# Conceptualizing biogeochemical reactions with an Ohm's law analogy

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**Abstract**

In studying problems like plant-soil-microbe interactions in environmental biogeochemistry and ecology, one usually has to quantify and model how substrates control the growth of, and interaction among, biological organisms. To address these substrate-consumer relationships, many substrate kinetics and growth rules have been developed, including the famous Monod kinetics for single substrate-based growth, Liebig's law of the minimum for multiple-nutrient co-limited growth, etc. However, the mechanistic basis that leads to these various concepts and mathematical formulations and the implications of their parameters are often quite uncertain. Here we show that an analogy based on Ohm's law in electric circuit theory is able to unify many of these different concepts and mathematical formulations. In this Ohm's law analogy, a resistor is defined by a combination of consumers' and substrates'kinetic traits. In particular, the resistance is equal to the mean first passage time that has been used by renewal theory to derive the Michaelis-Menten kinetics under substrate replete conditions for a single substrate as well as the predation rate of individual organisms. We further show that this analogy leads to important insights on various biogeochemical problems, such as (1) multiple-nutrient co-limited biological growth, (2) denitrification, (3) fermentation under aerobic conditions, (4) metabolic temperature sensitivity, and (5) the accuracy of Monod kinetics for describing bacterial growth. We expect our approach will help both modelers and non-modelers to better understand and formulate hypotheses when studying certain aspects of environmental biogeochemistry and ecology.

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**Key Points:**

- Ohm's law is proposed to formulate biogeochemical reactions.
- Ohm's law successfully models multiple substrates co-limited growth.
- Ohm's law may help building unified biogeochemical models.

**Abstract**: In studying problems like plant-soil-microbe interactions in environmental biogeochemistry and ecology, one usually has to quantify and model how substrates control the growth of, and interaction among, biological organisms. To address these substrate-consumer relationships, many substrate kinetics and growth rules have been developed, including the famous Monod kinetics for single substrate-based growth, Liebig's law of the minimum for multiple-nutrient co-limited growth, etc. However, the mechanistic basis that leads to these various concepts and mathematical formulations and the implications of their parameters are often quite uncertain. Here we show that an analogy based on Ohms' law in electric circuit theory is able to unify many of these different concepts and mathematical formulations. In this Ohm's law analogy, a resistor is defined by a combination of consumers' and substrates' kinetic traits. In particular, the resistance is equal to the mean first passage time that has been used by renewal theory to derive the Michaelis-Menten kinetics under substrate replete conditions for a single substrate as well as the predation rate of individual organisms. We further show that this analogy leads to important insights on various biogeochemical problems, such as (1) multiple-nutrient co-limited biological growth, (2) denitrification, (3) fermentation under aerobic conditions, (4) metabolic temperature sensitivity, and (5) the accuracy of Monod kinetics for describing bacterial growth. We expect our approach will help both modelers and non-modelers to better understand and formulate hypotheses when studying certain aspects of environmental biogeochemistry and ecology.

**Plain Language Summary**

Currently, scientists often use ad-hoc or empirical approaches to conceptualize and formulate biogeochemical processes encountered in environmental sciences. Here we propose that many biogeochemical processes can be coherently conceptualized and formulated using an analogy

based on the Ohm's law, a mathematical theory that is widely used to model electric circuits, and also the land-atmosphere exchange of water and energy. We show that this Ohm's law analogy is able to explain observations such as why microbial growth would follow the Monod kinetics, how sometimes fermentation could dominate aerobic respiration when glucose in great supply, how plant and microbes grow under multiple substrates co-limitation, etc. Since this Ohm's law analogy unifies the mathematical foundation of biogeophysics and biogeochemistry, we believe it can potentially lead to more robust land ecosystem models for projecting the climate change.

## 1. Introduction

In earth system modeling, biogeochemistry strongly affects mass and energy exchanges between ecosystems and the physical climate system [*Heinze et al.*, 2019]. Morphologically, biogeochemistry has three pillars: biology, geophysics, and chemistry. In the context of mathematical modeling, geophysics and chemistry generally have much stronger theoretical foundations than biology [*Brutsaert*, 2005; *Stumm and Morgan*, 1996; *Vallis*, 2006], even though all three are macroscale responses that emerge from atomic interactions, which in an ideal (but impractical) scenario can be predicted by solving the Schrödinger equation of all atoms together (so that arguably they all are subtopics of physics) [*Feynman et al.*, 2011b].

In seeking a better understanding of ecological dynamics, e.g., competition and symbiosis, mathematical formulations of the consumer-substrate relationship are essential for both theoretical modeling and interpreting empirical experiments [*Tilman*, 1982]. In the past, three approaches have been used to obtain such relationships. The first approach is by fitting certain empirical response functions to observational data [e.g., *Monod*, 1949]. The second approach is based on an ad-hoc heuristic conceptualization of the problem, e.g., the logistic equation was derived by adding a quadratic term to dissipate the exponential growth of a

population when Pierre-Francois Verhulst (1804-1849) was helping his teacher Alphonse Quetelet (1975-1874) to model human population dynamics [*Cramer*, 2002]. The third approach is based on systematic applications of some theory, such as the law of mass action [*Atkins et al.*, 2016], statistical mechanics [*Ma*, 1985], and renewal theory [*Doob*, 1948]. Notably, Michaelis-Menten kinetics (and some of its extensions) can be derived by applying any of these theories (see reviews in [*Kooijman*, 1998; *Swenson and Stadie*, 2019; *Tang and Riley*, 2013; 2017]), with the renewal theory even being able to show that Michaelis-Menten kinetics is the statistical mean of the stochastic description of a single enzyme molecule processing the substrate molecules [*English et al.*, 2006; *Reuveni et al.*, 2014].

Compared to the empirically-based and ad-hoc approaches, which generally provide limited understanding of the processes implied by the parameters, theory-based approaches have the advantage of linking various related albeit fragmented knowledge (that is abstracted from a much wider range of observations compared to the limited amounts of observational data used by the empirically-based approaches), thereby enabling a deeper understanding of the processes and systems of interest. For instance, when law of mass action is used to derive the Michaelis-Menten kinetics, using the related theory of chemical reaction rates (e.g., Smoluchowski's diffusion model of chemical reaction [*von Smoluchowski*, 1917]), *Tang and Riley* [2019b] were able to upscale the microbially-enabled reactions from one permease to a single bacteria cell and then to a representative soil volume (~O(1 $cm^3$)), and used the results to explain why substrate affinity parameters are highly variable in soil. Additionally, the theory-based approach has been used to derive the temperature response function of microbial activity [*Ghosh and Dill*, 2010], and to explain why Michaelis-Menten kinetics are more appropriate for microbial uptake of

small molecules, while reverse Michaelis-Menten kinetics are more appropriate for enzyme degradation of organic polymer particles [*Tang and Riley*, 2019a].

In this paper, we first introduce an analogy that uses the Ohms' law from electric circuit theory to interpret the resource-consumer relationship. Similar analogies have been widely used by land models to represent the physics of land-atmosphere exchanges of water, gases, and energy [e.g., *Lawrence et al.*, 2019; *Riley et al.*, 2011; *Shuttleworth and Wallace*, 1985; *Wu et al.*, 2009]. (So that in a certain sense, the Ohm's law is unifying all three aspects of biogeochemistry into physics.) We then exploit this analogy to explain several interesting biogeochemical phenomena that are observed in various context. We conclude the paper with recommendations of other potential applications of this analogy.

Although the example problems below are solved with the Ohm's law analogy, we note that they can all be solved using the more accurate Equilibrium Chemistry Approximation (ECA) kinetics [*Tang and Riley*, 2013] or the synthesizing unit plus ECA (SUPECA) kinetics [*Tang and Riley*, 2017]. However, the Ohms' law analogy proposed here is more intuitive and can provide an alternative to the ECA and SUPECA kinetics in formulating biogeochemical models.

