Biogeochemistry of tropical lakes

W. M. Lewis, Jr.

Introduction

Biogeochemical processes are driven jointly by mass flux and metabolism, but biogeochemical contrasts across latitude are more strongly related to metabolism than to mass flux. Metabolism can be expressed in terms of metabolic potential, which is regulated by temperature, irradiance, and chemical feedstocks (nutrients, electron acceptors, organic matter). Metabolic potential of autotrophs in tropical lakes for a given nutrient supply is 2–4 times higher than in lakes of middle latitude, mainly because tropical lakes have a higher rate of nutrient resupply to the mixed layer caused by their higher rates of vertical mass exchange between layers. Hypolimnetic waters of tropical lakes are warm and thus have much higher metabolic potential than hypolimnetic waters of mid-latitude lakes. Oxic metabolism often is suppressed by rapid loss of oxygen during stratification in tropical lakes. Prominence of deepwater anoxia in the tropics magnifies the importance of biogeochemical processes involving electron acceptors other than oxygen.

Key words: latitude, metabolism, nutrient cycling, photosynthesis, tropical lakes

Basis of lacustrine biogeochemical comparisons across latitude

Biogeochemistry is the byproduct of metabolism and mass flux, but latitudinal contrasts among lakes are more pronounced for metabolism than for mass flux. From an ecosystem perspective, lake metabolism can be classified as anabolic (growth) or catabolic (respiration). Because autotrophic and heterotrophic growth have different biogeochemical consequences, they are separated for latitudinal comparisons (Table 1). For catabolic metabolism, oxic and anoxic respiration are also sufficiently distinct biogeochemically to require separate consideration.

Lake metabolism is regulated primarily by temperature, solar irradiance, and chemical feedstocks, the most important of which are nutrients, electron acceptors, and organic matter (Table 1). Given what is known of metabolic processes and their rate controls, combined with discoveries about tropical lakes over the last few decades, some general conclusions about the biogeochemistry of tropical lakes can be reached, as summarized here.

Table 1. Summary of metabolism and metabolic rate-control factors to be used in evaluating metabolic capacity in lakes.

<table>
<thead>
<tr>
<th>Metabolism per Unit Mass</th>
<th>Growth</th>
<th>Respiration</th>
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<tbody>
<tr>
<td></td>
<td>Autotrophic</td>
<td>Oxic</td>
</tr>
<tr>
<td></td>
<td>Heterotrophic</td>
<td>Anoxic</td>
</tr>
</tbody>
</table>

Rate Controls on Metabolism

Temperature
Solar Irradiance
Feedstocks
Nutrients
Electron Acceptors
Organic Matter

Lake types

Detailed treatment of biogeochemical processes in tropical lakes would require recognition of various substantially different lake types (Fig. 1). The present analysis focuses only on one lake type, which consists of a natural basin approximately 30 m deep (basic type: Fig. 1). Such a lake, if located at middle latitude, would contain an epilimnion, metalimnion, and hypolimnion over a growing season of about 6 months. The same separation of layers would occur in a tropical lake, except that the duration of the stratification period would be considerably longer (e.g., 10.5 mo; LEWIS 1996). Seasonality in temperature for lakes within 20° latitude of the equator is so subtle that tropical lakes were first thought unlikely to show seasonal stratification and predictable seasonal mixing.
(Hutchinson & Löffler 1956). This initial assertion proved false (Talling 1966, Lewis 1987). Whereas a specific minimum depth is necessary for maintenance of stable seasonal stratification, seasonal stratification is the rule for tropical lakes deeper than about 15 m.

Deviations from the basic lake type could be important biogeochemically (Fig. 1). Some lakes have insufficient depth to sustain stratification; such lakes consist of a mixed layer in contact with sediment. Other lakes, which are unusual statistically but include some of the world’s most important tropical lakes, have very large hypolimnetic volumes. Another distinct type is the river lake, which is strongly influenced biogeochemically by the annual flood cycle. A final type is the reservoir, which may show unpredictable density layering caused by deepwater withdrawal as well as very strong hydraulically-driven mass flux if it is located on the main stem of a river.

