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# Reviewing the organic matter processing by wetlands

## Revendo o processamento da matéria orgânica pelas áreas úmidas

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**Abstract: Aim:** Cycling processes in wetlands are highly dynamic and involve complex interactions between hydrological processes, biogeochemical transformations, and microbial communities. This review attempts to assess the interactions between elements within biogeochemical cycles and the possible routes in which organic matter is processed in waterlogged soils. **Methods:** The input and cycling of organic matter in flooded soils were approached in this review. We used a non-systematic literature survey to indicate the possible biogeochemical routes of organic matter processing in waterlogged soils. **Results:** We explore hydrological processes, oxygen availability, biogeochemical routes of the organic matter process, and the inputs and exports of organic matter in flooded soils from wetlands. **Conclusions:** The anaerobic degradation of organic resources predominantly occurs within submerged soils. Under conditions of maintenance of natural rates of primary production and allochthonous detritus input, storing organic detritus in flooded soils prevails over mineralization. The importance of hydrology for the export of organic carbon is evident. In wetlands, the export of organic matter is predominantly associated with dissolved organic matter and methane production.

**Keywords:** waterlogged soils; hydrological regime; biogeochemical reactions; carbon and nutrient cycling; anaerobiosis; decomposition.

**Resumo: Objetivo:** Os processos de ciclagem em áreas úmidas são altamente dinâmicos e envolvem interações complexas entre processos hidrológicos, transformações biogeoquímicas e comunidades microbianas. Esta revisão avaliou as interações entre os elementos no contexto dos ciclos biogeoquímicos e as possíveis rotas em que a matéria orgânica é processada em solos alagados. **Métodos:** Nessa revisão foram abordados os processos de entrada e ciclagem de matéria orgânica em solos inundados. Utilizamos um levantamento bibliográfico não sistemático para indicar as possíveis rotas biogeoquímicas de processamento da matéria orgânica em solos alagados. **Resultados:** Exploramos processos hidrológicos, disponibilidade de oxigênio, rotas biogeoquímicas do processo de matéria orgânica e as entradas e exportações de matéria orgânica em solos alagados de áreas úmidas. **Conclusões:** A degradação anaeróbica dos recursos orgânicos ocorre predominantemente em solos submersos. Em condições de manutenção das taxas naturais de produção primária e adução de detritos alóctones, o armazenamento de detritos orgânicos em solos alagados prevalece sobre a mineralização. A importância da hidrologia para a exportação de carbono orgânico é evidente. Nas áreas úmidas, a exportação de matéria orgânica está predominantemente associada à matéria orgânica dissolvida e a produção de metano.

**Palavras-chave**: solos alagados; regime hidrológico; reações biogeoquímicas; ciclagem de carbono e nutrientes; anaerobiose; decomposição.

## 1. Introduction

Wetlands are biogeochemical hotspots, receiving and transforming autochthonous and allochthonous carbon and nutrients. The dynamic of the availability of oxygen within sediments promotes biochemical transformations that affect the availability of nutrients for productivity (Elsey-Quirk & Cornwell, 2022). Intense biogeochemical cycling in wetlands can make these environments efficient sites for microbial processing of organic matter and nutrients (Yarwood, 2018; Deemy et al., 2022). High productivity and soils waterlogged conditions transform many freshwater wetlands into significant carbon sinks. The quantity of carbon that wetlands store or emit depends considerably on the hydrogeochemical characteristics of the ecosystem (Bernal & Mitsch, 2012). Flooded soils are a critical part of wetland functioning, and biogeochemical processes are responsible for carbon sequestration and the uptake of nutrients (Mobilian & Craft, 2022). Hydrology dynamics and water chemistry regulate biogeochemical cycling and trophic wetlands dynamics (Deemy et al., 2022). Wetland soils presented anaerobic conditions where oxidation-reduction reactions mediated by microorganisms are particularly important. These processes control the storage, transformation, or release of several elements (Mobilian & Craft, 2022). Reduction-oxidation chemistry combines both biochemistry and geochemistry. The driving force of redox reactions is respiration, i.e., a complex series of electron-transfer reactions that ultimately couple microbial metabolism to the transformation of organic matter in the environment (Bleam, 2017). Energy can be liberated or stored in the environment by redox reactions (Borch et al., 2010). This review includes information focusing on biogeochemistry processes that modulate organic matter decomposition in wetlands waterlogged soils. We used a non-systematic literature survey to indicate and summarize the main possible biogeochemical routes of organic matter processing in wetlands waterlogged soils.

