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Modeling Simultaneous Saccharification and Fermentation of Softwood

Pär O. Pettersson,*[,1] Robert Eklund,[1,3] and Guido Zacchi[2]

[1]Department of Technology, Physics and Mathematics, Mid Sweden University, 891 18 Örnsköldsvik, Sweden, Email: par.pettersson@mh.se;
[2]Department of Chemical Engineering 1, Lund University, Sweden; and
[3]Present address: Applied Physics and Electronics, Umeå University, Sweden

Abstract

Simultaneous saccharification and fermentation (SSF) of wood has been modeled for the past 15–20 years, but the substrates used for model evaluation have so far not included pretreated softwood. In the present study, data from lab-scale batch SSF of SO_2-impregnated, steam-pretreated spruce chips were used to evaluate a model found in the literature. The model, which was somewhat modified, consists of a number of nonlinear, coupled ordinary differential equations, which were solved numerically. Some parameter values were fitted to data by use of least-squares minimization. A difficulty in parameter estimation was the lack of cellobiose measurements, something that was relieved by adding assumptions about parameter relations. The simulated concentration profiles agreed well with the measured concentrations of glucose and ethanol. It is therefore concluded that the basic model features apply to softwood SSF. The model predicts rate saturation with respect to enzyme concentration at concentrations above 60 FPU/g cellulose, although this was not observed in the experimental data, which only comprised enzyme concentrations up to 32 FPU/g cellulose.

Index Entries: Simultaneous saccharification and fermentation; softwood; kinetic model.

Introduction

Using enzymes to produce sugars from wood may be limited by a variety of factors, especially end-product inhibition. If the desired final product is ethanol, the problem of product inhibition can be overcome by fermenting the sugars as they are formed. This process is called simultaneous saccharification and fermentation (SSF), and has been explored for

*Author to whom all correspondence and reprint requests should be addressed.

the last two decades. As many other biochemical processes, SSF is not fully understood, and kinetic models can enhance our understanding and help optimize the process. Efforts to model SSF have been made by several research groups *(1–8)*, but no one has applied SSF models to pretreated softwood data. Softwood is generally more recalcitrant to chemical decomposition than hardwood is, and earlier models might not be valid for this substrate. Schell et al. (9) used parts of the model developed by Philippidis et al. *(1–4)* to model enzymatic hydrolysis of pretreated fir. The purpose of the present work was to evaluate the entire model developed by George Philippidis et al. *(1)* (henceforth referred to as GP) for softwood SSF. This model includes product inhibition of cellulase, β-glucosidase, and yeast, as well as Michaelis–Menten dependence on the cellulase concentration. It also takes into account the dependence of substrate and enzyme concentration, and it has successfully described SSF of unpretreated wastepaper *(4)*. The data used in the present work were collected from 1-L batch experiments using SO_2-impregnated, steam-pretreated spruce, in which the enzyme concentration was varied *(10)*. Some parameters were fitted to data by use of least-squares minimization. The model was slightly modified to fit our experimental situation.

Materials and Methods

Experimental Data

The data used in this work were collected by Kerstin Stenberg, Lund University, Sweden, and are described in detail elsewhere *(10)*. The experimental procedure is briefly presented here. The material used was fresh-chipped spruce, with glucan and lignin concentrations of 44.7% and 27.7%, respectively. The chips were impregnated with sulfur dioxide in a plastic bag for 20 min, and thereafter steam pretreated for 5 min at 215°C. This pretreatment was performed in batch, and the pretreated material from all batches were mixed together. The glucan and lignin contents in the solid material after pretreatment were 57% and 39%, respectively. The SSF runs were performed in 1-L fermentors containing a total weight of 750 g. The whole slurry from the pretreatment stage, diluted to different dry weights of solid material (2, 5, 7.5, and 10%), was used as substrate. The enzyme preparations used were Novozym 188 with a β-glucosidase activity of 392 IU/g *(11)*, and Celluclast with a cellulase activity of 75 FPU/g *(12)* and a β-glucosidase activity of 12 IU/g *(11)*. The amount of Novozym added was 4% w/w dry matter (DM), corresponding to a β-glucosidase activity of 28 IU/g cellulose, and the amounts of Celluclast added were 4, 8, 16, and 24% w/w DM, corresponding to cellulase activities of 5, 10, 21, and 32 FPU/g cellulose, respectively. Baker's yeast was added at a concentration of 5 g DM/L. The SSF experiments were run for 96 hours at the constant temperature of 37°C, and samples were withdrawn at 15 points in time and analyzed for glucose and ethanol concentrations by HPLC using an Aminex HPX-87H column (Bio-Rad, Hercules, CA) (Table 1).