## 2 Methods

### 2.1 A brief review of Ohm's law and circuit theory

We below briefly review Ohm's law and the theory of series and parallel resistor circuits. More detailed descriptions of circuit theory can be found in *Feynman et al.* [2011a].

Ohm's law describes the relationship between voltage ($V$), electric current ($I$), and resistor ($r$):

$$I = \frac{V}{r}. \tag{1}$$

To simplify the presentation, we assume that all variables are properly defined with their international units.

For a series concatenation of resistors $r_j$, application of Ohm's law yields

$$I = \frac{V}{\sum_j r_j}. \tag{2}$$

For a parallel concatenation of resistors $r_j$, application of Ohm's law leads to

$$I = V\left(\sum_j \frac{1}{r_j}\right), \tag{3}$$

and the electric current through each resistor is

$$I_j = \frac{V}{r_j}. \tag{4}$$

From equations (3) and (4), we can further derive

$$\frac{I_j}{I} = \frac{1}{1+\left(\sum_{l\neq j}\frac{r_j}{r_l}\right)}, \tag{5}$$

which states that when all other resistors are fixed, the fraction of current through $r_j$ increases with decreasing $r_j$. We will see later that this inference is very useful to explain shifts in metabolic pathways in biological organisms.

**2.2. Michaelis-Menten kinetics interpreted with Ohm's law**

Michaelis-Menten kinetics represents the single-enzyme catalyzed single-substrate reaction velocity $v$ as

$$v = \frac{v_{max}ES}{K+S}, \tag{6}$$

where, in the original application by *Michaelis and Menten* [1913], $v_{max}$ is the maximum specific hydrolysis rate enabled by the invertase and $E$, $S$, and $K$ are enzyme concentration, substrate concentration, and half saturation coefficient, respectively. We note that, for enzymes, $K$ also includes contributions from the dissociation process [e.g., *Briggs and Haldane*, 1925].

By defining $k_f = v_{max}/K$, equation (6) can be rewritten as

$$v = \frac{E}{\frac{1}{v_{max}} + \frac{K}{v_{max}S}} = \frac{E}{\frac{1}{v_{max}} + \frac{1}{k_f S}}. \tag{7}$$

We then note that equations (7) and (1) are of the same form. Therefore, for Michaelis-Menten kinetics, if we apply the Ohm's law analogy by regarding $E$ as voltage and $v$ as current, the corresponding resistance is

$$r = \frac{1}{v_{max}} + \frac{1}{k_f S} = r_E + r_S, \tag{8}$$

where $r_E$ represents the resistance as an intrinsic property (i.e., a kinetic trait) of the enzyme, and $r_S$ represents the resistance introduced by the effective substrate delivery rate towards the enzyme. Further, $r_E$ and $r_S$ are of the unit of time, where (in the renewal theory [e.g., *Kooijman*, 1998]) $r_E$ is the mean time for the enzyme to convert the enzyme-bound substrate molecules into product molecules and $r_S$ is the mean time for the substrate molecules to approach the enzyme molecule and form enzyme-substrate complexes. Together, $r$ is the mean first passage time of the stochastic description of how a single enzyme catalyzes the degradation of the substrate molecules [e.g., *Kooijman*, 1998; *Ninio*, 1987; *Qian*, 2008]. In particular, in many reactions, $k_f$ is approximately proportional to the substrate diffusivity [*Alberty and Hammes*, 1958; *Chou and Jiang*, 1974], such that $k_f S$ is the diffusive substrate flux sensed by enzyme molecules. We then observe that $r_S$ increases with the decrease of diffusive substrate flux, which can result from lower substrate concentration, or lower diffusivity (due to tortuosity, adsorption, or lower moisture in porous media like soil).

That the resistance $r$ in equation (8) is of the time unit has also motivated some researchers to apply the time budget idea to derive predator-prey relationships [e.g., *Holling*, 1959; *Murdoch*, 1973], where $r_E$ is referred as the mean time spent on handling the prey, and $r_S$

is the mean time for the predator to encounter the prey. However, few studies have pointed out the linkage between the time-budget analysis and Ohm's law, except that, based on a suggestion by *Thomsen et al.* [1994], *Almeida et al.* [1997] made an analogy of the membrane electron-transport chain to an electric circuit, and successfully used it to model denitrification. Recently, this method has been used by *Domingo-Felez and Smets* [2020] to build the Activated Sludge Model-Electron Competition (ASM-EC) model, which demonstrated the efficacy of this analogy in constructing robust biogeochemical models. Further, we noticed that the molecular biology of membrane electron transport chains and redox reactions are quite similar to the working principles of chemical batteries [*Schmidt-Rohr*, 2018], thereby motivating us to explore more extensively the applicability of Ohm's law analogy below.

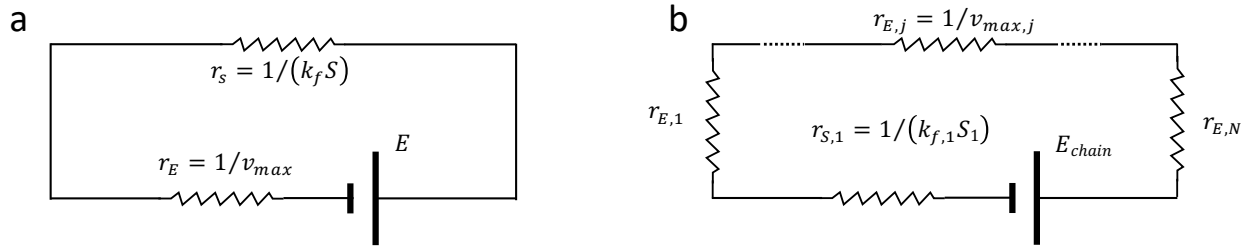


Figure 1**. a.** circuit schema for the Michaelis-Menten kinetics; **b**. series resistor-based schema for an enzyme chain and its reaction on substrate $S_1$, where dotted lines indicate multiple resistors $r_{E,j}$ concatenated in series. Symbols are explained in the main text**.**

In the Ohm's law analogy, kinetic interactions between an enzyme and its substrate molecules can be summarized as the battery-resistor relationship shown in Figure 1a, where the battery potential is enzyme concentration $E$, and the battery's resistance is $r_E$, while the appliance (i.e., substrate) has resistance $r_S$. However, we note that this analogy is accurate only when the substrate is non-limiting for the enzymes (i.e., when MM kinetics are more appropriate [*Tang and Riley*, 2019a]). For cases when substrate is limiting, the reverse Michaelis-Menten kinetics are more appropriate [*Tang*, 2015], and the roles of substrate and enzyme in the analogy

are reversed (such as for enzyme hydrolysis of polymeric organic matter; [*Tang and Riley*, 2019a]). (We note that the ECA kinetics are able to more accurately handle the wide range of substrate abundances with respect to enzymes [*Tang*, 2015].) We next show how the Ohm's law analogy will help us formulate biogeochemical kinetics for various situations.