## 2. Wetlands and Hydrological Processes

The global wetland area is more than $12.1 \times 10^6$ km$^2$, being 54% permanently inundated and 46%, temporarily flooded. About 92.8% of continental wetland area is inland, and only 7.2% is coastal (Davidson et al., 2018). Due to seasonal variations in the water regime (e.g., water from rivers, runoff, groundwater, and rainfall; Kirk, 2004), soil submersion occurs in wetlands (i.e., swamp, peatland, bog, fen, or water, whether natural or artificial, permanent, or temporary, with static or flowing fresh, brackish, or saline waters; sensu Ramsar Convention Secretariat, 2010). Wetlands are found in topographic areas with low slopes, which receive high rainfall inputs. The low topographic relief reduces runoff losses and precipitation surpluses evapotranspiration rates. The major factor regulating the seasonal fluctuation in the vertical and horizontal extent of a wetland is its topography. It also influences the spread over which water can increase before depth rises, where runoff effectively removes any additional water inflow (Los Huertos & Smith, 2013).

Wetlands expand and contract or appear and disappear, resulting from wet-dry cycles, which occur with different intensities at varying times (Klammler et al., 2020). Wetlands that receive relatively large precipitation, or runoff inflows, are protected from these cycles (Duever, 1988). Typically, the vertical change in water level is relatively small, usually less than 1-2 m, depending on the type of wetland. An exception is the varzea region, along the Amazon River, which presents annual fluctuations of up to 20 m (Junk, 1984). In general, the receptive capacity of a wetland for hydrological flows is probably one of the most important determinants of potential primary productivity (Casco & Neiff, 2006; De Gallardo et al., 2023). Peat with favorable runoff conditions has long been more productive than elevated swamps with stagnant water. Wetlands with stagnant (non-flowing) or continuously deep waters have low productivity, while wetlands on slow-flowing slopes or rivers subject to flood have high productivity (Mitsch & Gosselink, 2015).

## 3. Oxygen Availability in Wetlands Soils

Soil properties have evident effects on the decomposition of organic matter and plant detritus. In non-flooded soils, the size of the particles (e.g., silt, clay, sand), the presence of oxygen, the degree of moisture, the pH, the availability of oxygen and nutrients play essential roles in determining the order of magnitude of the rates of reactions linked to decomposition (Smyth et al., 2011). In general, organic carbon accumulation is higher in flooded soils because decomposition is limited by the high degree of humidity (Chapin et al., 2002). In flooded soils, gas exchange between soil and air is drastically reduced and, oxygen and other atmospheric gases can enter the soil only by molecular diffusion in the interstitial water. This process is slower than diffusion in gas-filled pores (Hogarth, 2001). Thus, the oxygen diffusion rate abruptly decreases when the soil reaches water saturation (Neira et al., 2015).

The oxygen deficits in soils may occur shortly after waterlogging after microorganisms deplete oxygen (Kirk, 2004; Mitsch & Gosselink, 2015). Past studies have indicated anaerobiosis in submerged soils occurs within a day (Evans & Scott, 1955; Takai et al., 1956). Anaerobiosis is usually reported in flooded rice fields, swamps, and mangroves for a long time (Armstrong & Boatman, 1967; Holguin et al., 2001; Kirk, 2004; Ferreira et al., 2010). The dissolved oxygen is usually not detected 1 cm below the surface of sediments (Horppila et al., 2015).

A comparison of oxygen consumption rates of sediments with oxygen diffusion rates in saturated soils corroborates that submerged soils are anoxic below the soil-water interface (Sahrawat, 2004). In a saturated medium, soil and sediment core samples lack free oxygen (Sexstone et al., 1985). The low oxidation-reduction potentials observed in sediments (Fenchel et al., 2012) and submerged soils of rice paddies (Ponnamperuma, 1972) are further evidence of the lack of molecular oxygen in waterlogged soils and sediments. The flux and type of organic matter are important variables in wetlands soils. Large fluxes of organic matter, in more rapid consumption of the available oxygen (Tostevin & Poulton, 2019). Despite the availability of dissolved oxygen in the water column and water-sediment interface, the anaerobic degradation of organic resources predominantly occurs within submerged soils.

Submerged soil is not uniformly oxygen-deprived; the oxygen concentrations can be high in the surface layer (from millimeters to a few centimeters thick; O'Geen et al., 2010). Below the surface layer, the oxygen concentration suddenly drops to practically zero (Reddy et al., 2000). The color of the oxygenated layer of the sediment, the chemical properties and oxidation-reduction potential undergo similar sudden changes with depth in submerged soils (Mobilian & Craft, 2022).

The chemical and microbiological transformations in the surface layer resemble those of aerobic soils. The most important chemical difference between submerged and well-draining soil is that waterlogged soil predominates in the reduced state (Figure 1). Except for the oxidized layer on the surface, a submerged soil is gray or greenish (Mobilian & Craft, 2022), has a low oxidation-reduction potential, and encompasses the reduced compounds of $NO_3^-$, $Mn^{4+}$, $Fe^{3+}$, $SO_4^{2-}$ and $CO_2$, i.e., $N_2$, $NH_4^+$, $Mn^{2+}$, $Fe^{2+}$, $H_2S$ and $CH_4$ (DeLaune & Reddy, 2005).