Table 1
Experimental Data for SSF of Steam-Pretreated Softwood[a]

	Data set A 5 FPU/g glucan		Data set B 10 FPU/g glucan		Data set C 21 FPU/g glucan		Data set D 32 FPU/g glucan	
Hours	Glucose	Ethanol	Glucose	Ethanol	Glucose	Ethanol	Glucose	Ethanol
0	4.15	1.77	4.77	1.35	5.45	1.11	5.93	0.96
2	1.11	5.19	3.16	3.65	4.07	3.44	4.67	3.55
4	0.56	7.44	0.94	6.96	1.49	6.16	1.8	7.25
6	0.56	7.76	0.62	7.82	0.84	8.45	1.03	9.69
8	0.54	8.38	0.65	7.54	0.88	9.9	0.92	10.69
22	0.49	10.37	0.63	11.1	0.81	13.09	0.82	15.13
27	0.56	11.09	0.66	12.34	0.8	14.56	0.8	15.93
33	0.48	10.01	0.62	12.9	0.76	14.91	0.77	16.84
47	0.5	12.09	0.52	13.26	0.73	15.34	0.64	17.56
50	0.53	12.61	0.54	14.24	0.76	16.43	0.69	18.75
54	0.53	12.55	0.53	14.32	0.76	16.52	0.66	16.66
72	0	12.8	0.43	14.99	0.96	16.67	0.39	18.66
75	0	12.39	0.52	15.16	1.06	18.06	0	19.24
80	0	12.61	0.51	15.38	1.02	17.19	0	19.11
96	0.25	12.17	0.36	15.58	1.18	17.58	0	18.68

[a]All numbers in g/L.

$$\text{Cellulose(C)} \xrightarrow{r1} \text{Cellobiose(B)} \xrightarrow{r2} \text{Glucose(G)} \xrightarrow{r_G} \text{Ethanol(E)} \,\&\, \text{Cell mass(X)}$$

$$\text{Mannose(M)} \xrightarrow{r_M} \text{Ethanol(E)} \,\&\, \text{Cell mass(X)}$$

Fig. 1. Kinetic scheme of the model.

Model Description

Figure 1 shows the reactions involved in the model. Cellulose (C) is cleaved into cellobiose (B), which in turn produces two glucose (G) units. Both glucose and mannose (M) are fermented by the yeast, resulting in the formation of cell mass (X) and ethanol (E). The mass balances of the model are given by Eqs. 1–6, and the rates are expressed by Eqs. 7–13. Equations 7, 9, and 11–13 include terms for product inhibition. Equation 8 considers adsorption–desorption equilibrium of cellulase on the substrate, and equation 10 includes a term for the irreversible adsorption of β-glucosidase to lignin. The model was explained in detail by Philippidis et al. *(1)*. The parameter values are listed in Table 2.

$$\frac{d(C)}{dt} = -r_1 \tag{1}$$

$$\frac{d(B)}{dt} = 1.056\, r_1 - r_2 \tag{2}$$

$$\frac{d(G)}{dt} = 1.053\, r_2 - r_G \tag{3}$$

$$\frac{d(M)}{dt} = -\, r_M \tag{4}$$

$$\frac{d(X)}{dt} = r_X \tag{5}$$

$$(E) - (E)_0 = 0.511\left(1\text{–}1.559\, Y_{XG}\right)\left(\begin{array}{c}\left[(G)_0 - (G)\right] + \left[(M)_0 - (M)\right] + \\ 1.053\left[(B)_0 - (B)\right] + 1.111\left[(C)_0 - (C)\right]\end{array}\right) \tag{6}$$

