Abstract  In oil production, a substantial part of the oil originally in place is not recovered after water flooding. A potential tertiary method for enhancing oil recovery is to utilize the activity of microorganisms, which are either present in or injected into the oil reservoirs. This is microbial enhanced oil recovery (MEOR), where microorganisms convert substrate to recovery enhancing products and more bacteria within the reservoir. We develop a mathematical model describing the process of microbial petroleum recovery. The one-dimensional isothermal model comprises displacement of oil by water containing bacteria and substrate for their feeding. The metabolites of bacterial activity (surfactants) result in decrease of the residual oil saturation and in better petroleum recovery. Several MEOR effects exist, where one important is reduction of water-oil interfacial tension by microorganisms producing surfactant. Different methods for incorporating surfactant induced reduction of interfacial tension into models are investigated. Surfactant is partitioned between both phases determined by a distribution coefficient. However, the effect from the metabolites is not necessarily restricted to influence only interfacial tension, but it can also be an approach for changing wettability or viscosity. The computations predict that substantial amount of surfactant is produced in the reservoir affecting the final recovery. A considerable effect is not reached at the entrance of the reservoir like under surfactant flooding, but rather after a given period of time needed for bacterial growth. Efficient surfactants decreasing interfacial tension several orders of magnitude should be produced by bacteria in order to achieve reasonable improvement of the recovery, where bacterial growth rate should be maintained in the reservoir. The partitioning of surfactant and the injection composition are found to have a significant influence on the saturation distribution in the reservoir as well as on the ultimate oil recovery.

Keywords  Microbial enhanced oil recovery · reactive transport · porous media · modeling · bacteria · surfactant · interfacial tension · relative permeability

1 Introduction

The biotechnology research has advanced and the oil industry has matured to consider microorganisms in the context of oil production. Both indigenous and injected microorganisms are used and it depends on their applicability of the specific reservoirs. In microbial enhanced oil recovery (MEOR), bacteria are often used as they are small and have several useful features.

The MEOR purpose is, like other EOR methods, to mobilize the residual oil and thus reduce its content and/or increase the sweep efficiency. MEOR addresses the same physical parameters as chemical EOR, where they are subject to the same in situ technical difficulties. The essential difference between MEOR and chemical EOR resides in the method of introducing the recovery-enhancing chemicals into the reservoir. Enhancement of the oil recovery through microbial action can be performed through several mechanisms:
• Reduction of oil-water interfacial tension and alteration of wettability by surfactant production and bacterial presence.
• Selective plugging by bacteria and their metabolites.
• Viscosity reduction by gas production or degradation of long-chain saturated hydrocarbons.
• Generation of acids that dissolve rock improving absolute permeability.

Especially, the two first mechanisms are believed to have the greatest impact on recovery. Islam (1990) presented a mathematical model for MEOR, where bacterial growth lead to plugging, reduction of oil viscosity and interfacial tension, and production of gas. Interfacial tension was directly correlated with bacterial concentration avoiding direct use of surfactants in the model, but it was concluded that surfactant mechanism seemed the most promising to improve the oil recovery. Chang et al. (1991) developed a mathematical model describing adsorption, growth and decay of microorganisms, consumption of nutrients, and other physical processes. Porosity and permeability was changed due to deposition of microorganisms. They demonstrated that the oil recovery increased by bacterial plugging. Beheshrt et al. (2008) have developed a MEOR model, where several mechanisms are taken into account; surfactant production and adsorption, salinity effects, adsorption of microorganisms, reduction of interfacial tension, and wettability changes. Polymer is additionally injected creating an EOR effect reducing permeability and viscosity. With this combination of methods, the oil recovery was shown to increase.

In this work, bacteria produce surfactants by consumption of substrates. Surfactant decreases oil/water interfacial tension and can be distributed between both phases. Several methods are used to model relative permeability changes as a function of interfacial tension. We use a correlation between surfactant concentration and interfacial tension. Generally, a reduction of interfacial tension decreases residual oil saturation and straightens the relative permeability curves approaching full miscibility (Coats, 1980; Al-Wahaibi et al., 2006). Some methods use interpolation of different parameters and others apply capillary number and residual oil dependencies or use a capillary number dependent interpolation function (Al-Wahaibi et al., 2006). This work investigates three methods; 1) capillary number and normalized residual oil saturation correlation, 2) Coats interpolation between relative permeability curves, and 3) interpolation of parameters of Corey type relative permeability curves (Green and Willhite, 1998; Coats, 1980). We investigate different distributions of surfactant between phases and the effect of bacterial growth rate. The saturation profiles with specific MEOR features are presented together with the improved oil recovery curves.