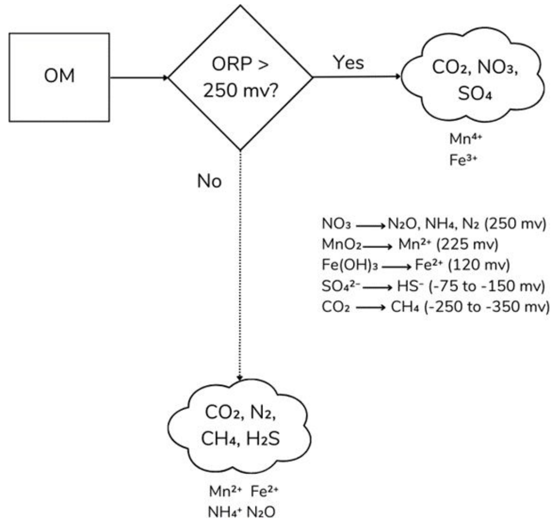


**Figure 1.** The products (inside the clouds) of organic matter (OM) cycling and elemental speciation due to oxidation-reduction potential (ORP). Solid arrow: predominantly higher rate processes (i.e., aerobic mineralization). Dashed arrow: processes with low rates (predominantly), i.e., anaerobic respiration and fermentation. The ORP reference values (e.g., 250 mv) were adopted from Mitsch & Gosselink (2015).

## 4. Microbial Metabolism: Biogeochemical Routes

Microbial metabolism in anaerobic sediments, such as waterlogged wetlands, plays a crucial role in regulating several essential biogeochemical cycles, i.e., carbon, nitrogen, phosphorus, and sulfur (Inglett et al., 2005). Flooded soils support intense heterotrophic activity and many transformations are directly mediated by aerobic and anaerobic microorganisms (D'Angelo & Reddy, 1999). The reduction of submerged soil and sediment is a consequence of the anaerobic respiration of bacteria (Reddy & DeLaune, 2008). During anaerobic respiration, organic matter is oxidized, and the components of the medium are reduced (Boon, 2006; Madsen, 2015; Reddy & DeLaune, 2008; Hanson et al., 2013). Examples include: (i) denitrification (Equation 1); (ii) the (dissimilatory) reduction of nitrate and nitrite to ammonium (Equations 2 and 3) (iii) the reductions of manganese dioxide (Equations 4 and 5); (iv) the reduction of ferric hydroxide (Equations 6 and 7); (v) sulfate reduction (Equations 8 to 10) and (vi) carbon dioxide reduction (Equation 11):

$$C_6H_{12}O_6 + 6NO_3^- \rightarrow 2N_2 + 2NO_2^- + 4CO_2 + 2CO_3^{2-} + 6H_2O + Energy(\Delta G'_0 = -590\ kcal\ mol^{-1}) \quad (1)$$

$$4CH_2O_2 + NO_3^- + 2H^+ \rightarrow 4CO_2 + NH_4^+ + 3H_2O + Energy(\Delta G'_0 = -226\ kcal\ mol^{-1}) \tag{2}$$

$$3CH_2O_2 + NO_2^- + 2H^+ \rightarrow 3CO_2 + NH_4^+ + 2H_2O + Energy(\Delta G'_0 = -166\ kcal\ mol^{-1}) \tag{3}$$

$$C_6H_{12}O_6 + 12MnO_2 + 24H^+ \rightarrow 6CO_2 + 12Mn^+ + 18H_2O + Energy(\Delta G'_0 = -484\ kcal\ mol^{-1}) \tag{4}$$

$$CH_3COO^- + 4MnO_2 + 9H^+ \rightarrow 2CO_2 + 4Mn^+ + 6H_2O + Energy(\Delta G'_0 = -137\ kcal\ mol^{-1}) \tag{5}$$

$$C_6H_{12}O_6 + 24Fe(OH)_3 + 48H^+ \rightarrow 6CO_2 + 24Fe^{2+} + 66H_2O + Energy(\Delta G'_0 = -40\ kcal\ mol^{-1}) \tag{6}$$

$$CH_3COO^- + 8Fe(OH)_3 + 17H^+ \rightarrow 2CO_2 + 8\ Fe^{2+} + 22H_2O + Energy(\Delta G'_0 = -11\ kcal\ mol^{-1}) \tag{7}$$

$$2(CH_2O) + H_2SO_4 \rightarrow 2CO_2 + 2H_2O + H_2S + Energy(\Delta G'_0 = -21\ kcal\ mol^{-1}) \tag{8}$$

$$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O + Energy\left(\Delta G'_0 = -20\ to\ -40\ kcal\ mol^{-1}\right) \tag{9}$$

$$CH_3COO^- + SO_4^{2-} + 3H^+ \rightarrow 2CO_2 + 2H_2O + H_2S + Energy(\Delta G'_0 = -13.7\ kcal\ mol^{-1}) \tag{10}$$

$$2CH_3CH_2OH + CO_2 + 17H^+ \rightarrow CH_4 + 2CH_3COO^- + 2H^+ + Energy\left(\Delta G'_0 = -24\ kcal\ mol^{-1}\right) \tag{11}$$