$$r_1 = \frac{k_1^{'}(C)e^{-\lambda t}}{1 + \dfrac{(B)}{K_{1B}} + \dfrac{(G)}{K_{1G}}} \frac{K_{1E}}{K_{1E} + (E)} \tag{7}$$

$$k_1^{'} = \frac{k_1 \cdot enzc}{K_{eq} + enzc} \tag{8}$$

$$r_2 = \frac{k_2^{'}(B)}{K_M\left[1 + \dfrac{(G)}{K_{2G}}\right] + (B)} \tag{9}$$

$$k_2^{'} = k_1 \cdot enzg \cdot \left[1 - K_L \cdot (L)\right] \tag{10}$$

$$r_X = \mu_m (X) \frac{(G + M)}{K_G + (G + M)} \frac{K_E}{K_E + (E)} \tag{11}$$

$$r_G = \frac{(G)}{(G) + (M)}\left[\frac{r_X}{Y_{XG}} + m_s (X)\right] \tag{12}$$

$$r_M = \frac{(M)}{(G) + (M)}\left[\frac{r_X}{Y_{XG}} + m_s (X)\right] \tag{13}$$

$$\text{esidual} = \min_{\theta}\ \frac{1}{N}\sum\left[y\left(t_i, \theta\right) - \tilde{y}_i\right]^2 \tag{14}$$

Table 2
Parameter Values from Philippidis et al. *(4)*, except *enzc* and *enzg*, Whose Values Correspond to the Experimental Conditions of Stenberg et al. *(10)*[a]

Parameter	Value	Parameter	Value
k_1	0.0827 h^{-1}	K_{1E}	50.35 g/L
k_2	0.00406 g/(IU h)	K_{1B}	5.85 g/L
λ	0.02 h^{-1}	K_{1G}	53.16 g/L
K_{eq}	544.89 IFPU/L	K_{2G}	0.62 g/L
K_L	0.0053 L/g	K_E	50 g/L
enzc	142.5, 285, 598.5	K_G	3.7310^{-5} g/L
	912 FPU/g cellulose	μ_m	0.19 h^{-1}
enzg	798 IU/g cellulose	m_s	0
K_m	10.56 g/L	Y_{XG}	0.113 g/g

[a]In the present work, k_1, k_2, λ, K_{eq} and μ_m are fitted to data.

A few things in this model differ from the original one. The old notations for enzyme concentration and activity have been replaced by the new variables *enzc* and *enzg*, which represent cellulase and β-glucosidase activity concentration, respectively. In this work, no direct formation of glucose from cellulose is assumed. Furthermore, mannose fermentation is modeled here, since 6 g/L mannose is present at the beginning of the SSF. Equations 4 and 13 are thus new, and Eqs. 6, 11, and 12 have been modified from GP, to include the concentration of mannose. It is assumed that mannose does not inhibit the hydrolysis enzymes, but that it inhibits the yeast in the same way as glucose does. This may be an oversimplification, but it is perhaps a reasonable one.

Simulation and Estimation Procedure

Philippidis et al. *(1–4)* used a number of special experiments to target one or a few parameters at a time. In this work, we used most of their values, assuming that they describe our process reasonably well. As for the reuse of the inhibition parameter values $K_{m,}$ K_{1B}, K_{1E}, K_{1G}, and K_{2G}, other researchers too have used them for enzyme systems other than that for which they were extracted, apparently successfully *(4, 7)*. The other parameter values reused here are the enzyme parameters K_{eq} and K_L, as well as the microorganism (Saccharomyces cerevisiae) parameters K_E,K_G, m_s, and Y_{XG}.

To estimate the remaining parameters of the model (k_1, k_2, μ_m and λ), we used the ethanol and glucose concentrations, determined at 15 different time points during each experiment. Unfortunately, no measurements on cellobiose or remaining glucan were made. The data at hand represent four levels of solids concentration, and four levels of enzyme loading, in a total of 16 experiments. At low solids concentration, lactic acid fermentation competed successfully with ethanol fermentation, and at high solids

concentration, glucose was not fermented at all due to low dilution of the inhibitors in the hydrolysate *(10)*. Therefore, only the four experiments involving 5% solids concentration were considered ideal for modeling. These represent cellulase activities of 5, 10, 21, and 32 FPU/g cellulose, respectively, and the four data sets are labeled A, B, C, and D respectively (Table 1). When simulating a certain experiment, the parameter *enzc* was adjusted to describe the cellulase activity concentration of that experiment. The parameter *enzg*, which describes the β-glucosidase activity concentration, was not changed, since the variations of Celluclast 2L loading did not significantly alter the total β-glucosidase activity concentration.