Metabolic potential

A useful metric for comparing groups of lakes that differ in some important respect (e.g., latitude) is metabolic potential. For present purposes, metabolic potential (m) is equated to metabolic output (anabolic or catabolic) per unit biomass under specific conditions for one or more rate-limiting factors. Maximum metabolic potential, m_{max}, refers to conditions under which all potentially limiting factors are optimal. Metabolic potential can be referenced to an index value of 1.0, which corresponds to m_{max}.

Metabolic potential, as defined here, applies to ecosystems or to a specific ecosystem component (e.g., phytoplankton). It is understood that the m_{max} for a given organism is dependent not only on rate-controlling environmental factors, but also on its size. If the size spectra for organisms are similar in the metabolically dominant communities of 2 or more lake ecosystems, m can be compared among them without any explicit treatment of organism size. There is currently no indication that tropical lakes differ significantly from lakes of higher latitude in their size spectra; therefore, community or ecosystem-level comparisons are made here without explicit consideration of size spectra.

Metabolic controls

The 3 classes of metabolic regulators (Table 1) can be placed into a hierarchy based on their scope of regulation. Temperature is first in the hierarchy because it regulates all processes across its full range of variation. Photosynthetically available radiation (PAR) is second in the hierarchy; it regulates across the full range of variation but is applicable only to photosynthesis. Feedstocks are third in the hierarchy because they regulate only when scarce.

Control by temperature

Both anabolic and catabolic processes show maximum rates near 25 °C in aquatic communities (Talling & Lemoalle 1998). Stenotherms are known, especially among fishes and larger invertebrates, but their niches are filled by ecological equivalents in ecosystems that are beyond their thermal tolerance ranges.

The mixed layers of tropical lakes near sea level reach maximum diel average temperatures of 25–30 °C (Lewis 1987). Although shallow, unstratified lakes may become somewhat warmer, an intermediate value of 27 °C serves as an approximation of the expected maximum diel average temperature for mixed layers of lakes within about 20° latitude of the equator at low elevation. For present purposes, m_{max} is assumed to occur when water temperature is ≥ 27 °C.

Thermal dependence of metabolism generally corresponds to a Q_{10} of 2 across large (interlatitudinal) temperature ranges (Lewis 1996), and the expected change in metabolic rate can be viewed as a function of temperature at Q_{10} = 2 (Fig. 2).

Because lakes are not consistent in temperature across months or depths, application of the concept of metabolic potential to lakes requires a time-depth map of temperature in lakes. Representative examples of temperatures for a tropical (0–20° latitude) and a mid-latitude lake
Fig. 2. Maximum expected metabolic rates as a function of temperature ($Q_{10} = 2$) for a range of diel mean temperatures.

(40–50°) show that temperature remains near optimum consistently in the tropical lake, as expected (Fig. 3). Temperature approaches optimum briefly in the mixed layer of the mid-latitude lake but is well below optimum in most months for the mixed layer and in all months for deeper water.

The sensitivity of photosynthesis to temperature when nutrients are abundant is relevant to the biogeochemical distinctions between temperate and tropical lakes. The photochemical component of photosynthesis is not sensitive to temperature (Falkowski & Raven 2007). Even so, the maximum rate of net photosynthesis shows a thermal response similar to that of respiration (i.e., $Q_{10} = 2$). The explanation for temperature sensitivity of photosynthesis lies in electron transport, which must accompany photochemistry for photosynthesis to proceed. Electron transport is impeded by membrane changes and molecule collision rates, both of which are sensitive to temperature (Falkowski & Raven 2007). Thus, for mixed layers, photosynthesis can be assigned a $Q_{10}$ of 2.

Although field data for photosynthesis show maxima at temperatures nearer to 20 °C than to 30 °C, a modest suppression of photosynthesis at the highest temperatures is probably explained by weak nutrient supplies at high temperatures (Falkowski & Raven 2007). For present purposes, it is assumed that the highest mixed-layer temperatures (>27 °C) for lakes correspond to the highest potential for photosynthesis, and thus to the highest column of rates of net photosynthesis. Rates at lower temperatures are assumed to follow from a $Q_{10}$ of 2.