In addition to anaerobic respiration, chemosynthesis also occurs; instead of organic matter, bacteria oxidize reduced inorganic compounds, such as ammonium (Equation 12; Madsen, 2015), sulfides, elemental sulfur (Equation 13) and other reduced sulfur compounds, such as thiosulphate (Wetzel, 2001).

$$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O + Energy(\Delta G'_0 = -86.2\ kcal\ mol^{-1}) \tag{12}$$

$$5S^o + 6NO_3^- + 2CO_3^{2-} \rightarrow 5SO_4^{2-} + 2CO_2 + H_2O + 3N_2 + Energy(\Delta G'_0 = -179\ kcal\ mol^{-1}) \tag{13}$$

In anaerobic environments, such as water-saturated wetlands soils, fermentations occur when the electron acceptors are organic compounds (Schlegel, 1997). In this case, the oxidation may be incomplete, generating intermediate organic products (such as lactic acid and ethanol; Equations 14 and 15, respectively; Conn et al., 1987). Substrate catabolism may be incomplete (Denef et al., 2009), and the products (organic or inorganic) enter the anabolic routes of the decomposers and, consequently, are resynthesized and incorporated by these organisms (Fenchel, 2008). Other products are incorporated and/or converted into the class of non-cellular organic compounds, such as humic substances (Assunção et al., 2017).

$$C_6H_{12}O_6 \rightarrow 2CH_3CHOHCOOH + 2H_2O + Energy(\Delta G'_0 = -32.4\ kcal\ mol^{-1}) \tag{14}$$

$$C_6H_{12}O_6 \rightarrow 2CH_3CH_2OH + 2CO_2 + Energy(\Delta G'_0 = -25.4\ kcal\ mol^{-1}) \tag{15}$$

The oxidation of organic matter (e.g., glucose, palmitic acid, and lactic acid; Equations 16, 17 and 18, respectively) is interrupted by soil submersion, and the aerobic microorganisms consume the oxygen in the soil and become quiescent or die. Facultative and obligate anaerobes then proliferate, using carbon compounds and oxidized components of the soil as substrate and dissimilation products of organic matter as electron acceptors in respiration (Sahrawat, 2004).

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + Energy(\Delta G'_0 = -686\ kcal\ mol^{-1}) \tag{16}$$

$$C_{16}H_{32}O_2 + 23O_2 \rightarrow 16CO_2 + 16H_2O + Energy(\Delta G'_0 = -2338\ kcal\ mol^{-1}) \tag{17}$$

$$CH_3CHOHCOOH + 3O_2 \rightarrow 3CO_2 + 3H_2O + Energy(\Delta G'_0 = -319.5\ kcal\ mol^{-1}) \tag{18}$$

The requirements for organic matter reduction soil are: (i) the absence of oxygen; (ii) the presence of organic matter, and (iii) anaerobic bacterial activity (Sigee, 2005). Metabolic routes, reaction rates and the degree of organic matter reduction are influenced by the nature and content of organic matter, temperature, nature and content of electron acceptors, and pH (Wilson et al., 2011; Szafranek-Nakonieczna & Stepniewska, 2014; Boye et al., 2018; Li et al., 2021b). Growth rates (i.e., anabolism) are not invariant properties of organisms; they are markedly influenced by the prevailing environmental conditions, particularly by the complexity of the medium (substrate) and by the nature of the primary source of carbon and energy (Mandelstam et al., 1982).

Usually, heterotrophic bacteria grow faster in a medium containing nutrients and complex organic compounds (e.g., amino acids, purines, pyrimidines, and vitamins). Facultative anaerobic bacteria growth in the presence of oxygen is generally faster than in its absence. Presumably, this reflects the greater efficiency with which organisms can generate ATP in an aerobic environment;

comparisons of the energy yields of aerobic oxidations (e.g., Equations 16 to 18; Conn et al., 1987) with those of anaerobic respirations (e.g., Equations 1, 4 and 6) and fermentations (Equations 14 and 15) illustrate these processes. Substances such as nitrate, whose assimilation requires extra energy demands on organisms, generally support growth at a lower rate than those such as ammonia, whose assimilation requires less energy input (Mandelstam et al., 1982).

Microorganisms can use a wide variety of organic compounds as a source of energy. The catabolism of these substances leads to the production of intermediate compounds that act as raw material suppliers for biosynthetic reactions and energy production (Williams & del Giogio, 2005). The $CO_2$ molecules produced in the decomposition (anaerobic: Equations 1 to 8 or aerobic decay: Equations 16 to 18; Figure 2) associate with water molecules and form carbonic acid; carbonic acid dissociations produce bicarbonates and carbonates; such dissociations generate $H^+$ (Equation 19), thus acidify the medium (Langmuir, 1997).