All mathematical work was performed in *MATLAB 5* (The MathWorks, Inc.). Simulation of the model (a system of nonlinear ordinary differential equations) was done by the command *ode23s*, which handles stiff systems. Parameter estimation was performed using least-squares minimization of the residual as described by Eq. 14. y signifies simulated and $\tilde{y}$ measured concentrations of ethanol and glucose. y is a function of time and θ, which signifies the model parameter(s) that are to be estimated. N is the total number of data points used in the minimization. Data from one or more data series may be used. The minimization routine was MATLAB's *fminsearch*, which uses a Nelder–Mead simplex (direct search) method.

Results and Discussion

Simulation Results

Early attempts to estimate λ (which describes the rate of decrease in the specific surface area of cellulose) and the rate constants k_1 and k_2, revealed that k_2 was not bounded by the data at hand. k_2 grew ever larger as the optimization proceeded, resulting in the simulated cellobiose concentration reaching zero very fast. This is not acceptable, and additional information was needed. Philippidis et al. *(4)*, using unpretreated waste paper, found that $k_1 = 0.0827\ h^{-1}$ and $k_2 = 0.00406$ g/(IU h), i.e., $k_2 \approx 0.05 \cdot {}_1$. In this work we assumed $k_2 = 0.1 \cdot k_1$, thereby binding k_2 to k_1. This relation between the two variables gives cellobiose concentration curves that are reasonable according to experience *(3)*. There are more sophisticated methods for dealing with this kind of problem, including regularization *(13)*, but given the scarcity of data, there is little gain in pursuing this further. The same situation occurred when trying to estimate the cellulase enzyme saturation constant K_{eq}, which is strongly correlated to k_1. K_{eq} describes the efficiency of the cellulase-substrate binding, and has been found to have a significant impact on hydrolysis yield *(4)*. K_{eq} was set to 1090 IFPU/L [twice the value used in GP *(4)*], which gave a good fit to the data. It should be realized, however, that this may differ significantly from the actual value. Schell et al. *(9)* estimated $K_{eq} = 132{,}000$ IFPU/L for Douglas fir, but they also reported that the estimation procedure was somewhat problematic. Yet another parameter that is likely to differ from the values of GP is the maximum specific growth rate, μ_m. This parameter was also fitted to data,

Table 3
Residuals When Applying Parameters θ_i^* and θ_{A-D}^* to the Four Data Sets[a]

	Value of θ	Data set A	Data set B	Data set C	Data set D
θ_A^*	0.252 0.094 0.035	**0.17**	0.52	0.99	0.70
θ_B^*	0.170 0.063 0.018	0.36	**0.19**	0.42	0.51
θ_C^*	0.183 0.062 0.024	0.39	0.22	**0.40**	0.55
θ_D^*	0.218 0.070 0.025	0.28	0.33	0.60	**0.36**
θ_{A-D}^*	0.200 0.067 0.025	0.28	0.22	0.45	0.41

[a]θ_i^* is the optimal parameter estimation for data set i, θ_{A-D}^* is the optimal parameter estimation for all data sets. $\theta = (k_1, \mu_m, \lambda)$.

although it is reported to have a relatively small effect on the overall process *(4)*. *T*hus, the parameters that had to be estimated by least-squares minimization were k_1, μ_m and λ, which are collectively denoted as the vector parameter $\theta = (k_1\ \mu_m\ \lambda)$.

Estimating many parameters in a nonlinear model is often difficult, as the global minimum may be missed if the initial guess is bad. In our case, the terrain proved to be rather good, i.e., there was no great multitude of sharp, local minima. Convergence was fair, although the model was very stiff.