For a lake with equal epilimnetic and hypolimnetic volumes, a simple estimate of the annual mean value of $m$ ($\bar{m}$), can be made for comparison with $m_{\text{max}}$, assuming optimum conditions for irradiance and nutrients. When averaged over a year’s time, tropical lakes show only small deviations ($\bar{m} = 0.90$) from $m_{\text{max}}$ based on temperature (other factors are assumed optimal for purposes of this calculation), whereas a lake of middle latitude shows 55% of $m_{\text{max}}$ based on temperature ($\bar{m} = 0.55$) in the upper water column and 20% of $m_{\text{max}}$ ($\bar{m} = 0.20$) in the lower water column (Fig. 3).

**Control by irradiance**

For water near the surface of a lake, optimum irradiance as judged by maximum net photosynthesis typically is less than the maximum ambient irradiance on a clear day because of the onset of light inhibition at the highest irradiances. For an entire mixed layer, however, maximum photosynthetic output per unit mass corresponds to maximum irradiance, given that photoinhibition is a phenom-
enon of the uppermost 1 or 2 m in a water column (Kalff 2002). Therefore, $m_{\text{max}}$ for photosynthesis of autotrophs corresponds to maximum water-column irradiance under nutrient-saturated conditions at high temperature.

Irradiance, as measured in latitudinal bands over the terrestrial part of the earth’s surface, shows a latitudinal pattern but not a tropical/nontropical dichotomy (Lewis 1996). Within the tropics, total irradiance is suppressed 20–25% by atmospheric moisture as compared with the highest irradiiances, which are observed in the subtropics where atmospheric moisture is minimal. Furthermore, daylength partly compensates for angular exposure of mid-latitude lakes. Thus, at middle latitudes the total annual irradiance is little different from that of the tropics.

The biogeochemically relevant conclusion for irradiance is that distinctive properties of tropical lakes with respect to photosynthesis relate to dependence of photosynthesis on temperature or nutrient supply and not to contrasts in irradiance between low latitudes and middle latitudes. The degree of thermal stimulation for photosynthesis under nutrient-saturated conditions for a mixed layer over an annual interval is identical to that forecast for general metabolic control based on $Q_{10}$ and water temperature.

In the mixed layers of lakes, the present analysis indicates that the balance between photosynthesis and respiration is essentially the same in temperate and tropical lakes, provided that neither process is substrate-limited. Because catabolic processes occur 5 times faster in the deep waters of tropical lakes, however, the lake as a whole, if consisting of both eutrophic and aphotic zones, will show a stronger bias toward respiration in a tropical lake than in a temperate lake. Thus, a working hypothesis would be that carbon turnover is faster in tropical lakes as a whole, and carbon storage is weak, but depletion of efficient electron acceptors in deep water may offset thermal magnification of deepwater metabolism.

**Control by nutrients**

Among the feedstocks, nitrogen (N) and phosphorus (P) are critical regulators of biogeochemical processes related to photosynthesis. If the available forms of either of these elements are depleted to the point of physiological scarcity, photosynthesis is suppressed. The mechanism of suppression is similar to that of lowering temperature: photosynthetic potential is reduced by an amount reflecting the degree of scarcity (Falkowski & Raven 2007). Recycling of N and P within the mixed layer ensures that the supply of physiologically available N and P never becomes zero, but it may be so low as to support only negligible growth rates among autotrophs.

Although phosphorus has long been considered most likely to limit the growth of autotrophs on an annual basis in lakes, there are many examples of N limitation for phytoplankton communities at temperate latitudes (Elser et al. 1990, Lewis & Wurtsbaugh 2008). Some evidence indicates that N and P are closely balanced in their capacity to limit production in oligotrophic lakes at temperate latitudes, but anthropogenic influences leading to eutrophication tend to bias lakes toward a low N:P ratio, increasing the probability of N limitation (Downing & McCauley 1992).

Limitation of autotrophs by N deficiency may be more pronounced at tropical latitudes than at middle latitudes, but this remains a controversial subject (Lewis 2000). Tropical warmth favors N fixation in the mixed layer, but also favors denitrification in deep water and high rates of ammonification throughout the water column. The higher probability of extended anoxia in tropical lakes deep enough to stratify may be one explanation for a greater incidence of N limitation in tropical lakes, in that anoxia reduces the inorganic nitrogen inventory through denitrification (Lewis 2002). Whereas the generality of N limitation in the tropics is not yet resolved, examples of nitrogen limitation in the literature are sufficient to suggest that the biogeochemistry of nitrogen is of special interest at tropical latitudes.