In water-saturated soils, typical of wetlands, the degree of acidity partially depends on the amount of decomposed organic material and the degradation velocity. The degree of acidity is mainly proportional to the production of $CO_2$. Other processes also contribute to the increase in the acidity are: (i) leaching (dissolutions) of detritus and subsequent dissociation of organic acids; (ii) nitrification (Equation 20); (iii) oxidations of sulfur compounds (Equations 21 to 23) and (iv) cation hydrolysis (Mihelcic, 1999; Cunha-Santino & Bianchini Júnior, 2002; Konhauser, 2007).

Increases in water electrical conductivity values due to soil submersion are related to releasing ions and compounds from leaching and mineralization processes. Changes in the color of water result from the formation and dissolution of inorganic colloids (e.g., iron and sulfur salts; Ciminelli et al., 2014; Li et al., 2021a; Equations 24 and 25), the release of pigments from plants detritus (Killops & Killops, 2013) and the formation of organic colloids (e.g., humic substances; Cunha-Santino et al., 2013).

$$CO_2 + H_2O \rightarrow H_2CO_3 + H_2O \rightarrow H^+ + HCO_3^- + H_2O \rightarrow H^+ + CO_3^2 \tag{19}$$

$$NH_4^+ + 2O_2 \rightarrow NO_3^- + H_2O + 2H^+ \tag{20}$$

$$H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+ \tag{21}$$

$$S^0 + H_2O + 1½O_2 \rightarrow SO_4^{2-} + 2H^+ \tag{22}$$

$$S_2O_3^{2-} + H_2O + 2O_2 \rightarrow 2SO_4^{2-} + 2H^+ \tag{23}$$

$$CH_2O + 8H^+ + 4FeOOH \rightarrow CO_2 + 4Fe^{2+} + 7H_2O \tag{24}$$

$$3H_2S + 2FeOOH \rightarrow 2FeS + S^0 + 4H_2O \tag{25}$$

In anaerobic environments (e.g., sediments and saturated soils), the rates of detritus mineralization (which are derived mainly from the growth rates of microorganisms) usually are lower than those observed under aerobic conditions (Wetzel, 2001; Kirk, 2004; Mitsch & Gosselink, 2015).

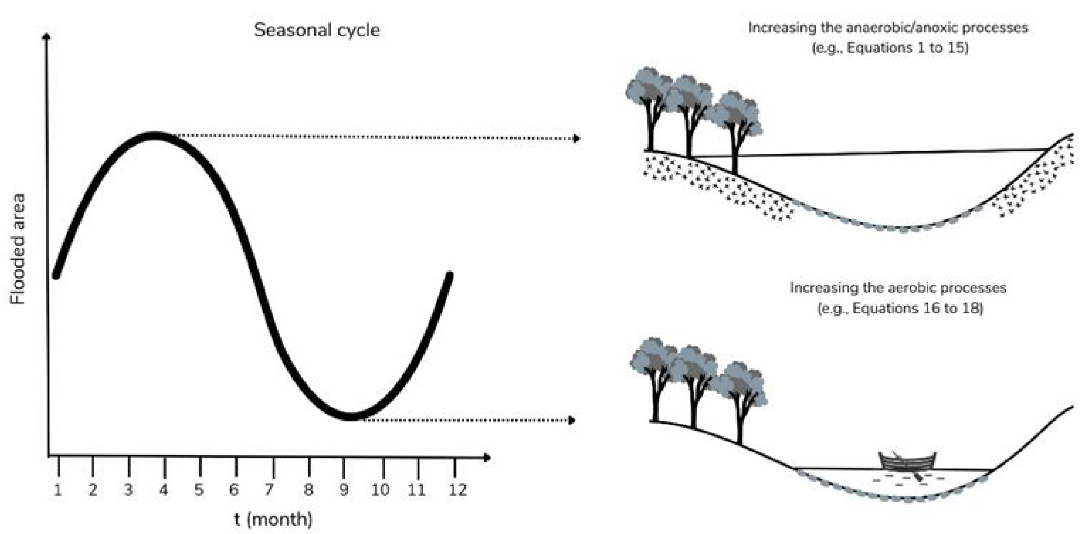


**Figure 2.** Seasonal change in the predominant metabolic reactions in wetland soil as a function of the flood pulse (sensu Neiff, 1999). Hatched soil: predominantly anoxic or anaerobic processes.