## 3. Applications

### 3.1 Series resistor circuit-based formulation of chain-like enzyme reactions

Many metabolic pathways consist of a chain of reactions. Such examples include the Calvin-cycle (in photosynthesis), membrane electron transport chain, glycolysis, citric acid cycle, etc., and note that most of these reaction pathways involve cofactors [*Madigan et al.*, 2009; *Taiz and Zeiger*, 2006]. Nonetheless, assuming that at each step the enzyme and its co-factor together form an integrated enzyme unit to process the substrate delivered from a prior step, and the whole chain of enzymatic reactions are in detailed balance (i.e., the whole chain is in steady state without overflow [*Cao*, 2011], an assumption that is often made in flux balance models [*Orth et al.*, 2010]), we can then use the series circuit analogy to calculate the overall enzyme kinetics straightforwardly. According to the schema for this configuration (Figure 1b), when the whole enzyme chain is taken as a catalysis unit, the abundance of enzyme at the first step represents the voltage of the battery, and the total resistance is

$$r_{chain} = \left(\sum_{j=1}^{N} r_{E,j}\right) + r_{S,1} = r_E + r_{S,1}, \tag{9}$$

where $r_{E,j} = v_{max,j}^{-1}$ such that the first right hand side term is the total resistance represented by the maximum catalysis rate of the overall enzyme chain, and $r_{S,1} = \left(k_{f,1}S_1\right)^{-1}$ is the resistance due to the incoming substrate flux to the first enzyme in the chain. For the overall chain, the specific reaction rate for substrate processing is then

$$\frac{v_{chain}}{E_{chain}} = \frac{1}{r_{chain}} = \frac{\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)^{-1} S_1}{\frac{K_1}{v_{max,1}\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)} + S_1} \quad , \tag{10}$$

where $K_1 = v_{max,1}/k_{f,1}$. Equation (10) can be simplified as

$$\frac{v_{chain}}{E_{chain}} = \frac{v_{max,chain} S_1}{K_{chain} + S_1}, \tag{11}$$

with

$$v_{max,chain} = \left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)^{-1} < min_j\{v_{max,j}\}, \tag{12}$$

and

$$K_{chain} = \frac{K_1}{v_{max,1}\left(\sum_{j=1}^{N} v_{max,j}^{-1}\right)} = \frac{K_1}{1 + \sum_{j=2}^{N} v_{max,1}/v_{max,j}}. \tag{13}$$

From equation (10), we assert that an enzyme chain is equivalent to an enzyme unit with kinetic traits $v_{max,chain}$ and $K_{chain}$. Moreover, from equations (12) and (13), we infer that increasing the chain length decreases the overall reaction rate $v_{max,chain}$ (which is even slower than the slowest step) and the half saturation coefficient $K_{chain}$ of the enzyme chain.

Several interesting inferences can be additionally drawn from equations (9)-(13). First, the second law of thermodynamics suggests that a thermal engine has higher thermodynamic efficiency when it runs slower (and the highest efficiency can only be achieved when the system is in thermodynamic equilibrium, i.e., not running at all [*Salamon et al.*, 2001]). Since a longer reaction chain slows down the overall transformation rate from a given substrate to its final product, (as an example,) application of the above equations to electron transport chains leads us to assert that a longer chain will likely be thermodynamically more efficient (this argument echoes the Ladder theorem in finite time thermodynamics; [*Salamon et al.*, 2017]). In contrast, shorter electron transport chains imply faster use of substrates even though they result in less efficient substrate use. Therefore, the length of electron transport chains can characterize the

208 tradeoff between substrate use rate and substrate use efficiency, an important selection factor for
209 organisms during their evolution. Indeed, in one chemostat based study, *Chen et al.* [2017] found
210 that Vibrionales bypass respiratory complex III to consume part of the oxygen using a
211 cytochrome bd terminal oxidase to speed up growth, but the bioenergetic efficiency becomes
212 ~32% as compared to ~80% for the longer canonical respiratory chain. Similarly, observations
213 indicate that the less efficient fermentation pathway which has fewer enzymes involved is faster
214 than the aerobic respiration pathway that has many more enzymes involved (thus is longer and
215 more efficient; [*Madigan et al.*, 2009]). We will later (in section 3.5) use the parallel circuit
216 analogy to explain why such bypassing of more efficient pathways will occur under substrate
217 abundant conditions.

218 The second inference to be made is about the temperature sensitivity of parameters
219 $v_{max,chain}$ and $K_{chain}$. In the simplest one-step case, $v_{max,chain}$ equals $v_{max,1}$, and $K_{chain}$ equals
220 $K_1$. According to transition state theory [e.g., *Eyring*, 1935], $v_{max,1}$ would have the following
221 temperature dependence,

$$v_{max,1} = v_{max,1,ref} T \cdot exp\left(-\frac{\Delta G_1}{RT}\right), \tag{14}$$

222 where $v_{max,1,ref}$ is some reference reaction rate, $T$ is temperature, $\Delta G_1$ is the Gibbs energy of
223 activation, and $R$ is the universal gas constant. Similarly, for a reaction pathway consisting of a
224 chain of enzymes, each $v_{max,j}$ will have a temperature dependence similar to that in equation
225 (14), that is

$$v_{max,j} = v_{max,j,ref} T \cdot exp\left(-\frac{\Delta G_j}{RT}\right), \tag{15}$$

226 which when entered into equation (12), $v_{max,chain}$ will then be of the form

$$v_{max,chain} = \left[\sum_{j=1}^{N}\left(v_{max,j,ref}^{-1} exp\left(\frac{\Delta G_j - \Delta G_1}{RT}\right)\right)\right]^{-1} T \cdot exp\left(-\frac{\Delta G_1}{RT}\right). \tag{16}$$

227 Therefore, if $(\Delta G_j - \Delta G_1)/(RT) \ll 1$, the temperature dependence of $v_{max,chain}$ will be
228 approximately like that in equation (14).

229 The temperature dependence of $K_1$ is determined by the temperature dependencies of
230 $v_{max,1}$ and $k_{f,1}$. Inside the microbial cytoplasm and cell membrane (and also for whole microbial
231 cells in most natural environments), $k_{f,1}$ is closely related to diffusivity [*Madigan et al.*, 2009].
232 Thus, according to the Stokes-Einstein equation of diffusivity ($D = (k_B T)/(6\pi\eta a)$, where $k_B$ is
233 the Boltzmann constant, $\eta$ is the dynamic viscosity, and $a$ is the radius of the spherical particle)
234 [*Feynman et al.*, 2011c], $k_{f,1}$ can be approximated with a linear dependence on temperature
235 divided by the temperature sensitivity of $\eta$ (which is $exp(B/(T - T_{VF}))$, where $B$ and $T_{VF}$ are
236 empirical parameters, according to the semi-empirical Vogel-Fulcher-Tamman-Hesse equation
237 [*Garcia-Colin et al.*, 1989]). When the temperature dependence of $k_{f,1}$ is combined with the
238 Eyring-type temperature dependence of $v_{max,1}$, the definition of $K_1$ ($= v_{max,1}/k_{f,1}$) suggests
239 that its temperature dependence is of the Arrhenius type (because $exp(B/(T - T_{VF}))$ of the
240 viscosity is very similar to the Arrhenius equation, and the linear temperature dependence of $k_{f,1}$
241 cancels out the linear part of the temperature dependence of $v_{max,1}$). Once again, if
242 $(\Delta G_j - \Delta G_1)/(RT) \ll 1$, $K_{chain}$ will probably have an Arrhenius-type temperature sensitivity as
243 well.