2 Model Description

The reactive transport model describes convection, bacterial growth, substrate consumption, and metabolite production, where metabolite is surfactant. It is two-phase flow comprising five components; oil \( o \), water \( w \), bacteria \( b \), substrate \( s \) and metabolite/surfactant \( m \). The water phase may consist of water, bacteria, substrate and metabolite. The oil phase consists primarily of oil, but contains also metabolite, see figure 1 illustrating components and phases of the flow system. Surfactant can lower the oil/water interfacial tension \( \sigma \) that has an effect on relative permeability curves. Only metabolite will have index for both component and phase as it is the only component existing in both phases. The following model assumptions are made:

• Fluid flow is one dimensional.
• Bacterial growth rate can be described by Monod kinetics being independent on temperature, pressure, pH and salinity.
• Metabolite is surfactant and can be distributed between both phases according to a distribution constant \( K_i \) and masses of water and oil.
• Neglecting adsorption of bacterial and thus plugging porous medium by bacteria.
• No substrate and metabolite adsorption to pore walls.
• Fractional flow function is used as capillary pressure is considered negligible.
• Negligible diffusion and chemotaxis.
• Isothermal system with incompressible flow.
• No volume change on mixing.
The transport equations for each component is given as:

\[
\frac{\partial}{\partial t} \left( \phi \sum_{j=1}^{n_p} \omega_{ij} \rho_j s_j \right) + \frac{\partial}{\partial x} \left( v \sum_{j=1}^{n_p} \omega_{ij} \rho_j f_j \right) = \phi q_i, \quad i = \{o, w, b, s, m\}
\]

where \( j \) is the phase, \( i \) is the component, \( n_p \) is the number of phases, \( \omega_{ij} \) are component mass fractions in phase \( j \), \( v \) is the linear velocity, \( \rho_j \) is the phase density, \( f_j \) is the fractional flow function of phase \( j \), \( x \) is the length variable, \( t \) is the time, \( \phi \) is the porosity, and \( q_i \) is the source term for component \( i \) also comprising the reaction terms.

2.1 Bacterial growth, consumption and production

A growth rate expression for microorganisms is the well-known Monod expression derived from enzyme kinetics (Chang et al., 1991; Islam, 1990; Nielsen et al., 2003; Zhang et al., 1992). The growth rate is

\[
\mu = \frac{\mu_{\text{max}} C_s}{K_s + C_s},
\]

\( K_s \) is half-saturation constant, \( \mu_{\text{max}} \) maximum growth rate, and \( C_s \) is the limiting substrate mass concentration in the water phase. Other forms of the growth rate term exist, where e.g. substrate and metabolite inhibition occurs or there are more limiting substrates (Nielsen et al., 2003). The model is simplified, so only the important metabolic products and substrates needs to be modeled.

The growth rate enters the conservation law for bacteria. The corresponding source term \( q_b \) is expressed as

\[
q_b = Y_{sb} C_b \mu,
\]

where \( Y_{sb} \) is the yield of bacteria on substrate. The source terms for the other equations are:

\[
q_m = Y_{sm} C_b \mu,
\]

\[
q_s = -q_b - q_m,
\]

and \( C_b \) is the bacterial mass concentration of the water phase, \( Y_{sm} \) is the yield of surfactant (\( m \)) on substrate (Nielsen et al., 2003; Zhang et al., 1992). Converted substrate become either bacteria or surfactant.