The tendency is for a greater stock of organic matter to occur in sediments, submerged soils, and hydrosols. The accumulation of plant residues in soils and sediments generally results from a long time of degradation of plant resources compared to the rates of input of allochthonous detritus and those from autochthonous primary production, i.e., chemosynthesis, oxygenic (Equation 26) or anoxygenic (Equations 27 to 29) (Conn et al., 1987). The lack of oxygen has drastic consequences for the decomposition of organic material. Obligate aerobic decomposers are limited to the more aerated patches of sediment. Fungi and bacteria that can break down refractory organic molecules mainly belong to this group. Although the half-life of such substances increases strongly in anaerobic soils, the more easily degradable organic matter will be transformed by anaerobes (facultative or obligate). These organisms use other electron acceptors to replace oxygen, which leads to interactions of the carbon cycle with those of nitrogen, manganese, iron, and sulfur (Verhoeven, 2009), as demonstrated by Equations 1 to 10.

$$6CO_2 + 12H_2O + Energy(\Delta G'_0 = +686\ kcal\ mol^{-1}) \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2 \tag{26}$$

$$CO_2 + 2H_2S + Energy(\Delta G'_0 = +686\ kcal\ mol^{-1}) \rightarrow CH_2O + 2S^o + H_2O \tag{27}$$

$$2CO_2 + Na_2S_2O_3 + 5H_2O + Energy(\Delta G'_0 = +686\ kcal\ mol^{-1}) \rightarrow CH_2O + 2H_2O + 2NaHSO_4 \tag{28}$$

$$CO_2 + 2CH_3CH_2OH + Energy\left(\Delta G'_0 = +686\ kcal\ mol^{-1}\right) \rightarrow CH_2O + 2CH_3CHO + H_2O \tag{29}$$

## 5. Organic Matter Decomposition

The organic matter generated by plants can be mineralized or accumulate in the soil matrix as sequestered organic carbon and other elements (Elsey-Quirk & Cornwell, 2022). Slow cycling of organic resources may indicate inherent resistance to enzymatic attack but may also be due to environmental factors, e.g., moisture, pH, temperature, particle size, and nutrient and oxygen availability (Li et al., 2022). Natural polymers (e.g., lignin, cellulose, hemicellulose, pectin) can bind to inorganic ions, clay, or other organic residues that protect these materials from degradation. Plant detritus can also be naturally enclosed to other molecules, e.g., cellulose is usually tightly associated with lignin, which limits cellulase access.

As oxygen-dependent peroxidases and dioxygenases primarily degrade lignin, lignified cellulose is not readily decomposed in anaerobic environments. Other oxidants, such as nitrate, metal oxides or sulfate (e.g., Equations 1 and 2, 4, 5, and 8, respectively) do not seem to promote anaerobic degradation of these resources, which leads to lignocellulose accumulation in water-saturated soils and sediments, as bogs (Kirk, 2004).

The storage of organic matter in soils and sediments constitutes an essential reservoir of carbon in the biosphere (Fenchel, et al., 2012). Storage is derived from balancing detritus input and mineralization (Six & Jastrow, 2002; Kirk, 2004). Element turnover is often quantified as mean residence time (MRT) or half-life (t½). The MRT of an element is defined as: (i) the average time the element resides in the medium at a steady state or (ii) the average time required to replenish the contents of the element at a steady state completely. The half-life of soil organic matter (Soil OM) is the time required for decomposing 50% of the currently existing stock.

The typical model used to describe the dynamic behavior or turnover of the Soil OM is the first-order model, which assumes a constant (zero-order) input with a proportional (constant) mass loss per unit of time. For Soil OM, the MRT = 1/k; where k = coefficient of mass loss of organic matter ($t^{-1}$); Six & Jastrow (2002). Depending on latitude, humidity, management, soil type and composition and method used for evaluation, the MRT of Soil OM ranges from tens to thousands of years (Stevenson, 1994; Six & Jastrow, 2002; Torn et al., 2009).

Evidence suggests that the persistence of organic carbon oxidation in the environment (soil and sediment) is determined by the interaction between substrates, microbial communities, and abiotic conditions. Therefore, organic matter turnover must be seen as dependent on microbial ecology and the state of a specific environment. Varying degrees of structural organization, microbial ability, and resource constraints within a given environment (soil aggregate, soil horizon) make it likely that identical organic compounds can be recycled at different rates due to variations in driving force (i.e., controlling environmental variables).

Soil organic matter can be classified as a reservoir of reduced carbon in different states (Kleber, 2010). This categorization leads to observing the structural heterogeneity of the Soil OM and organic detritus. On a carbon basis, it is possible to distinguish that decomposing resources are formed by labile organic carbon (LC), soluble organic carbon (which will be released in dissolved form; DOC) and refractory particulate organic carbon (POCR; comprising basically of structural compounds); Bianchini Júnior & Cunha-Santino (2011). Mass losses due to decomposition must be represented by a set of equations corresponding to the sum of several exponential functions (Heitkamp et al., 2012) that separately consider the different resources with their specific compositions (i.e., LC, DOC and POCR content); Equation 30.

$$CO_t = \sum_{i=1}^{n}\sum_{j=1}^{m} CO_j \times e^{-k_j t} \qquad (30)$$

where: COt = remaining organic carbon at time t; i = the sum index for resource type (e.g., leaves, branches, Soil OM); n = number of detritus types; j = sum index for organic carbon category (LC, DOC and POCR); m = number of types of organic carbon; COj = initial mass of organic carbon j of resource i; kj = COj mass loss coefficient of resource I and t = time.