244 When the above inferences are put into equation (11), we can then infer the temperature
245 dependence of $v_{chain}$. From chemical thermodynamics, the temperature dependence of $v_{chain}$
246 depends on chemical kinetics (as characterized by the Michaelis-Menten term, i.e., $\frac{v_{max,chain} S_1}{K_{chain} + S_1}$ in
247 this example) and thermodynamics (as a function of the Gibbs free energy) of the enzyme
248 catalyzed reaction. However, because enzymes are proteins, their conformational states are also

temperature dependent [*Murphy et al.*, 1990]. Thermodynamically, the undenatured (aka catalytically active) fraction of an enzyme population of length $n_x$ (as measured by the number of amino acid residues) can be described as [*Murphy et al.*, 1990]

$$f_{ax} = \frac{1}{1+exp\left(-\frac{n_x \Delta G_x}{RT}\right)}, \tag{17}$$

where

$$\Delta G_x = \Delta H^* - T\Delta S^* + \Delta C_p[(T - T_H^*) - Tln(T/T_S^*)], \tag{18}$$

and

$$\Delta C_p = -46.0 + 30(1 - 1.54{n_x}^{-0.268})N_{CH,x}, \tag{19}$$

with heat capacity $\Delta C_P$ defined as the energy required to reorganize the water molecules surrounding the protein [*Ratkowsky et al.*, 2005]. $\Delta C_P$ increases with the non-polar accessible area of the molecule, as measured by $N_{CH,x}$, the average number of non-polar hydrogen atoms per amino acid residue. $\Delta C_p$ also measures the hydrophobic contribution, with higher values implying higher hydrophobicity (and notice that greater $N_{CH,x}$ implies higher hydrophobicity). Other parameters include $\Delta S^*$ as the enthalpy change at $T_S^*$ (the convergence temperature for entropy) and $\Delta H^*$ as the enthalpy change at $T_H^*$ (the convergence temperature for enthalpy), which can be considered to be constant under environmental conditions [e.g., *Ratkowsky et al.*, 2005]. Assuming $N_{CH,x}$ and $n_x$ can be obtained from proteomic data for each type of enzyme [e.g., *Sawle and Ghosh*, 2011], we can then calculate $f_{ax,j}$ for all enzymes involved in the chain. Therefore, putting together the kinetic, thermodynamic, and catalytically active enzyme fraction functions, we obtain

$$v_{chain} = \frac{v_{max,chain}S}{K_{chain}+S} F_T \prod_j f_{ax,j}, \tag{20}$$

where the thermodynamic temperature dependence of the reaction is

$$F_T = 1 - exp\left(-\frac{\Delta G_{reac}}{RT}\right), \tag{21}$$

with $\Delta G_{reac}$ being the Gibbs free energy of the overall reaction being catalyzed, which is defined by the chemical activity of initial substrates and final products [e.g., *Jin and Bethke*, 2007].

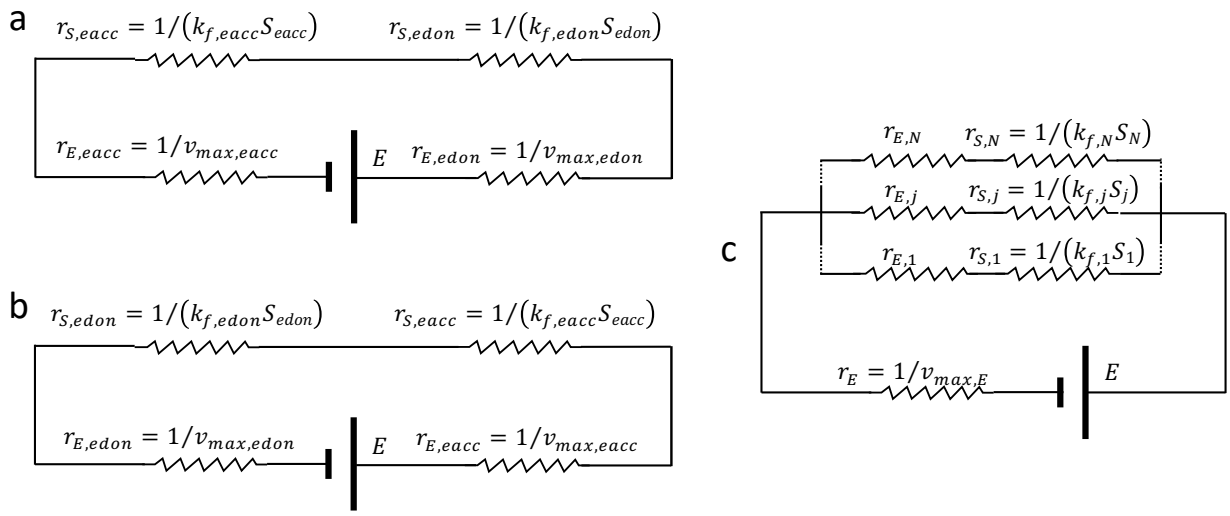


Figure 2. **a**. type-1 circuit schema for redox-type reaction; **b**. type-2 circuit schema for redox-type reaction; **c**. circuit schema for parallel resistor-based schema for competitive enzymatic reactions. Type-1 and Type-2 schema are equivalent, and are not differentiated in the Ohm's law analogy. Symbols are explained in the main text.

Unless equation (20) is applied to organisms capable of growing on alternative electron acceptors or donors, and the system is undergoing fast transition in redox status (e.g., at the depth of the soil water table), $F_T$ is very close to 1, and can be ignored. Therefore, the temperature dependence of $v_{chain}$ is dominated by the kinetic term (i.e., that of the Michaelis-Menten term) and the temperature dependent fraction of active enzymes ($\prod_j f_{ax,j}$). The kinetic term increases with temperature, while the fraction of active enzymes first increases, then decreases with temperature. The overall temperature sensitivity of the reaction chain will be of the form predicted by the macromolecular rate theory (MMRT) (with fine tuning from substrate availability through the kinetic term which MMRT does not consider) [*Arcus et al.*, 2016; *Schipper et al.*, 2014]. Therefore, for a population of cells that are not under substrate limitation

and steadily growing (so that one metabolic pathway dominates the metabolism), one should expect a MMRT type temperature dependence of the metabolic rates. This thus explains why *Ratkowsky et al.* [2005] was able to use the following equation to model bacterial growth rates under unlimited substrate supply:

$$g = \frac{cTexp(-\Delta H_A/RT)}{1+exp\left(-\frac{n}{RT}\left(\Delta H^* - T\Delta S^* + \Delta C_p\left[\left(T-T_H^*\right)-Tln\left(T/T_S^*\right)\right]\right)\right)}, \quad (22)$$

where $g$ is growth rate, $c$ is an empirical constant, and $\Delta H_A$ is substrate dependent activation energy. However, unlike it was historically assumed that properties of some single control enzyme determine the overgrowth [*Johnson and Lewin*, 1946], here $n$ and $\Delta C_p$ represent mean values of protein length and their thermal property, under possible influences from other molecules, such as phospholipids [e.g., *Mansy and Szostak*, 2008].

**3.2 Series resistor-based formulation of enzyme catalyzed redox reactions**

Many biogeochemical processes are of the redox type, including photosynthesis, aerobic respiration, nitrification, anaerobic denitrification, etc. [*Madigan et al.*, 2009; *Taiz and Zeiger*, 2006]. Basically, enzyme catalyzed redox reactions facilitate electron transfers from electron donors to electron acceptors. This process can be summarized with the schema Figure 2a that has one resistor representing electron donors ($r_{S,edon}$), and the other resistor ($r_{S,eacc}$) representing electron acceptors, with the enzyme being the battery. By applying the Ohm's law analogy, the reaction rate is

$$v = \frac{E}{r_{eacc}+r_{edon}}, \quad (23)$$

where $r_{eacc} = \frac{1}{v_{max,eacc}} + \frac{1}{k_{f,eacc}S_{eacc}}$, and $r_{e,acc} = \frac{1}{v_{max,edon}} + \frac{1}{k_{f,edon}S_{edon}}$. When the two are combined, equation (23) can be rewritten as

$$v = \frac{E}{r_E + \frac{1}{k_{f,eacc}S_{eacc}} + \frac{1}{k_{f,edon}S_{edon}}}. \tag{24}$$

with $r_E = \frac{1}{v_{max,eacc}} + \frac{1}{v_{max,edon}}$, $r_{S,eacc} = \frac{1}{k_{f,eacc}S_{eacc}}$, and $r_{S,edon} = \frac{1}{k_{f,edon}S_{edon}}$. We note that in this series resistor-based formulation, the total resistance (or mean first passage time) does not include the discount resulting from the concurrent binding of electron donors and acceptors to the enzyme (i.e., configuration Figure 2b is as good as Figure 2a, and they have the same resistance). However, this discount can be incorporated by renewal theory (or law of mass action), which leads to the synthesizing unit (SU) model [*Kooijman*, 1998] below

$$v = \frac{E}{r_E + \frac{1}{k_{f,eacc}S_{eacc}} + \frac{1}{k_{f,edon}S_{edon}} - \frac{1}{k_{f,eacc}S_{eacc} + k_{f,edon}S_{edon}}}. \tag{25}$$

Compared to equation (24), the SU model (i.e., equation (25)) is numerically more accurate (in approximating the law of mass action, the standard method that deals with biogeochemical reactions [*Koudriavstev et al.*, 2001]). Equations (24) and (25) differ by the additional term $-1/\left(k_{f,eacc}S_{eacc} + k_{f,edon}S_{edon}\right)$ that accounts for the co-existence of schemas in Figure 2a and Figure 2b.