2.2 Relative Permeabilities

For the relative permeability curves for oil \( k_{ro} \) and water \( k_{rw} \), the Corey correlations are used (Lake, 1989).

\[
k_{ro} = k_{rowi} \left( \frac{1 - s_w - s_{or}}{1 - s_{wci} - s_{or}} \right)^b
\]

\[
k_{rw} = k_{rwor} \left( \frac{s_w - s_{wc}}{1 - s_{wci} - s_{or}} \right)^a
\]

where \( s \) is water saturation, \( k_{rowi} \) endpoint relative permeability for oil (at \( s_{wci} \)), \( k_{rwor} \) endpoint relative permeability for water (at \( 1 - s_{or} \)), \( s_{wci} \) initial water saturation, \( s_{or} \) residual oil saturation, and exponents for water and oil is \( a \) and \( b \), respectively. The fractional flow function of phase \( j \) is \( f_j \) and is calculated from the relative permeabilities for water and oil.
2.3 Partitioning of surfactant

Partitioning of surfactant depends on the distribution constant $K_i$. Surfactant in water and oil phase are $\omega_{mw}$ and $\omega_{mo}$, respectively, and it distributed according to:

$$\frac{\omega_{mW}}{\omega_{mo}} = K_i \frac{\omega_w}{\omega_o}$$

where surfactant exists in small amounts compared to water and oil. A large distribution coefficient means that most surfactant is present in the water phase. The relative permeabilities depend on the water phase mass concentration, so when surfactant is moved into the oil phase, there will be a smaller effect from the surfactant. The surfactant concentration in the water phase must reach a certain threshold, before surfactant reduces interfacial tension. Therefore, the distribution works as a disappearance term, where the amount of efficient surfactant is reduced.

2.4 Surfactant effect

The surfactant affects the relative permeability curves through interfacial tension reduction. In many cases, the correlation curve between surfactant concentration and interfacial tension looks as shown in figure 2. Water flooded systems have interfacial tensions between oil and water that are around 20-30 mN/m. In order to increase recovery significantly, a good surfactant should decrease interfacial tension three or four orders of magnitude (Fulcher et al., 1985; Shen et al., 2006).

![Figure 2: Different curves for concentration of surfactant $C_m$ against interfacial tension $\sigma$. After a certain concentration of surfactant is reached, the further concentration increases does not change $\sigma$ (critical micelle concentration has been reached) (Lake, 1989).](image)

Relative permeability curves show a clear dependence on $\sigma$. A lower $\sigma$ decreases capillary resistance, which results in relative permeability curves with reduced curvature and smaller residual saturations. When $\sigma$ reaches zero, curves approach a unit slope line for which the relative permeability is simply equal to the phase saturation (Al-Wahaibi et al., 2006).

2.4.1 The capillary number method

The capillary number $N_{ca}$ is ratio of viscous to capillary forces and thus being dependent on changes in interfacial tension $\sigma$.

$$N_{ca} = \frac{\mu_w v}{\sigma_{ow}}$$

where $N_{ca}$ is the dimensionless capillary number, $\mu$ is viscosity of displacing fluid and $v$ is the ‘characteristic’ linear velocity (Green and Willhite, 1998). Experiments show a dependency between capillary number and normalized...
residual oil saturation \( s_{or}/s_{orw} \), where \( s_{orw} \) is the residual oil saturation after water flood. Green and Willhite (1998) present several data showing this dependency. Figure 3 shows an approximated graph, that is transferred from the curve by Taber presented by Green and Willhite (1998).

Fig. 3: Green and Willhite (1998) have collected curves for dependencies between \( s_{or}/s_{orw} \) and \( N_{ca} \), where \( s_{orw} \) is the residual oil saturation at the water flooded saturation. It shows the applied curve (cyan, dash) in this work and the curve by Taber (full, black) transferred from Green and Willhite (1998).

2.4.2 Coats’ interpolation between relative permeability curves

Coats’ correlation is stated to be used in many commercial simulators for modeling the effect of miscibility on relative permeability (Al-Wahaibi et al., 2006), even though it is not based on any theory, but developed to describe the highlighted changes in relative permeability curves by interfacial tension reductions (Coats, 1980). Coats (1980) models the changes of two-phase gas and oil relative permeability curves due to reductions of interfacial tension. The method is shown for water and oil (also referring to the interpretations by Al-Wahaibi et al. (2006)):

\[
f(\sigma) = \left( \frac{\sigma}{\sigma_{\text{base}}} \right)^n \tag{9}
\]

\[
s_{wc}^* = f(\sigma)s_{wc}
\]

\[
s_{or}^* = f(\sigma)s_{or} \tag{10}
\]

\[
k_{rw} = f(\sigma)k_{rw(\text{base})} + [1 - f(\sigma)]k_{rw(\text{misc})} \tag{12}
\]

\[
k_{ro} = f(\sigma)k_{ro(\text{base})} + [1 - f(\sigma)]k_{ro(\text{misc})}, \tag{13}
\]