When using just one data set (from one experiment) to estimate θ, θ adopts well to this particular data set. Table 3 shows the resulting estimates of θ, as well as the residuals of these four estimates, as evaluated for the four data sets. Using all four data sets for the estimation resulted in the estimate $\theta_{A-D}^* = [0.200\quad 0.0670\quad 0.0249]$, which is also shown in Table 3 together with the resulting residuals. This set of parameter values was used to simulate the SSF and the result is shown in Figs. 2–6 together with the experimental data. In Figs. 2–5, simulated glucose and mannose concentrations and measured glucose concentrations were omitted for clarity. Figure 6 shows these values for data set B. The curves were almost the same for the other data sets (not shown). When all the data are used for parameter estimation, there are no fresh data to use for model validation. It is therefore a good idea to save one data set for validation. Two such

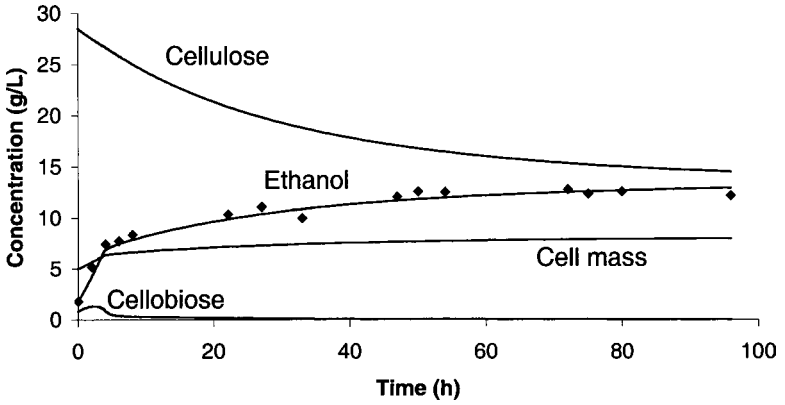

Fig. 2. The simulated runs (lines) and the measurements of ethanol (dots) for data set A (5 FPU/g cellulose). For clarity, simulated glucose and mannose concentrations are not shown, nor are glucose measurements.

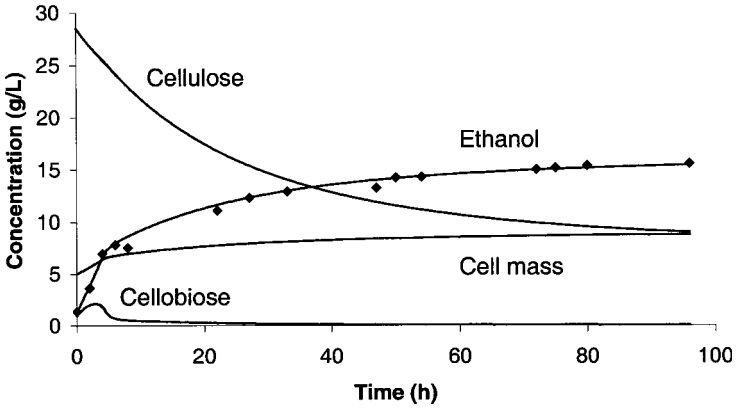

Fig. 3. The simulated runs (lines) and the measurements of ethanol (dots) for data set B (10 FPU/g cellulose). For clarity, simulated glucose and mannose concentrations are not shown, nor are glucose measurements.

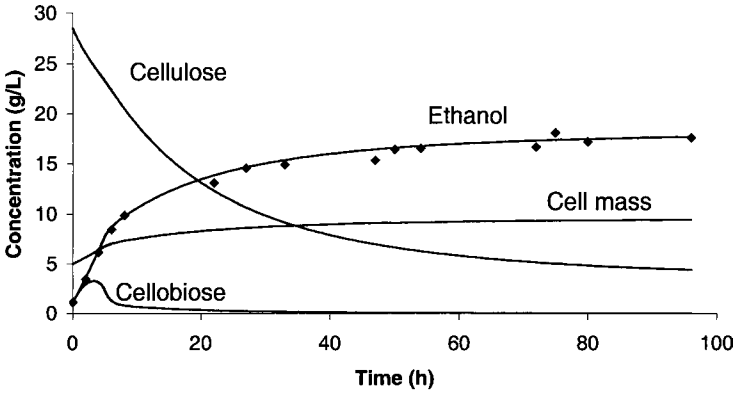

Fig. 4. The simulated runs (lines) and the measurements of ethanol (dots) for data set C (21 FPU/g cellulose). For clarity, simulated glucose and mannose concentrations are not shown, nor are glucose measurements.