Equation (24) was derived as early as in *Alberty* [1953], and is called the additive model. It was found as the superior formulation to model multiple nutrient limitations of microbial and plant growth in *O'Neill et al.* [1989] (where electron donors and acceptors are replaced with complementary nutrients, such as nitrogen and phosphorus). In particular, the additive model equation (24) can be extended to include arbitrary number of nutrients:

$$v = \frac{E}{r_E + \sum_j \frac{1}{k_{f,j}S_j}}. \tag{26}$$

where $S_j$ can be essential nutrients including carbon, nitrogen, phosphorus, potassium, chloronium, etc. *Smith* [1976; 1979] used equation (26) to model plant growth and microbial

growth under carbon, nitrogen, phosphorus, and potassium co-limitation. Based on past successful applications [*Franklin et al.*, 2011; *Kooijman*, 1998], the SU model (i.e., equation (25)) may be argued as mathematically more rigorous than the series resistor-based additive model (i.e., equation (24) or (26)). However, given the usually significant uncertainty of ecological data, the series resistor-based additive model may be equally good. Indeed, when we applied both the SU model and the resistor-based additive model to the measured algal growth rates under various levels of phosphorus and vitamin $B_{12}$ additions [*Droop*, 1974], both models can be satisfyingly calibrated with respect to the growth data (Figure 3a and b). Further, when the normalized growth rates are contoured as a function of the normalized substrate fluxes, the SU and resistor-based additive models show very similar growth patterns (Figure 3c and d). The SU model and additive model also performed equally well for the plant growth data from *Shaver and Melillo* [1984] (Figure 4). Moreover, when the SU model and additive model are used to model aerobic heterotrophic respiration using the parameterization from *Tang and Riley* [2019b], we once again find the two models resulted in very similar goodness of fit with respect to the measurements (Figure 5). These lines of evidence suggest that one can probably use these two models alternatively. In particular, both can be a substitute for Liebig's law of the minimum that is used by most existing biogeochemical models [*Achat et al.*, 2016].

Additionally, we note that equation (26) can be extended into a photosynthesis model to replace the Farquhar or Collatz model that is formulated based on Liebig's law of the minimum, which has to arbitrarily smooth the abrupt transitions from one limiting process to another [e.g., *Collatz et al.*, 1990; *Collatz et al.*, 1992; *Farquhar et al.*, 1980; *Kirschbaum and Farquhar*, 1984]. In this context, we contend that it is possible to use the same kinetics to formulate models

of plant photosynthesis, microbial substrate dynamics, and biomass growth, a strategy that will likely enhance the mathematical coherence in modeling plant-soil-microbial interactions.

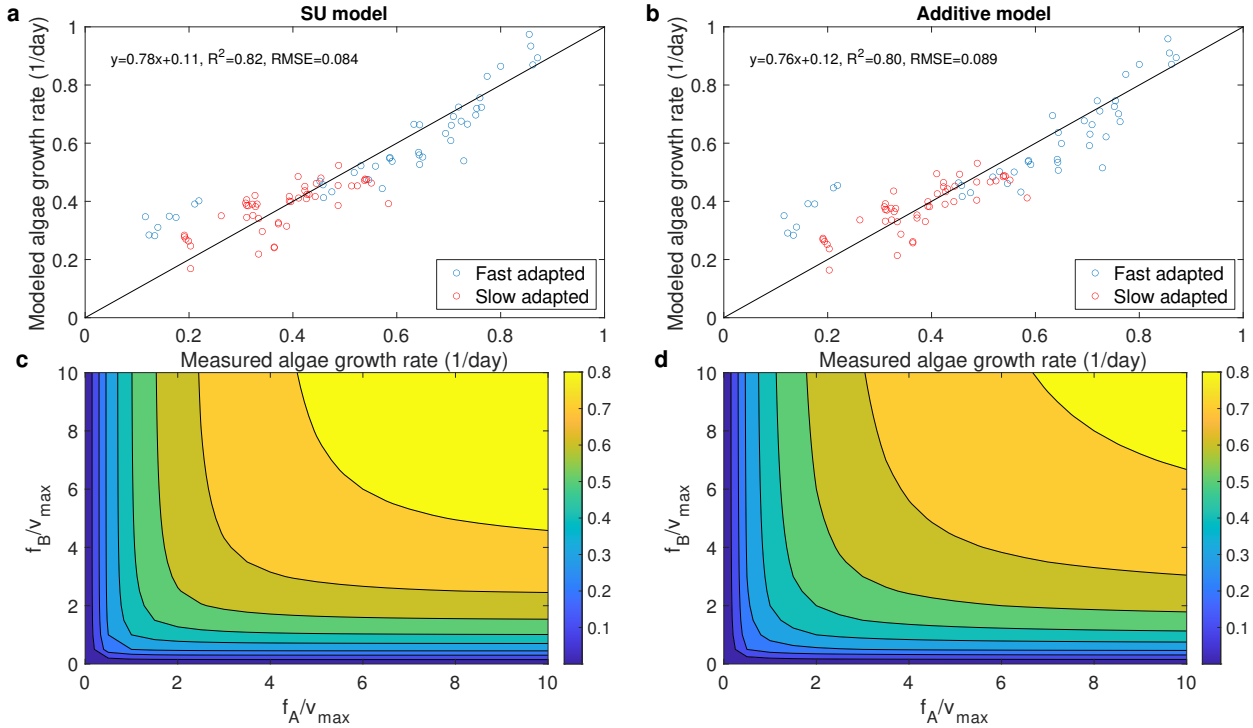


Figure 3 **a** comparison of the calibrated synthesizing unit (SU) model prediction for the algal growth rates data from *Droop* [1974]; **b** same as **a** but from the calibrated resistor-based additive model; **c** contour of normalized growth rate as a function of normalized fluxes of substrates A and B for the SU model; **d** same as **c** but for the resistor-based additive model. The additive model is presented as equation (24), and the SU model is presented as equation (25). Model parameters are in Table S1 of the supplemental material.