where \( \sigma \) is current interfacial tension, \( f(\sigma) \) interpolation function with values between 0 (at low interfacial tension) and 1 (at high interfacial tension), \( s_j \) initial residual saturation, \( s_j^* \) predicted residual saturation at \( \sigma \), \( n \) is an adjustable exponent in the range of 4-10, \( k_{rw(\text{base})} \) is the relative permeability curve at highest interfacial tension \( \sigma_{\text{base}} \) being a function of both \( s_j^* \) (cf. Corey equations (6) and (7)), and \( k_{rw(\text{misc})} \) is the linear relative permeability curve at lowest interfacial tension also being a function of both \( s_j^* \) (Coats, 1980; Al-Wahaibi et al., 2006).

The procedure is initiated by an interpolation by residual saturations between initial values and zero. They are used to correct the relative permeability curve range from initial interfacial tension to current interfacial tension resulting in curves that stretch between \( s_{wc}^* \) and \( (1 - s_{or}^*) \). Following, the interpolation function, eqn. (9), is used to interpolate between \( \text{base} \) and \( \text{misc} \) relative permeability curves for water and oil, eqns. (12) and (13). This means that \( s_{or}, s_{wc} \) and to some extent the exponents all are functions of interfacial tension, while the capillary number method only changes \( s_{or} \) directly.
Table 1: Parameters.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_s$</td>
<td>1 kg/m$^3$</td>
</tr>
<tr>
<td>$\mu_{\text{max}}$</td>
<td>0.2 d$^{-1}$</td>
</tr>
<tr>
<td>$K_i$</td>
<td>1 -</td>
</tr>
<tr>
<td>$\phi$</td>
<td>0.4 -</td>
</tr>
<tr>
<td>Reservoir length</td>
<td>400 m</td>
</tr>
<tr>
<td>Reservoir width</td>
<td>100 m</td>
</tr>
<tr>
<td>Reservoir height</td>
<td>100 m</td>
</tr>
<tr>
<td>Volumetric injection velocity</td>
<td>800 m$^3$/d</td>
</tr>
<tr>
<td>$\mu_w$</td>
<td>1 cP</td>
</tr>
<tr>
<td>$\mu_o$</td>
<td>3 cP</td>
</tr>
<tr>
<td>$\rho_w$</td>
<td>1000 kg/m$^3$</td>
</tr>
<tr>
<td>$\rho_o$</td>
<td>800 kg/m$^3$</td>
</tr>
<tr>
<td>$\sigma_{\text{base}}$</td>
<td>29 mN/m</td>
</tr>
<tr>
<td>$Y_{\text{sm}}$</td>
<td>0.18 kg/kg</td>
</tr>
<tr>
<td>$Y_{\text{sb}}$</td>
<td>0.82 kg/kg</td>
</tr>
<tr>
<td>$\nu_b$</td>
<td>$0.5 \cdot 10^{-5}$ m$^3$/m$^3$</td>
</tr>
<tr>
<td>$\nu_s$</td>
<td>$10^{-5}$ m$^3$/m$^3$</td>
</tr>
<tr>
<td>$\nu_m$</td>
<td>0 m$^3$/m$^3$</td>
</tr>
<tr>
<td>$n$</td>
<td>10 -</td>
</tr>
<tr>
<td>$k_{\text{rwor}}$</td>
<td>0.5 -</td>
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<tr>
<td>$k_{\text{rowi}}$</td>
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</tr>
<tr>
<td>$a$</td>
<td>2 -</td>
</tr>
<tr>
<td>$b$</td>
<td>2 -</td>
</tr>
<tr>
<td>$s_{\text{wi}}$</td>
<td>0.3 -</td>
</tr>
<tr>
<td>$s_{\text{or}}$</td>
<td>0.4 -</td>
</tr>
</tbody>
</table>

2.4.3 Interpolation of parameters of Corey type relative permeabilities

The difference between capillary number and Corey interpolation method is the translation of interfacial tension reduction to changes in the relative permeability curves. The methods are different with regard to e.g. sensitivity. We have chosen to use the interpolation function presented by Coats (1980).

$$f(\sigma) = \left( \frac{\sigma}{\sigma_{\text{base}}} \right)^n$$

and $n$ will be within the range for the approach by Coats (1980). The interpolation can be performed for each parameter given in the Corey type permeabilities, cf. eq. (6) and (7).