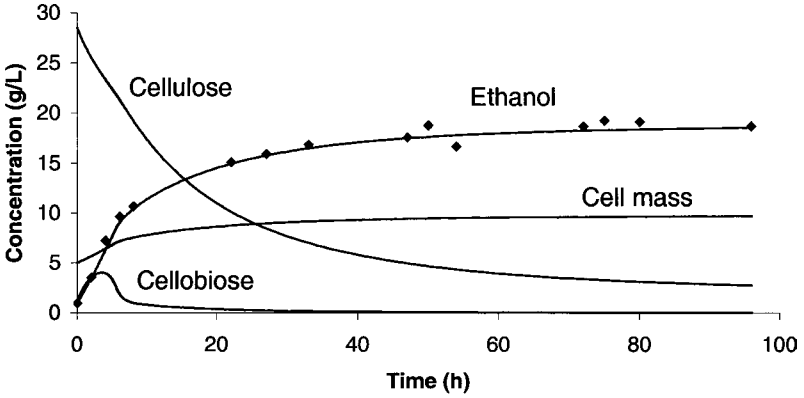

Fig. 5. The simulated runs (lines) and the measurements of ethanol (dots) for data set D (32 FPU/g cellulose). For clarity, simulated glucose and mannose concentrations are not shown, nor are glucose measurements.

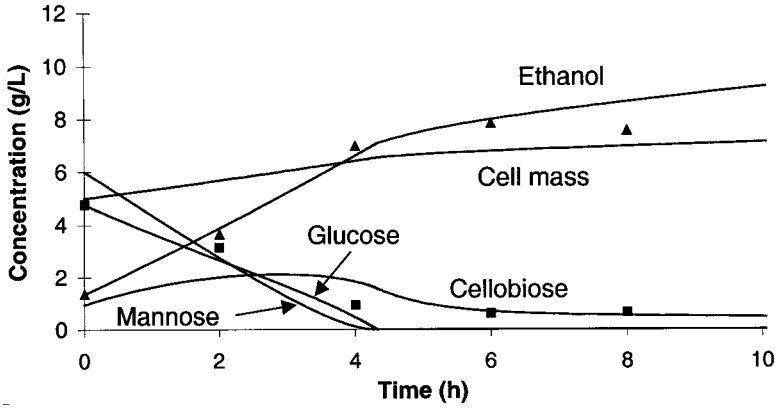

Fig. 6. Simulated concentrations (lines), glucose (squares) and ethanol (triangles) measurements during the first 10 h, data set B (10 FPU/g cellulose). Cellulose is omitted for clarity.

estimations/validations were made, in which data sets B and C respectively, were not included during parameter fitting, but were used for model validation. These two new estimates only differ slightly from the estimate that uses all data sets, and the residuals do not change significantly (Table 4). It is obvious that the model can correctly predict a new set of data, and that it can do so for enzyme concentration levels that lie between those used for identification. This does not mean that the model is mechanistically correct, but can help to predict ethanol concentration profiles in the enzyme concentration range used.

Sensitivity Analysis of the Model

To investigate the sensitivity with respect to the three estimated parameters (k_1, μ_m, and λ), the residual was calculated using disturbed parameter values. One value was changed by 10%, and the other two were

Table 4
Parameter Estimation Using Three Data Sets, Checking the Residual of the Fourth[a]

Data sets used for estimation	Data set used for validation	Estimated θ	Residual for this estimate	Residual for θ_{A-D}*
A, C, D	B	0.210 0.068 0.027	0.24	0.22
A, B, D	C	0.208 0.069 0.026	0.50	0.45

[a]$\theta = (k_1, \mu_m, \lambda)$.

