 6CO_2 + 12M_n^{2+} + 18H_2O$	−1916
$Fe(OH)_3$	$C_6H_{12}O_6 + 24Fe(OH)_3 + 48H^+ = 6CO_2 + 24Fe^{2+} + 66H_2O$	−418
SO_4^{2-}	$C_6H_{12}O_6 + 4H_2O \rightarrow 2CH_3COO^- + 2HCO_3^- + 4H_2 + 4H^+$	−207
	$CH_3COO^- + SO_4^{2-} + 3H^+ = 2CO_2 + H_2S + 2H_2O$	−63
CO_2	$C_6H_{12}O_6 + 4H_2O \rightarrow 2CH_3COO^- + 2HCO_3^- + 4H_2 + 4H^+$	−207
	$2CH_3COO^- + 2H_2O \rightarrow 2CH_4 + 2HCO_3^-$	−31

synthesize enzymes to hydrolyze polymers such as polysaccharides. Also, many groups of sulfate-reducing bacteria cannot use monomers such as monosaccharides (e.g., glucose) as substrates for energy, and thus sulfate reducers are dependent on fermenting bacteria to produce simple organic compounds (e.g., acetate, propionate).

Sulfate reducers are widely studied groups of microorganisms with special significance in coastal wetland ecosystems due to the high concentration of sulfate in seawater. Sulfate reduction can occur over a wide range of pH, temperature, and salinity. One product of sulfate reduction, hydrogen sulfide, is extremely toxic to aerobic organisms, because it reacts with the heavy metal groups of the cytochrome system. Hydrogen sulfide is very reactive with metals and usually results in the precipitation of metallic sulfides (e.g., FeS).

The terminal step in the anaerobic degradation of organic macromolecules, in the absence of all other electron acceptors, is the conversion of acetate and H_2/CO_2 to methane. This is an intricate process involving a net of interactions, possibly encompassing the largest set of microbial dependencies. Methanogens are obligate anaerobes that grow autotrophically (they use CO_2 as C source and as electron acceptor) and heterotrophically (they use organic substrates as energy source).

Like sulfate reducers, methanogens cannot directly utilize large-molecular-weight polymers; so methanogens must depend on at least three groups of microbes, including hydrolytic, fermentative, and H_2-producing acetogenic bacteria. Methanogens are typically found in the archaeal families of Methanobacteriaceae, Methanomicrobiaceae, Methanosaeteaceae, and Methanosarcinaceae.

Fermentation pathways vary depending on the original substrate, and quantity and presence of alternate electron acceptors. Denitrification, and Fe(III) and Mn(IV) reduction may utilize any of these fermentation products as the final step in respiration. Acetate and H_2, and other small organic acids are utilized directly by sulfate-reducing bacteria, while methanogens can only use acetate and H_2. Acetogenic bacteria cleave organic acids and alcohols into acetate, H_2, and CO_2. This conversion is only possible in the presence of sulfate-reducing bacteria or methanogens that consume H_2, resulting in low hydrogen concentrations, ensuring that acetogenesis is thermodynamically favorable.

Agronomic, Ecologic, and Environmental Significance

Anaerobic soils occupy an important niche in the biosphere, and their importance in wetlands and paddy soils is widely recognized by scientists, environmental managers, and policy-makers. Agronomically, anaerobic soils commonly known as paddy soils are widely used throughout the world for rice production. Anaerobic soils in wetlands are primary drivers of natural ecosystem function, as many of the biogeochemical processes have important feedback to ecosystem productivity and function.

Anaerobic soils are primary nutrient sources to plants grown in the paddy soils or wetlands. The decomposition process described here results in production of bioavailable nitrogen and phosphorus, which supports the productivity of plants. Furthermore, the extent of Fe(III) and/or Mn(IV) reduction can strongly influence the distribution of toxic trace metals and availability of P.

Environmentally, anaerobic soils may have both positive and negative attributes. One negative aspect is that wetlands are one of the primary sources of methane, a potent greenhouse gas. Approximately 25% of methane emitted to the atmosphere is derived from wetlands. Alternatively, anaerobic soils in wetlands also function as sinks, sources, transformers of nutrients and contaminants, and their role in improving water quality is widely recognized. This function of anaerobic soils has resulted in developing low-cost constructed wetland technology for water treatment. At present several thousands of such wetlands are in operation throughout the world.

See also: **Carbon Cycle in Soils:** Dynamics and Management; **Hydric Soils; Microbial Processes:** Environmental Factors; **Nitrogen in Soils:** Cycle; **Organic Soils; Paddy Soils; Sulfur in Soils:** Overview; **Wetlands, Naturally Occurring**

Further Reading

Cowardin LM, Carter V, Golet FC, and LaRoe ET (1979) *Classification of Wetlands and Deepwater Habitats of the United States.* Fish and Wildlife Service, US Department of Interior. Washington, DC: US Government Printing Office.

Federal Register, Notice (1994) *Changes in Hydric Soils of the United States.* Federal Register, vol. 59. Washington, DC: US Government Printing Office.

Federal Register, Notice (1995) *Hydric Soils of the United States.* Federal Register, vol. 60. Washington, DC: US Government Printing Office.

Holmer M and Storkholm P (2001) Sulphate reduction and sulphur cycling in lake sediments: a review. *Freshwater Biology* 46: 431–455.

Lovley DR (1991) Dissimilatory Fe(III) and Mn(IV) reduction. *Microbiological Reviews* 55(2): 259–287.

National Technical Committee for Hydric Soils (1991) *Hydric Soils of the United States.* USDA–SCS Miscellaneous Publication 1491. Washington DC: USDA–SCS.

Ponnamperuma FN (1972) The chemistry of submerged soils. *Advances in Agronomy* 24: 29–96.

Reddy KR and D'Angelo EM (1994) Soil processes regulating water quality in wetlands. In: Mitsch W (ed.) *Global Wetlands – Old World and New,* pp. 309–324. New York: Elsevier.

Reddy KR, D'Angelo EM, and Harris WG (2000) Biogeochemistry of wetlands. In: Sumner ME (ed.) *Handbook of Soil Science,* pp. G89–G119. Boca Raton, FL: CRC Press.

Schwertmann U (1993) Relations between iron oxides, soil color, and soil formation. In: Bigham JW and Crolkosz EJ (eds) *Soil Color,* pp. 51–70. Madison, WI: Soil Science Society of America.

US Department of Agriculture, Natural Resource Conservation Service (1998) *Field Indicators of Hydric Soils in the United States.* version 4.0. Ft. Worth, TX: USDA–NRCS.

Vepraskas MJ (1992) *Redoximorphic Features for Identifying Aquic Conditions.* Technical Bulletin 301, North Carolina Agricultural Research Service. Raleigh, NC: North Carolina State University.