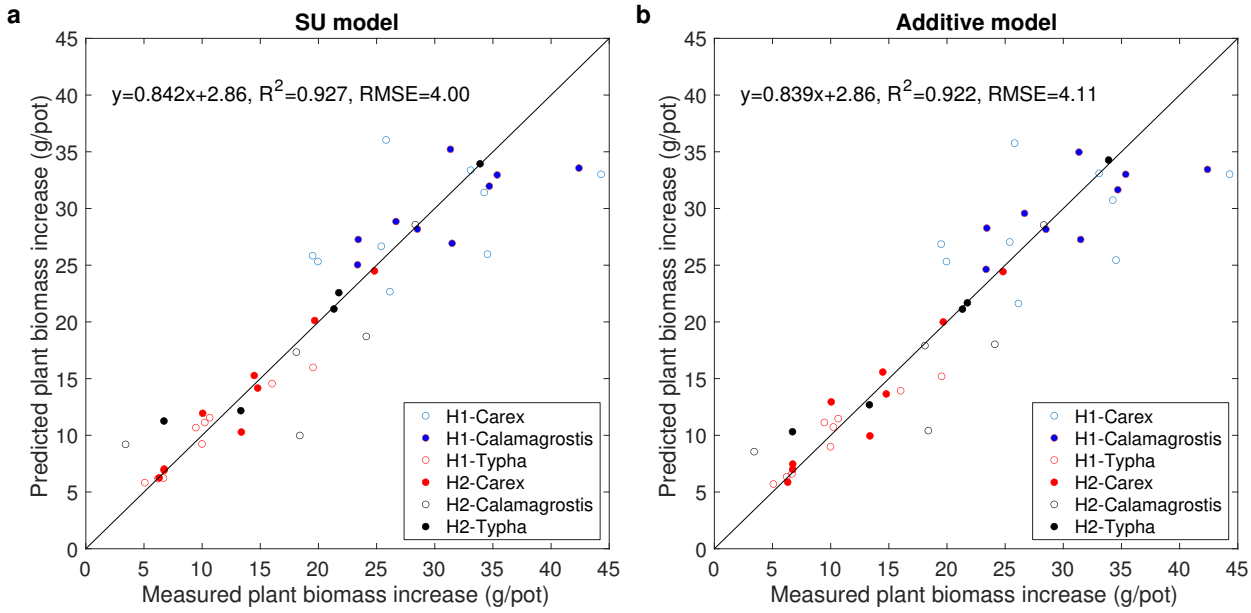


Figure 4 **a** SU model predicted vs measured plant growth; **b** Additive model predicted vs measured plant growth. The data is from *Shaver and Melillo* [1984]. Model parameters are in Table S1 of the supplemental material.

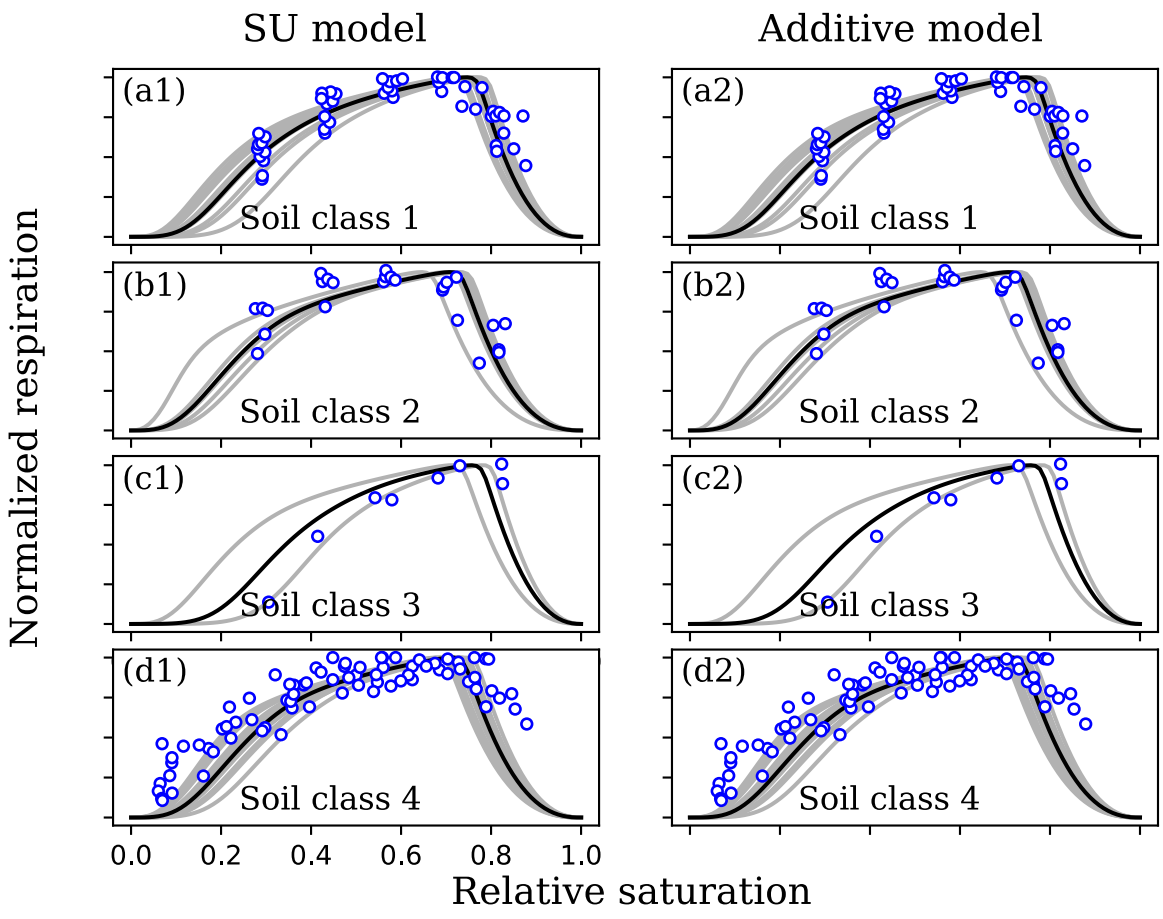


Figure 5. Left panels are SU model-based prediction of respiration-soil-moisture relationship; right panels are based on the resistor-based additive model. The two models used identical parameters, which are detailed in *Tang and Riley* [2019b]. The statistics for model-data fitting (in terms of linear regression and root mean square error) between two models are identical to 0.01 (see Table S2 of the supplemental material).

### 3.3 Parallel resistor-based formulation of competitive kinetics

Many microorganisms can feed on multiple substrates. For example, *E.coli* and yeasts are able to perform both aerobic and anaerobic respiration [e.g., *Dashko et al.*, 2014; *Unden and Bongaerts*, 1997]. Meanwhile, some enzymes can react on different substrates, e.g., enzyme ribonuclease is able to degrade various RNA molecules [*Etienne et al.*, 2020]. Thus, we next show that such problems can be formulated using the parallel circuit (plus one series resistor) analogy.