Table 5
Sensitivity of Model Parameters[a]

Parameter	Value	Residual	Relative deviation $(res-res_{min})/res_{min}$
k_1	0.9×0.200	0.408	+20.7%
	0.200	0.338	Minimum
	1.1×0.200	0.395	+16.6%
μ	0.9×0.0670	0.348	+8.5%
	0.0670	0.338	Minimum
	1.1×0.0670	0.362	+6.8%
λ	0.9×0.0249	0.355	5.0%
	0.0249	0.338	Minimum
	1.1×0.0249	0.354	4.8%

[a]*res* is the residual as described by Eq. 14, and *resmin* = 0.338 is the residual obtained for the optimal value of $\theta = (k_1, \mu_m, \lambda)$.

kept constant (Table 5). The fact that the relative changes of the residual are in the same order of magnitude as the relative changes in parameter value suggests that the estimation problem is well-conditioned. We also found that no parameter was unnecessary, and we did not observe any extreme parameter sensitivity.

Sensitivity of the System Identification

A weakness in the present system identification is that the parameter k_2 is not identifiable. This problem was overcome by assigning a fix relation between k_1 and k_2, but this is not an ideal solution. Instead, more data should be collected. In order to test the influence of cellobiose measurements, simulated cellobiose measurements were created and used in the parameter estimation. The cellobiose data were first disturbed by Gaussian

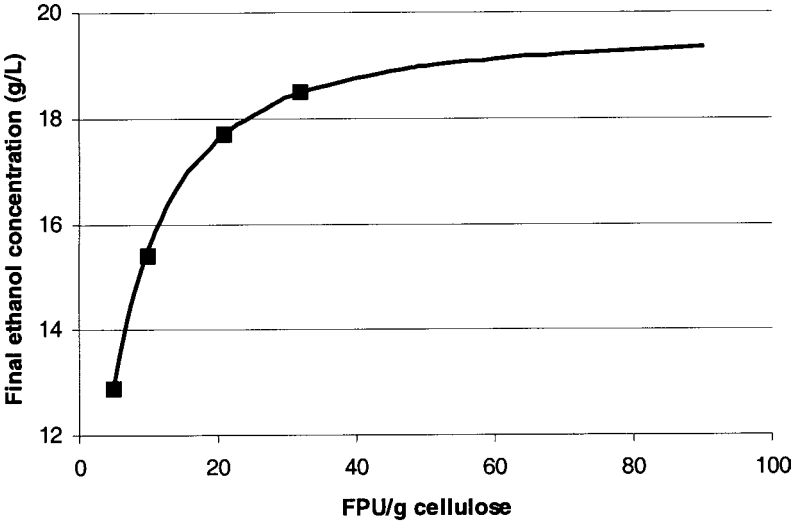

Fig. 7. Simulated final (96 h) ethanol concentration as a function of cellulase activity concentration. Initial values of glucose and ethanol were 4.15 and 1.77 g/L respectively. Experimental values are also shown (dots), where similar initial values were used (Table 1).

noise with a standard deviation of 10%. Using these "synthetic" data along with the real data, k_2 was clearly identifiable (data not shown). It can therefore be concluded that cellobiose measurements are important in finding the parameter values of this model.

Experimental estimates of remaining cellulose (or rather remaining cellulose + cell growth) would probably also aid in parameter estimation. Stenberg et al. *(10)* only did this for the experiment on 32 FPU/g cellulose (data set D). They estimated the final cellulose concentration to be 17% of the initial one, assuming there was no cell growth. This calculates to 4.85 g/L of remaining cellulose and cell growth. The corresponding simulated number is 7.48 g/L (2.76 g/L of remaining cellulose and 4.72 g/L of cell growth). This difference may in part be attributed to the parameter Y_{XG}, which is the yield coefficient of cell mass from glucose. When its value is lowered from 0.113 to 0.08 (θ being kept at its old value), the estimated amount of remaining cellulose and cell growth is 6.11 g/L (2.77 g/L cellulose and 3.34 g/L cell growth), which is in closer agreement with the measured value. This illustrates that the parameter values borrowed from GP may not be fully adequate for our experimental conditions.