The composition of the detritus and the proportions of particulate organic carbon components (POC = LC + DOC + POCR) is defined as intrinsic factors (Gimenes et al., 2010) and determine the effect of detritus quality on degradation (Erhagen et al., 2013). The implications of abiotic variables (extrinsic factors; Gimenes et al., 2010) define the types and prevalence of decomposers and, consequently, the reaction rates expressed in the mass loss coefficients (k). The temperature is usually an essential extrinsic driving force in detritus cycling, followed by the availability of oxygen and nutrients (Bowie et al., 1985; Li et al., 2022); Equation 31. In aquatic environments with low temperature variations, such as tropical regions, oxygen availability modulates decomposition rather than temperature (Passerini et al., 2016).

$$k_t = k_{max} \times \theta^{\left(T - T_{Ref}\right)} \times f\left(\left[OD\right],\left[N\right],\left[P\right],\ldots,\left[S\right]\right) \qquad (31)$$

where: kt = kj at time t (Equation 30); $k_{max}$ = maximum value of kj at the reference temperature; T = temperature at time t; $T_{Ref}$ = reference temperature (e.g., 20°C); θ = temperature adjustment coefficient (derived from the $Q_{10}$ of the microbial community); [OD] = dissolved oxygen concentration, [N] = nitrogen concentration, [P] = phosphorus concentration and [S] = sulfur concentration.

Incubations performed with wetlands soil showed, on average, $CO_2$ production rates six times higher in aerobic environments. The mean rate of total anaerobic carbon loss ($CO_2$ + $CH_4$) was only 13% of that observed under aerobic conditions. Incubations showed higher $CO_2$ and $CH_4$ production rates at elevated temperatures, and the level of response varied with soil type and temperature. The anaerobic processes were more influenced by the increase in temperature than the aerobic (Inglett et al., 2012).

Other driving forces can be included or excluded from the model (Equation 31), depending on their importance to the environment to be simulated (e.g., pH, humidity, current velocity). The first term of Equation 31, which refers to the effect of temperature on reaction coefficients, is usually presented separately and described by exponential functions (derived from the van´t Hoff Equation), as it is assumed that reaction rates increase with increasing temperature.

Hyperbolic functions (Michaelis-Menten or Monod equation) are normally used to describe the relationships between [OD], [N], [P] and [S] and reaction rates (Davidson et al., 2012; second term of Equation 31). The abscissa corresponds to the concentration of each element and the respective coordinates of the values of the reaction coefficients (that vary, for each element, from zero to 1, making: $\frac{k}{k_{max}}$). From the concentrations of the variables in the medium, the final value of f([OD], [N], [P], …, [S]), which varies from zero to 1, is calculated by criteria such as mean arithmetic, harmonic mean, multiplication, and law of relative minimum (Jɸrgensen, 1980). Using these procedures, $k_t$ is updated as a function of temperature and other variables. The composition of the detritus, how mass losses occur (Equation 30), the effects of environmental conditions on decomposition (Equation 31) and how the various types of detritus (autochthonous and allochthonous) enter the soil, represent important temporal functions for the calculation of the stock of carbon of the submerged soils and sediments and the consequent exportations and emissions of gases of the greenhouse effect (GHG); Boon (2006).

## 6. Inputs and Exports of Organic Matter

Organic matter enters wetlands from various sources (i.e., point and diffuse) and in different ways (e.g., functions: impulse, step, linear, exponential, and periodic). The atmospheric sources (precipitation and dry deposition) that enter the air-water interface are partially dependent on the surface size of the aquatic environment and the amount of rainfall. In wetlands, detritus additions are naturally (and periodically) linked to: (i) the seasonality of the climate; (ii) GHG emissions (Bloom et al., 2012) and (iii) hydrological dynamics (Baker et al., 2009; Gilvear & Bradley, 2009; Grootjans & Van Diggelen, 2009).

Seasonal additions of detritus tend to be more evident in temperate than in tropical environments, where seasonal temperature variations are less intense (Gonçalves Junior et al., 2014). Hydrological dynamics (e.g., variations in aquifer height, fluviometric variations, runoff), which define the frequency and duration of floods, are an important source of allochthonous detritus (Barker & Maltby, 2009; Dise, 2009). Detritus enters a wetland from various sources and in several different ways. Sources of adduction related to the hydrological cycle, such as mass transported by flow or precipitation can often be characterized by periodic functions. The general pattern of high spring/summer runoff, with the relatively low and constant flow for other seasons, is repeated in a very predictable way. Sinusoidal functions can often represent the cycles of wet and dry periods. Therefore, the entries of organic allochthonous constituents can be characterized by temporal properties, that is, by their changes over time (Equation 32; Chapra, 2008):

$$w_t = \sum_{i=1}^{n} \left( v \frac{dc}{dt} \right) \tag{32}$$

where: $w_t$ = adduction rate (m $t^{-1}$); i = entry number; n = maximum number of entries; v = affluent volume; $\frac{dc}{dt}$ = time variation of element concentration.