\[
\begin{align*}
    s_{\text{or}}^* &= f(\sigma) \cdot s_{\text{or}} \quad (15) \\
    s_{\text{wi}}^* &= f(\sigma) \cdot s_{\text{wi}} \quad (16) \\
    k_{\text{rowi}}^* &= f(\sigma) \cdot k_{\text{rowi}} \quad (17) \\
    k_{\text{rwor}}^* &= f(\sigma) \cdot k_{\text{rwor}} \quad (18) \\
    a^* &= f(\sigma) \cdot a \quad (19) \\
    b^* &= f(\sigma) \cdot b \quad (20)
\end{align*}
\]

One advantage is that experimentally determined changes can easily be approximated by this method. In order to compare with the capillary number method, we have chosen that only equation (15) is used here.
2.5 Initial and Boundary Conditions

The parameters used in the simulations is shown in table 1. The reservoir is assumed initially not to contain any bacteria. Bacteria and substrate in water solution are continuously injected into the reservoir, where the injection composition is given as volumetric fractions, $v_i$. In literature regarding both enhanced oil recovery and wastewater treatment, many different injection concentrations are used ranging from $10^{-8} - 10^{-2}$ volumetric fraction (corresponding to $10^{-5} - 10^1$ kg substrate/m$^3$) (Beheshti et al., 2008; Chang et al., 1991; Soleimani et al., 2009; Sen et al., 2005; Sarkar et al., 1994). As a consequence, we have chosen a substrate volumetric fraction of $10^{-3}$ thus being in the low end of the interval.

2.6 Numerical Solution Procedure

The mathematical model developed is solved numerically using an implicit finite difference technique, where mass balances and the total volume balance are satisfied. Application of fractional flow functions excludes solution of the pressure equations, which ease calculations.

3 Results and discussion

The general features of the water phase saturation profile for surfactant dominated MEOR are to some extent similar to surfactant flooding. However, there is a difference in that bacteria is either injected or indigenous microorganisms is boosted by injection of substrates. Here, bacteria are injected together with substrates, and no surfactant (metabolite). A prime example of the water phase saturation profile can be seen if figure 4(a), where the capillary number method is used. The parameters applied are listed in table 1.

Fig. 4: Saturation profiles at different dimensionless times, $\tau$. The dimensionless reservoir length is $\xi$. The curves are the analytical Buckley-Leverett solution for pure water flood, the numerical solution to MEOR, and the corresponding residual oil saturation $s_{OR}$ for the MEOR solution. Recovery curves are for MEOR and water flooding.
As bacteria and substrate penetrate the reservoir, more bacteria and surfactant are produced. When enough surfactant is produced, the interfacial tension reduces significantly affecting the relative permeabilities. As is the case with water flooding, a water front is created. The interfacial tension reduction mobilizes oil, and water will build up instead producing a second water front with surfactant. This results in a traveling oil bank, which in some cases will catch up with the first front as a consequence of different front velocities. If the oil bank catches up with the first front, the new water front will be slowed down. On the other hand, as long as the oil bank does not catch up, the water front will be located at the front for pure water flooding.

The recovery curve is shown in figure 4(b). When the oil bank catches up with the water front, it results in production with the steeper recovery slope for a longer period of time, as water breakthrough occurs later. In addition, the recovery slope of the second part of the curve is larger compared to water flooding. The water saturation is lower until breakthrough of the surfactant water front, where the recovery curve then levels off. If the oil bank does not catch with the water front, the recovery curve is similar to water flooding recovery curve until the oil bank breakthrough. The actual recovery will then depend on the specific surfactant. Islam (1990) produces a recovery curve similar to the latter curve, where the oil bank does not catch up with the water front. The incremental recovery is around 40%, when the current correlation between surfactant concentration and interfacial tension is used.

3.1 Partitioning of surfactant

Figure 5 shows saturation profiles (left) and recovery curves (right) for the different cases of partitioning. When the distribution constant is small, surfactant is mainly located in the oil phase. Less surfactant is present in water phase and more surfactant should be produced in order to decrease residual oil saturation. Firstly, the time
before changes in residual oil occurs is longer. Secondly, the distance from the inlet, where the surfactant effect initiates, also increases. Hence, the oil bank is created later and the effect from surfactant is seen at later times in the recovery curve. This means that the first part of the recovery curve is similar to pure water flooding until breakthrough of the oil bank.