Optimization

According to the model obtained in this study, a high enzyme concentration gives a high ethanol concentration (data not shown). This is highly expected, and optimization with respect to enzyme concentration is entirely an economic issue. Since the cost of enzymes is high *(14)*, this is

probably one of the most important parameters to optimize. One aspect of enzyme concentration that would be interesting to study at this point is the rate saturation with enzyme concentration. Experiments have shown that there is such a saturation in SSF of hardwood *(15–18)*, but Stenberg et al. *(10)* did not reach substantial saturation in their experiments on SSF of softwood, using up to 32 FPU/g cellulose. Figure 7 shows the predicted final (96 h) ethanol concentration as a function of cellulase activity concentration, as well as the four experimental data points available. The result indicated that saturation does occur in softwood SSF as well, but it has to be remembered that the crucial parameter K_{eq} was set rather arbitrarily. Although the simulated curve perfectly matches the experimental data up to 32 FPU/g cellulose (Fig. 7), it cannot be concluded that it will accurately predict the rate saturation at higher cellulase activity concentrations.

A high solids concentration is also beneficial according to our model, but the results obtained by Stenberg et al. *(10)* showed that fermentation was strongly inhibited at a solids concentration of 10%, or even lower. This is probably due to the increase in inhibitory compounds present in the slurry and, consequently, the parameter μ_m is strongly dependent on the solids concentration (or rather on how much the slurry is diluted). In fact, a number of other parameters may depend on the solids concentration as well, although not as strongly as μ_m does. The inhibition, caused by the high concentration of inhibiting substances from the pretreatment step, is not easily modeled.

Conclusions

In spite of few data, it has been established that the model presented here succeeds in describing the SSF of softwood, and its dependence on enzyme concentration under the experimental conditions of Stenberg et al. *(10)*. Before using it for fine-tuned process optimization, more data and further validation are needed. Especially, measurements of cellobiose, in addition to glucose and ethanol, are required. Nevertheless, the model concepts that Philippidis et al. *(1)* developed appear to be adequate for softwoods as well as for hardwoods.

Acknowledgment

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Notation

(B) concentration of cellobiose (g/L)
(C) concentration of cellulose (g/L)
(E) concentration of ethanol (g/L)

enzc cellulase activity concentration (FPU/g cellulose)
enzg β-glucosidase activity concentration (IU/g cellulose)
(G) concentration of glucose (g/L)
k_1 maximum specific rate of cellulose hydrolysis to cellobiose (h^{-1})
k_2 specific rate of cellobiose hydrolysis to glucose (g/[IU h])
k_1' lumped specific rate of cellulose hydrolysis to cellobiose (h^{-1})
k_2' lumped specific rate of cellobiose hydrolysis to glucose (g/[L·h])
K_{eq} cellulase adsorption saturation constant (g/L)
K_E ethanol inhibition constant for the microorganism (g/L)
K_G glucose saturation constant for the microorganism (g/L)
K_L constant for β-glucosidase adsorption to lignin (g/L)
K_m cellobiose saturation constant for β-glucosidase (g/L)
K_{1B} inhibition constant of cellulase by cellobiose (g/L)
K_{1E} inhibition constant of cellulase by ethanol (g/L)
K_{1G} inhibition constant of cellulase by glucose (g/L)
K_{2G} inhibition constant of β-glucosidase by glucose (g/L)
(L) concentration of lignin (g/L)
(M) concentration of mannose (g/L)
m_s specific rate of substrate consumption for maintenance requirements (h^{-1})
r_G volumetric rate of glucose consumption (g/[L·h])
r_M volumetric rate of mannose consumption (g/[L·h])
r_X volumetric rate of cell mass production (g/[L·h])
r_1 volumetric rate of cellulose hydrolysis to cellobiose (g/[L·h])
r_2 volumetric rate of cellobiose hydrolysis to glucose (g/[L·h])
t time (h)
(X) concentration of cell mass (g/L)
Y_{XG} yield coefficient of cell mass from glucose (g/g)

Greek symbols

λ rate of decrease in cellulose specific surface area (h^{-1})
μ_m maximum specific growth rate of the microorganism (h^{-1})

Subscript

0 initial values

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