The origin of the detritus (autochthonous or allochthonous) can also interfere with cycling rates, with allochthonous resources being normally more inaccessible since potentially labile fractions have already been consumed, remaining detritus refractory fractions (Thurman, 1985; Gimenes et al., 2010). In wetlands, hydrology alters many variables related to detritus cycling, e.g., humidity depends on the flood regime, running water carries oxygen and nutrients, while in stagnant water, oxygen is quickly depleted, and nutrients are transformed into less available forms.

Hydrological changes induced by climatic and anthropogenic disturbances can also define the rates and predominant composition of GHG emissions; for example, drainage lowers the water table and raises the oxygen content of the soil, increasing $CO_2$ emissions. In temperate wetlands, the highest emissions were found where the water level remained close to the soil surface, suggesting that mainly litter and not burial organic matter contributes to $CH_4$ emission (Wang et al., 2021). $CH_4$ emissions from drained wetland soils are generally negligible because soil carbon is preferentially oxidized to $CO_2$ (Hiraishi et al., 2014).

Three different reactions generate $CH_4$ under strictly reductive conditions (Boon, 2006). The first uses $CO_2$, acetate (HCOO-), or carbon monoxide (CO) to produce $CH_4$ (Equation 33). In the second reaction, $CH_4$ can be produced by the reduction of the methyl group of methyl compounds, such as methanol (Equation 34). In the third reaction, $CH_4$ is produced by the breakdown of acetate into methane and carbon dioxide (Equation 35).

$$\begin{aligned} &CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O \\ &+Energy(\Delta G'_0 = -31.3\ kcal\ mol^{-1}) \end{aligned} \tag{33}$$

$$\begin{aligned} &4CH_3OH \rightarrow 3CH_4 + CO_2 + 2H_2O \\ &+Energy\left(\Delta G'_0 = -76.2\ kcal\ mol^{-1}\right) \end{aligned} \tag{34}$$

$$\begin{aligned} &4CH_3COO^- + H_2O \rightarrow 3CH_4 + HCO_3^- \\ &+Energy(\Delta G'_0 = -7.4\ kcal\ mol^{-1}) \end{aligned} \tag{35}$$

Anaerobic mineralization bioassays indicated that $CO_2$ is the main product, instead of $CH_4$ (Romeiro & Bianchini Júnior, 2006; Cunha-Santino & Bianchini Júnior, 2013; Bianchini Júnior & Cunha-Santino, 2016). The controlling factors of $CH_4$ production are: (i) availability of electron acceptors (Segers, 1998); (ii) quantity and quality of the organic matter supply (Bianchini Júnior et al., 2010); (iii) temperature (Romeiro & Bianchini Júnior, 2008); (iv) pH (Kiene, 1991; Cunha-Santino et al., 2006; Bloom et al., 2012); (v) coenzymes and prosthetic groups (Schlegel, 1997) and (vi) micronutrients (Banik et al., 1996; Basiliko & Yavitt, 2001). Interactions between these abiotic factors that influence metabolic pathways in generating of specific intermediate products can influence $CH_4$ production (Bergman et al., 1999). The intermediate compounds (e.g., methanol, propanol, formic acid, butyric acid) and acetate (Equation 34) is the main substrate for methanogenesis (Boone, 1991; Conrad, 1999).

The physical and biotic structure and resulting metabolism of a wetland ecosystem are tightly coupled to hydrological and chemical loads from the watershed (Wetzel, 2006). The importance of hydrology for the export of organic carbon is evident; in general, higher export rates are expected from wetlands that are open to water flow. Riparian wetlands provide large amounts of organic detritus to streams, including coarse detritus. It is evidence that watersheds that drain wetlands export more organic material but maintain more nutrients than watersheds that have no wetlands (Mitsch & Gosselink, 2015). In wetlands, the export of organic matter is predominantly associated with dissolved organic matter derived from relatively recalcitrant chemical compounds, often associated with the origin of lignin and cellulose structural tissues of higher plants and various products of bacterial degradation (Wetzel, 2006).

## 7. Final Considerations

The hydrological regime (i.e., periodic drought and flood; Dunn et al., 2023) that the wetlands are submitted (precipitation, evapotranspiration, inflows and outflows of surface and groundwater) directly interferes with: (i) the availability of oxygen; (ii) the prevalence of origin of detritus (autochthonous and allochthonous; Foti et al., 2012) and (iii) rates of detritus input (Gonçalves Junior et al., 2014). The balance between input and cycling of detritus determines the prevalence of redox potential in the aquatic system. Under conditions of maintenance of natural rates of primary production and allochthonous detritus input (i.e., without anthropogenic interventions), storing organic detritus in flooded soils prevails over mineralization. The organic matter metabolism of a wetland ecosystem is tightly coupled to hydrological and chemical loads from the watershed. The role of hydrology in the export of organic matter is clear. In wetlands, the export of organic matter is predominantly associated with dissolved organic matter and methane production during organic matter cycling.

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