A fixed nutrient inventory that is insufficient to provide constant nutrient saturation for both N and P over an entire growing season will suppress photosynthesis to some degree for a portion of the growing season. Three characteristics of the mixed layer are potentially important in differentiating tropical from middle latitude lakes: (1) high nutrient uptake potential related to high temperature, (2) high regeneration potential caused by high metabolic rates of grazers and decomposers (Kilham & Kilham 1989), and (3) nutrient renewal (resupply) by epi-limnetic thickening associated with temporary reduction in the stability of layering (Lewis 1987).

Depletion of nutrients from a fixed pool available at the start of a growing season would occur very quickly in either a tropical lake or a mid-latitude lake (Fig. 4). The tropical lake would achieve depletion more rapidly (tropical $m = 0.87$, time for $10^7$ biomass increase = 21 d; versus mid-latitude $m = 0.55$, time for $10^7$ increase = 32 d), but the total production under nutrient-saturated conditions would be similar because nutrient inventory, assumed the same for this example, sets the peak abundance of autotrophs. For either a tropical or mid-latitude lake, production for the growing season or year is much
more dependent on events that follow initial nutrient exhaustion than by the speed with which nutrients can be exhausted.

A mixed layer for a tropical lake could support $m=1.0$ for phytoplankton if continuously nutrient-saturating (Fig. 5). The annual mean value of $m$ in such a case, assuming adverse conditions for primary production during the seasonal mixing of approximately 6 weeks, would be only slightly less ($\overline{m}=0.9$) than for the growing season. For a lake of middle latitude, as derived from application of a $Q_{10}$ of 2 to the monthly expected temperatures in the mixed layer, the corresponding value for the growing season would be 0.55. For an annual mean, incorporating a discount of approximately 50% as necessary because of the shorter growing season (6 mo), $\overline{m}$ would be 0.27, or approximately 30% of that expected for a tropical lake.

Constant nutrient saturation for the entire growing season is possible but unusual for stratified lakes. More typically, growth overtakes nutrient supplies. Assuming no significant resupply of nutrients from points beyond the boundaries of the mixed layer, net photosynthesis that occurs after the uptake of most available nutrients is derived from recycling. Because mixed-layer recycling is a byproduct of the metabolism of grazers and decomposers, its potential rates can be forecast from $Q_{10}$. Recycling is accompanied, however, by progressive loss of nutrients to points below the mixed layer. Introduction of a fixed rate of loss over the entire growing season substantially affects predictions for metabolic potential (second set of graphs, Fig. 5). A 2% daily loss reduces the estimated $\overline{m}$ in the tropical lake over the growing season from 1.0 to 0.16. The relative reduction in $\overline{m}$ is smaller for the temperate lake because the growing season is half as long. Thus, with recycling discounted by 2% per day to account for nutrient loss, tropical and temperate lakes show similar $\overline{m}$ over the growing season on a given nutrient base. For the entire year, tropical lakes still would be expected to have a higher $\overline{m}$ than mid-latitude lakes simply because the growing season is longer.

A final factor to be considered is resupply of nutrients during the growing season. Nutrients can be resupplied from the watershed, but often resupply of this type is small and controlled more by hydrology and hydraulic residence time than by latitude. Resupply can also occur, however, through vertical exchange between the mixed layer and the waters below; this type of exchange has a strong latitudinal component.

Even though tropical lakes of appropriate depth sustain stratification for an entire season, the maximum possible stability of layering is much lower in tropical lakes than in lakes of higher latitude (Ruttner 1938). Furthermore, stability is subject to substantial episodic reductions caused by short-term heat loss during the stratification season (Lewis 1987, 1996). Because the upper and lower layers of stratified tropical lakes differ by only ~2°C, a heat loss that would be inconsequential in terms of stability for a temperate lake may cause a critical reduction in stability of layering in a tropical lake. A critical reduction in stability often leads to some entrainment of water into the mixed layer. This entrainment may be observed through a substantial thickening of the mixed layer, or it may involve only movement of a meter or less of water from the deeper water column into the mixed layer. Entrainment varies among lakes within the tropics and may even be affected by climate change (O’Reilly et al. 2003, Verburg et al. 2003).