For \( K_i = 10^{-2} \), surfactant is mainly present in the water phase. There is not produced enough surfactant in order to have a water phase surfactant concentration that can effect residual oil saturation. The water phase saturation profile and recovery curves results in being the same as under water flooding.

3.2 Growth rate

The growth rate can be difficult to maintain in a reservoir as reservoir conditions change markedly. This model does not take changes in the surroundings into account, but here we show the importance of being able to maintain a certain growth rate in order to enhance oil recovery.

Cases for different growth rates are shown in figure 6. A higher growth rate results in a faster surfactant production and the threshold is reached after a shorter distance from the reservoir entrance. This will to a greater extent resemble surfactant flooding. Reduction of the growth rate prolongs the time before the surfactant effect can be seen, but also how close to the entrance the residual oil decreases producing an oil bank. An order of magnitude reduction in growth rate to \( 0.02 \) \( d^{-1} \) shows no effect from surfactant as too little surfactant is produced at \( K_i = 10^{0} \). Recovery is then similar to pure water flooding.

3.3 Comparison of interpolation methods

Overall, the three methods affect saturation profiles in the same way, but the capillary number method makes sharper profile changes, cf. figure 7. Coats’ method and the Corey interpolation method are smoother and produce a larger zone of a reduced residual saturation. The final recovery ends up being improved significantly. The methods investigated are sensitive to distribution of surfactant, growth rate, substrate and bacterial concentration. The incremental recovery for the three methods has only minor differences ranging between 30 – 40\%, so the recovery outcomes are very alike.

3.4 Substrate and bacterial injection concentrations

The bacterial growth rate is dependent on both substrate and bacteria concentration. Therefore, the recovery should be very dependent on their injection concentrations. Figure 8 shows recovery curves using Coats’ method and the capillary number method at different concentrations. The curves show that both methods are very
sensitive to concentration differences, but Coats’ method has a bigger working range for the used correlations. Regardless, the graphs clearly demonstrate that injection concentration is a parameter that should be considered carefully.

4 Conclusion

According to predictions of our model, the additional recovery is achieved on a later stage, where the oil bank generated by the bacterial surfactant arrives. The particular results are very sensitive to the parameters selected for simulation, especially distribution coefficient for surfactant partition between phases, maximum growth rate and injection concentrations for substrate and bacteria. The parameters should be chosen such that sufficient surfactant is produced to ensure a significant improvement of oil recovery. The incremental recovery is found to be around 40%, when the distribution constant for surfactant is large ensuring that surfactant remains in the water phase.

Different methods for introducing the changes in the relative permeability curves have been investigated. The capillary number method produced more steep fronts and coming from faster changes in residual oil saturation. Coats’ method and the interpolation of Corey relative permeability parameters both demonstrated smoother changes and produce a larger zone of a reduced residual saturation. The final choice of method should depend on experimental data for specific surfactant systems and their relative permeability curves.
Nomenclature

<table>
<thead>
<tr>
<th>Symbols</th>
<th>Greek</th>
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<tbody>
<tr>
<td>$a$</td>
<td>Exponent, Corey curves</td>
</tr>
<tr>
<td>$b$</td>
<td>Exponent, Corey curves</td>
</tr>
<tr>
<td>$C$</td>
<td>Mass concentration</td>
</tr>
<tr>
<td>$f(\sigma)$</td>
<td>Interpolation function</td>
</tr>
<tr>
<td>$f_j$</td>
<td>Fractional flow function for phase $j$</td>
</tr>
<tr>
<td>$k_{rw}$</td>
<td>Relative permeability curve for water</td>
</tr>
<tr>
<td>$k_{ro}$</td>
<td>Relative permeability curve for oil</td>
</tr>
<tr>
<td>$K_{s}$</td>
<td>Partitioning constant for metabolite</td>
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<tr>
<td>$k_{rwor}$</td>
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<td>Time variable</td>
</tr>
<tr>
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</tr>
<tr>
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</tr>
<tr>
<td>$x$</td>
<td>Reservoir length variable</td>
</tr>
<tr>
<td>$Y_{sb}$</td>
<td>Yield of biomass on substrate</td>
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References