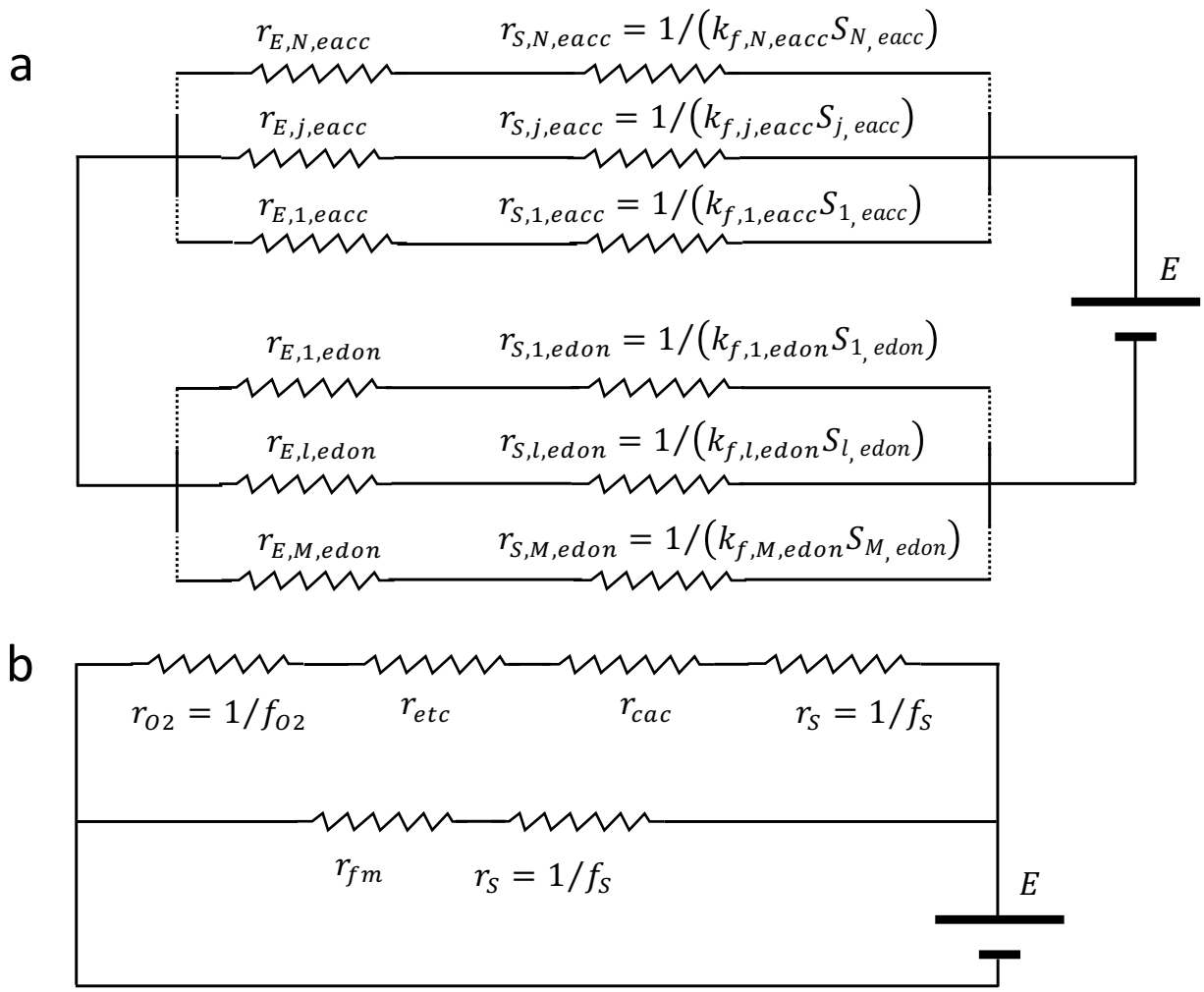


Figure 6. **a** mixed resistor circuit schema for redox reactions with alternative electron donors and acceptors; **b** circuit schema for the parallel fermentation and aerobic respiration pathways. Symbols are explained in the main text.

We first formulate the competitive Michaelis-Menten kinetics using the schema in Figure 2c. For this case, the total resistance is

$$r = r_E + r_S = r_E + \left(\sum_j \left(r_{E,j} + r_{S,j}\right)^{-1}\right)^{-1}, \tag{27}$$

where ${r_{S,j}}^{-1} = k_{f,j}S_j$, and $r_{E,j}$ is the resistance due to preprocessing of substrate $S_j$ before it is handed to the central enzyme $E$ (i.e., the enzyme that products of all substrates have to pass through), and $r_E = 1/v_{max,E}$ is the resistance due to the maximum substrate processing rate of

the central enzyme (which for redox-reactions could be determined by the time spent on processing the electron donors if $S_j$ here are electron acceptors). If $r_{E,j} = 0$, which is usually assumed for competitive Michaelis-Menten kinetics, the second term $r_S$ becomes $\left(\sum_j k_{f,j} S_j\right)^{-1}$, and the reaction velocity is

$$v = \frac{E}{r} = \frac{E}{\frac{1}{v_{max}} + \left(\sum_j k_{f,j} S_j\right)^{-1}}, \tag{28}$$

and the corresponding flux through pathway $j$ is

$$v_j = \frac{v r_S}{r_{S,j}} = v \frac{k_{f,j} S_j}{\sum_l k_{f,l} S_l} = E \cdot \frac{v_{max} S_j / K_j}{1 + \sum_l S_l / K_l}, \tag{29}$$

where $K_j = v_{max} / k_{f,j}$. It is easy to see that $v_j$ is the reaction velocity computed from the competitive Michaelis-Menten kinetics. We note that equation (29) is meaningful only when pathway $j$ produces new molecules. However, even for inhibitors, whose binding to enzymes does not produce new molecules, if we regard dissociation as a way of producing new molecules, then equation (29) is still mathematically meaningful.

### 3.4 Mixed series and parallel resistor-based formulation of redox reactions of alternative electron donors and acceptors

Many microorganisms (such as denitrifying bacteria; e.g., *Robertson and Groffman* [2015]) are able to grow on different electron donors and acceptors. Such problems can be solved using the SUPECA kinetics [*Tang and Riley*, 2017]. Below we formulate it using the schema of mixed series and parallel resistors.

Based on the schema in Figure 6a, the total resistance is

$$r = r_{edon} + r_{eacc} = \left(\sum_l {r_{l,edon}}^{-1}\right)^{-1} + \left(\sum_j {r_{j,eacc}}^{-1}\right)^{-1}, \tag{30}$$

where the resistance for electron donors is

$$r_{l,edon} = r_{E,l,eacc} + r_{S,l,eacc} = \frac{1}{v_{max,l,eacc}} + \frac{1}{k_{f,l}S_{l,eacc}}, \tag{31}$$

and the resistance for electron acceptors is

$$r_{j,eacc} = r_{E,j,edon} + r_{S,j,edon} = \frac{1}{v_{max,j,edon}} + \frac{1}{k_{f,j,edon}S_{j,edon}}. \tag{32}$$

Accordingly, the corresponding reaction flux through electron donor $j$ is

$$v_{j,edon} = \frac{E}{r}\frac{r_{edon}}{r_{j,edon}} = \frac{E}{r_{j,edon}}\frac{r_{edon}}{r_{edon}+r_{eacc}}, \tag{33}$$

while the corresponding reaction flux through electron acceptor $j$ is

$$v_{j,eacc} = \frac{E}{r}\frac{r_{eacc}}{r_{j,eacc}} = \frac{E}{r_{j,eacc}}\frac{r_{eacc}}{r_{edon}+r_{eacc}}. \tag{34}$$

Now considering an application that involves two electron acceptors, e.g., nitrate and nitrite in denitrification, we have

$$\frac{1}{r_{eacc}} = \frac{1}{r_{NO3}} + \frac{1}{r_{NO2}}, \tag{35}$$

which when combined with equation (34) leads to

$$v_{NO3} = \frac{E}{r_{NO3}+r_{edon}+r_{edon}r_{NO3}/r_{NO2}}, \tag{36}$$

and

$$v_{NO2} = \frac{E}{r_{NO2}+r_{edon}+r_{edon}r_{NO2}/r_{NO3}}, \tag{37}$$

which are just the equations (10) in *Almeida et al.* [1997] that have been successfully used to fit the measurement of denitrification rates from *Almeida et al.* [1995]. With proper number of resistors, the denitrifier model by *Domingo-Felez and Smets* [2020] can also be easily recovered from equations (30)-(34).

### 3.5 Other potential applications of the Ohm's law analogy

Besides the applications described above, we below use the Ohm's law analogy to derive some quite interesting results.