Incursion of the mixed layer into the water below, without full mixing of the lake, brings a new supply of nutrients into the mixed layer, thus providing new nutrient feedstock for primary production. These fertilization events are marked by measurable stimulation of primary production and a reset of phytoplankton successional processes (Lewis 1996).

Entrainment of nutrient-rich water into the mixed layer is known for temperate lakes, especially in the case of
upwelling caused by standing waves, but typically can be induced only by unusual weather conditions and not the moderate episodic cooling that suffices to cause such transfers in tropical lakes.

Scant information currently exists on the transfer of nutrients caused by episodic erosion of the thermocline in stratified tropical lakes. In Lake Lanao, Philippines, and Lake Valencia, Venezuela, where this phenomenon has been studied intensively (Lewis 1996), the total amount of exchange between the mixed layer and deeper layers over the course of an entire mixing season is approximately equal to the initial volume of the mixed layer. Consequently, the nutrient supply is magnified as much as 2-fold by episodic instability in the mixed layer.

The effect of resupply can be superimposed on recycling and a 2% daily loss of nutrients (Fig. 5). The resupply for calculation purposes is assumed to be equal to the original nutrient inventory of the tropical lake and 5% of the original nutrient inventory for the mid-latitude lake. Resupply doubles the metabolic potential of the tropical lake, thus establishing a 2-fold difference between the tropical and temperate lake for the growing season (bottom 2 panels, Fig. 5). If the longer growing season is factored into the comparison, the tropical lake shows as much 4 times the metabolic potential annually as the middle latitude lake.

Overall, current information suggests that the initial burst of production occurring in either a tropical or mid-latitude stratified water column will deplete nutrients from the mixed layer over a short interval under stable stratification (Fig. 6). Recycling is twice as fast during the growing season in tropical mixed layers than in temperate mixed layers, but recycling alone cannot maintain a metabolic advantage for the tropical lake because of the long duration of stratification, during which loss of nutrients from the mixed layer weakens metabolic potential. Offsetting long periods of stratification is episodic exchange between the mixed layer and waters below, which enriches the mixed layers of tropical lakes to a much greater extent than expected for temperate lakes.

**Fig. 5.** Phytoplankton metabolism (m) over the growing season or entire year under 3 conditions, relative to $m_{\text{max}} = 1.0$. 

The diagram shows the distribution of metabolic activity (m) in different layers of the water column (T = Tropical; ML = Mid-latitudes) for daily growing season and annual periods, illustrating the impact of upwelling, nutrient saturation, recycling, and resupply.
Taking these factors together, tropical lakes could be expected to generate 2–4 times as much production over a growing season as a temperate lake for a given nutrient supply. Evidence, although scant at present, suggests that the production multiple is closer to 2 than to 4 (Lewis 1996).

The 2–4 ratio of $\bar{m}$ for phytoplankton in tropical lakes relative to lakes of middle latitudes under similar nutrient loading indicates that tropical lakes produce significantly more organic matter from a given increment of nutrient loading than temperate lakes. In the mixed layer, the more rapid generation of organic matter is accompanied by a correspondingly higher rate of turnover. Because of nutrient resupply, however, a tropical lake should sustain higher mean autotroph biomass. This expectation is consistent with observations of lower temporal variability of phytoplankton biomass and higher ratios of mean to maximum biomass during the growing season of tropical lakes (Lewis 1990).

Control by electron acceptors

Events below the mixed layers of lakes require consideration of electron acceptor abundance and demands, beginning with oxygen. The hypolimnetic waters of tropical lakes, if fully saturated during mixing, can hold only approximately 60% of the oxygen concentration expected for a lake of middle latitude because of the effect of temperature on oxygen saturation (Lewis 1987). In addition, the oxygen inventory would be expected to degrade approximately 5 times faster in a tropical lake than a lake of middle latitude because of the relationship between temperature in $Q_{10}$ and decomposition processes. Thus, the hypolimnion of a tropical lake will become anoxic 5–10 times faster than in a middle latitude lake of similar morphometry and organic content. This is one of the most striking differences between temperate and tropical lakes.

Duration of stratification also influences oxygen content of the hypolimnion. Because the stratification season is very long in tropical lakes and the depletion of initial oxygen reserves can occur quickly, the deeper waters of tropical lakes, except under some special circumstances of extreme oligotrophy and large hypolimnetic volumes, can be expected to be consistently anoxic for periods of 9–10 months per year. In essence, the dominant hypolimnetic condition, even in the absence of human influence, is anoxia in the deep waters of most tropical lakes (Lewis 2000). Thus, biogeochemical processes in the deeper waters of tropical lakes are predominantly anoxic, whereas those of temperate lakes may be either anoxic or oxic, depending largely on the trophic state and mean depth of the lake.

Anoxic metabolism is prokaryotic and involves intensive use of electron acceptors other than oxygen, including nitrate, oxidized iron and manganese, sulfate, and organic matter. Because of the extended period of anoxia and high temperature, prokaryotic metabolism is more likely to bridge a wider range of redox potentials during the course of stratification than it would in lakes of middle latitude, especially those that are not eutrophic (Fig. 7). Thus, the metabolic potential of deep waters in tropical lakes is directly related to the abundance of electron acceptors; the efficient acceptors such as nitrate will support more robust metabolism than less efficient acceptors, such as organic matter. In many tropical lakes, exhaustion of the most efficient electron acceptors may occur before the new production reaching the deeper water is oxidized.
Contrasts in redox potential of hypolimnetic waters in tropical and mid-latitude lakes of similar morphometry and nutrient supply.

Control by organic matter

Predominance of anoxia in the deep waters of tropical lakes is likely to offset in part the tendency of tropical lakes to mineralize autochthonous organic matter. Whereas mineralization occurs rapidly in the mixed layer, it may occur more slowly in the hypolimnion because of the inefficiency of oxidation processes at lower redox potential (Stumm & Morgan 1996).

Extensive production of mineralized reduction products such as sulfide and ammonia in tropical lakes during the stratification season sets the stage for biogeochemical processes that involve reoxidation of these substrates during the mixing period. This phenomenon has not been studied extensively in the context of tropical lakes.

Conclusions

Biogeochemical peculiarities of tropical lakes that distinguish them from lakes of higher latitude are summarized in Table 2. In general, 3 classes of differences emerge: (1) the mixed layers of tropical lakes have metabolic potential for catabolic and anabolic processes that are 2–4 times higher than in lakes of middle latitude, (2) the main factor inhibiting realization of metabolic potential in the mixed layer is nutrient supply, which is relieved substantially in tropical lakes by episodic weakening of stability leading to interchange between layers during the stratification season, and (3) hypolimnetic waters of tropical lakes often are dominated by anoxic processes because of lower oxygen inventory at the time of stratification, more rapid elimination of dissolved oxygen, and a long interval of stratification.

References


Table 2. Metabolic ratios for a mid-latitude lake and a tropical lake.

<table>
<thead>
<tr>
<th>Metabolism</th>
<th>Ratio, Tropical: Mid-latitude</th>
<th>Biogeochemistry</th>
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<tbody>
<tr>
<td>Photosynthesis (Annual, ( \text{mm} ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Photosynthesis, maximum rates</td>
<td>1.8:1</td>
<td>C,N,P CNP</td>
</tr>
<tr>
<td>2. Photosynthesis, no recycle or resupply</td>
<td>1:1</td>
<td>C,N,P CNP</td>
</tr>
<tr>
<td>3. Photosynthesis with Boundary Exchanges</td>
<td>2-4:1</td>
<td>C,N,P CNP</td>
</tr>
<tr>
<td>Heterotrophy – Mixed Layer Potential</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Secondary Production</td>
<td>3.3:1</td>
<td>CNP, CNP (_h) + C,N,P</td>
</tr>
<tr>
<td>2. Decomposition</td>
<td>3.3:1</td>
<td>CNP, C,N,P</td>
</tr>
<tr>
<td>Heterotrophy – Hypolimnic Potential</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Oxic Potential</td>
<td>5:1</td>
<td>CNP, C,N,P</td>
</tr>
<tr>
<td>2. Anoxic Potential</td>
<td>10:1</td>
<td>CNP, C,N,P + S,N,Fe, Mn</td>
</tr>
<tr>
<td>3. Reoxidation Potential</td>
<td>10:1</td>
<td>S,N,Fe,Mn</td>
</tr>
</tbody>
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