411 First, we will explain why fermentation can occur even when there is still oxygen to
412 support the energetically more efficient aerobic respiration. Such a phenomenon is called the
413 Warburg effect (i.e., lactate producing aerobic fermentation) in proliferating mammalian cells (a
414 phenomenon important to the understanding of cancer development), or the Crabtree effect (i.e.,
415 ethanol fermentation) of unicellular yeast Sacchamoyces cerevisiae [e.g., *de Alteriis et al.*, 2018].
416 *E. coli* have also been observed to shift to the seemingly less efficient yet faster metabolic
417 pathways under high substrate concentrations [e.g., *Flamholz et al.*, 2013; *Labhsetwar et al.*,
418 2014]. Depending on the details to be represented, we acknowledge that there are multiple ways
419 to model such phenomenon even with the circuit analogy. We next present one of these
420 mathematical explanations to show that, under certain aerobic conditions, high glucose
421 concentration makes fermentation more favorable.
422 According to the schema in Figure 6b, the specific ATP generation rate from the
423 fermentation pathway is

$$v_{FM,ATP} = \frac{Y_{FM}}{\frac{1}{f_S}+r_{fm}}, \tag{38}$$

424 where $f_S$ is the incoming flux of pyruvate (produced from glycolysis) sensed by the two
425 metabolic pathways (which is proportional to the incoming glucose flux sensed by the organism
426 under steady-state), $r_{fm}$ is the resistance associated with the conversion of pyruvate into
427 fermentation products (which could be lactate, ethanol, or acetate depending on the organism;
428 [*Madigan et al.*, 2009]), and $Y_{FM}$ is the ATP yield of fermentation. Similarly, the specific ATP
429 generation rate from the aerobic respiration pathway is

$$v_{AO,ATP} = \frac{Y_{AO}}{\frac{1}{f_S}+r_{cac}+r_{etc}+\frac{1}{f_{O2}}}, \tag{39}$$

where $r_{acc}$ and $r_{etc}$ are resistance associated with the citric acid cycle, and the electron transport chain, respectively. $f_{O2}$ is the incoming oxygen flux, and $Y_{AO}$ is the ATP yield of aerobic respiration. Because the citric acid cycle involves many more enzyme-catalyzed steps than fermentation, $r_{cac} > r_{fm}$. Meanwhile, $Y_{AO}$ is about 20 times the value of $Y_{fm}$[*Madigan et al.*, 2009].

In a metabolically active organism, for fermentation to be more favorable than aerobic respiration, the following condition needs to be satisfied,

$$\frac{Y_{FM}}{Y_{AO}} > \frac{\frac{1}{f_S}+r_{fm}}{\frac{1}{f_S}+r_{cac}+r_{etc}+\frac{1}{f_{O2}}} > \frac{r_{fm}}{r_{cac}+r_{etc}+\frac{1}{f_{O2}}}, \tag{40}$$

where the term after the second ">" suggests that fermentation is more favorable only when oxygen is below a certain level of availability (note that $f_{O2}$ is approximately proportional to diffusion). When the oxygen availability is sufficiently low, higher substrate concentration (i.e., greater $f_S$) will make fermentation more effective in generating ATP. If we further consider that the fermentation pathway requires the organism to maintain a much smaller number of enzymes than required for the aerobic oxidation pathway (which is equivalent to increase the value of $Y_{FM}/Y_{AO}$, making the inequality (40) easier to be satisfied), we can expect fermentation to be preferred for high supply of glucose (i.e., greater $f_S$) even under certain aerobic conditions. (For anaerobic condition, $f_{O2}$ approaches zero, and the inequality (40) is easily satisfied). Given the significance of this problem in various contexts, including methane and hydrogen dynamics in environment and industrial biogeochemistry [*Lu et al.*, 2009; *Madigan et al.*, 2009], we expect to study this problem in a more quantitative and extensive way elsewhere.

Another very interesting application is to qualitatively explain why Monod kinetics can fit the substrate-growth rate relationship of an exponentially growing bacterial population

[*Monod*, 1949]. The argument goes like the following. For an exponentially growing bacterial population, the bacteria proteomes are in steady state. Meanwhile, from the Ohm's law analogy described here, we know that any functioning circuit-network can be equivalently represented by a bulk resistor. Therefore, we contend that however complex the circuit representation of a bacterial metabolism would be, it as a whole can be equivalently represented by a resistor $r_E$. When this $r_E$ is combined with the resistance associated with the incoming substrate flux (see equation (7)), we say that the bacterial growth would very likely follow the Monod kinetics. However, when the bacteria are in transition from one metabolic state into another, extra resistors are introduced accompanying the change of proteomes, and Monod kinetics will fail for such situations [e.g., *Erickson et al.*, 2017]. This argument also explains why models based on flux balance analysis with proteomic constraints can simulate steadily growing *E. coli* and yeast realistically [*Labhsetwar et al.*, 2014; *Labhsetwar et al.*, 2017].

**3.6 Limitations of the Ohm's law analogy**

While the Ohm's law analogy can be used to model many challenging biogeochemical processes, it is not appropriate for all types of networks. For instance, it is not able to properly couple two or more consumers (i.e., two or more batteries) within a single circuit network, even though the electric-circuit theory itself does not forbid such a configuration to occur (which can be solved with the Kirchhoff's law of voltage and current [e.g., *Feynman et al.*, 2011a]). Rather, such coupling can only be done by first representing the substrate dynamics of each consumer separately, and then coupling them together by differential equations. Such coupling could be critical when many consumers are competing for a limited substrate, even though none of the consumers is substrate-limited when other consumers are excluded [e.g., *Etienne et al.*, 2020]. The equilibrium chemistry approximation (ECA) kinetics [*Tang and Riley*, 2013] and its progeny

SUPECA kinetics [*Tang and Riley*, 2017] are more capable of resolving such situations. In soil biogeochemistry, one such situation is to model the interaction of a substrate molecule (e.g., ammonium, inorganic phosphorus, or dissolved organic carbon) that is simultaneously undergoing uptake by organisms and adsorption by mineral surfaces. Fortunately, a simple remedy is possible for the Ohm's law analogy from the ECA kinetics. In the ECA kinetics, microbial uptake of substrate $S$ under the influence of adsorption by mineral surface $M$ (with affinity parameter $K_M$) is

$$F = \frac{v_{max}SB}{K+S+MK/K_M+\alpha B}, \tag{41}$$

where $K$ is the half saturation constant for the uptake of $S$ by microbe $B$ in the absence of $M$, and $\alpha B$ is the within-population competition effect introduced by ECA. *Tang and Riley* [2019a] showed that $\alpha B$ is negligible due to the large size contrast between microbes (and likewise fine roots) and substrate molecules. When $\alpha B$ is ignored, equation (41) becomes

$$F = \frac{B}{\frac{1}{v_{max}}+\frac{1}{k_f S}\left(1+\frac{M}{K_M}\right)} = \frac{B}{\frac{1}{v_{max}}+\frac{1}{k_f^* S}}, \tag{42}$$

with

$$k_f^* = k_f \Big/ \left(1+\frac{M}{K_M}\right). \tag{43}$$

Now the Ohm's law analogy will still work if $1/k_f^* S$ is used to defined the substrate dependent resistance. Moreover, equation (43) suggests that mineral surfaces may slow the microbial uptake of substrate $S$ by effectively reducing the substrate delivery rate towards the microbes. However, when the sizes of substrates and competitors are similar (e.g., in some predator-prey relationships), the Ohm's law analogy will be too cumbersome to apply, and the ECA or SUPECA kinetics should be used. Nonetheless, it will be very interesting and helpful to

construct and compare models for the same system using both the Ohm's law analogy and ECA (or SUPECA) kinetics.

## 4 Conclusions

By applying the mathematical similarity between the Ohm's law and Michaelis-Menten kinetics, we show that the electric circuit analogy can be used to derive many interesting results of biogeochemical kinetics. We show this approach reproduces many successful applications in the literature, including aerobic heterotrophic respiration, multi-nutrient co-limited microbial (and plant) growth, denitrification dynamics, etc. This approach also sheds new insights on the Warburg and Crabtree effect in prokaryotes and eukaryotes, and conceptually explains why the Monod relationship accurately represents the kinetics of steadily-growing bacterial populations, and why flux balance modeling with proteomic constraints is able to accurately model microbial growth. Based on these results, we expect that the Ohm's law analogy will help build a unified kinetic modelling framework of microbial and plant biogeochemistry to make more robust predictions.

## Data Availability Statement

Data is available through *Shaver and Melillo* [1984], *Droop* [1974], *Franzluebbers* [1999], and *Doran et al.* [1990].

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**Author contributions**

JYT conceived the idea and did the analysis; JYT, WJR, GLM and ELB discussed the analysis and wrote the paper.

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