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► **To cite this version:**

Jérôme Harmand, Alain Rapaport, Thibault Nidelet. About overyielding with mixed cultures in batch processes. 8th IFAC Conference on Foundations of Systems Biology in Engineering (FOSBE 2019), Oct 2019, Valencia, Spain. pp.163-168, 10.1016/j.ifacol.2019.12.252 . hal-02318595

**HAL Id: hal-02318595**

**<https://hal.science/hal-02318595>**

Submitted on 17 Oct 2019

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# About overyielding with mixed cultures in batch processes

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**Abstract:** This paper investigates - via modeling - several possible explanations of overyielding observed in mixed cultures cultivated in batch reactors. It is first shown that the classical model of competition of  $N$  species for a single resource cannot explain such overyielding. Then, three hypotheses are introduced and discussed at the light of numerical simulations.

*Keywords:* Overyielding, competition, variable yield, mortality, batch processes.

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## 1. INTRODUCTION

Overyielding - the capacity of certain ecosystems to exhibit better performances than when their species are cultivated alone - has been studied for a long time in ecology, notably in plant ecology, cf. for instance Schmid *et al.* (2008). Because they can be easily manipulated, microbial ecosystems are now more and more used for studying ecological-related questions Jessup *et al.* (2004), for instance to study the effects of biodiversity on ecosystems performances. Although the relationship between biodiversity and system performances may exhibit different patterns (cf. Graham and Duda (2011)), it is often shown for microbial ecosystems that higher the diversity, better the performances of the ecosystem with possibly the emergence of overyielding as observed in environmental ecosystems such as the anaerobic digestion (Hamelin and Milferstedt (2015)). In systems fed with complex substrates, complementary and interaction effects are usually invoked to explain overyielding. In systems using less complex resources or artificially assembled communities, it is shown that a high biodiversity still yields better performances but the relationship can no longer be monotonic, cf. for instance Langenheder *et al.* (2010). Models that capture such overyielding phenomena are rare not to say absent of the literature. In the present paper, we propose a number of mechanisms able to explain overyielding. In Sec. 2, we define precisely what is meant here by *overyielding*, and then show that classical competition models are unable to exhibit such overyielding in batch bioreactors. Furthermore, it is shown that the introduction of direct or indirect interactions terms in the microbial kinetics does not affect the result. In Sec. 3, three extensions of the classical dynamics of microorganisms are considered, and we give conditions for which overyielding occurs. Their impacts on system performances are illustrated with simulations and the results are discussed in Sec. 4, before the conclusion is drawn.

## 2. COMPETITION FOR A SINGLE RESOURCE

### 2.1 The classical model

The standard competition model of  $n$  species on a single substrate in a batch reactor is given by the following dynamical system (see for instance Harmand *et al.* (2017)):

$$\begin{cases} \dot{X}_i = \mu_i(\cdot)X_i, & i = 1 \cdots n \\ \dot{S} = - \sum_{i=1}^n \frac{\mu_i(\cdot)}{Y_i} X_i \end{cases} \quad (1)$$

where  $S$  is the substrate concentration, while  $\mu_i(\cdot)$  and  $Y_i$  are the specific growth rate and yield of the  $i^{\text{th}}$  species, of concentration  $X_i$ . We do not consider here multi-steps reactions, where typically a species is using the product of another one to grow, such as in anaerobic digestion, where overyielding is ubiquitous in this case. We focus here on the first step where competitors can grow by their own when alone. In the simplest models (such as the Monod or the Haldane models), the growth functions  $\mu_i(\cdot)$  are assumed to fulfill the following properties.

*Hypothesis 1.* The functions  $\mu_i(\cdot)$  are functions of  $S$ , Lipschitz continuous from  $\mathbb{R}_+$  to  $\mathbb{R}_+$  with  $\mu_i(S) > 0$  for  $S > 0$ .

### 2.2 Definition of overyielding

Here we will say that there is biomass overyielding in a batch process if the total production of biomass using an inoculum composed of multiple species is greater than the biomass production obtained when the inoculum (of same total mass) is made up of a single species. In other words, we study the role of the diversity of the inoculum with respect to process performances in terms of biomass production (other criteria such as by-products or biogas production could also be chosen but are not considered here). For simplicity, we restrict our attention to single step reactions, which means that we investigate possible

mechanisms of overyielding in any biological system where the biomass growth is limited by a single limiting substrate (the extension to several limiting resources could be the matter of future work). In other terms, we study biomass overyielding in the framework of the competition of  $n$  species on a single resource, the performance index being the net quantity of biomass produced over a period of time  $[0, T]$  where  $T$  is sufficiently large to consider that the bio-conversion of the resource into biomass is (almost) ended. Traditionally, one makes the distinction between “overyielding” and “transgressive overyielding” as follows.

- overyielding is when the production of the ecosystem is above the averaged production of the isolated species, pondered by the initial composition of the ecosystem.
- transgressive overyielding is when the production is above the best production obtained among ecosystems with single species.

A schematic representation of such situations is given in Fig. 1. Here, we shall consider transgressive overyielding

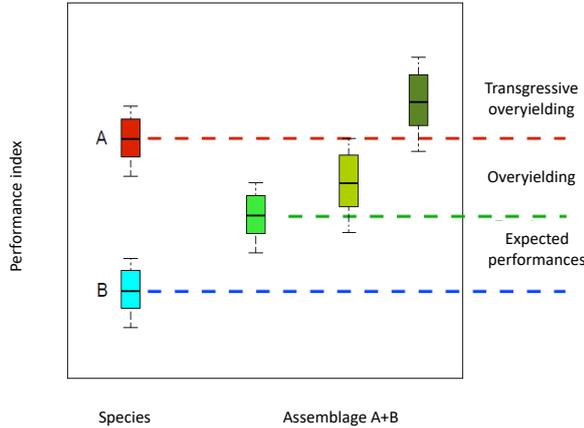


Fig. 1. Schematic representation of the overyielding.

only, as it appears to be the most interesting situation in practice, that we shall simply call “overyielding”.

Let us now formalize the overyielding from a mathematical viewpoint: let us denote by  $\mathcal{S}$  the simplex in the positive orthant of  $\mathbb{R}^n$

$$\mathcal{S} := \left\{ p \in \mathbb{R}_+^n; \sum_i p_i = 1 \right\} \quad (2)$$

and the vertices  $\sigma_i$  ( $i = 1 \dots n$ ) such that

$$\sigma_{i,i} = 1, \quad \sigma_{i,j} = 0, \quad j \neq i \quad (3)$$

We also denote by  $X$  the vector in  $\mathbb{R}_+^n$  of components  $X_i$ .

*Definition 2.* Let  $B_0, S_0$  be two positive numbers. For any  $p_0 \in \mathcal{S}$ , consider the solution of system (1) for the initial condition  $X(0) = p_0 B_0, S(0) = S_0$  and define the number  $R(p_0) := B_\infty - B_0$  where  $B_\infty := \lim_{t \rightarrow +\infty} B(t)$  with  $B(t) = \sum_i^n X_i(t)$ . System (1) presents *overyielding* for  $(B_0, S_0)$  when the following inequality is fulfilled.

$$\max_{p_0 \in \mathcal{S}} R(p_0) > \max_{i \in \{1 \dots n\}} R(\sigma_i) \quad (4)$$

### 2.3 Analysis of the classical model

In this section, we consider the model (1) under Hypothesis

1. For this model one has:

$$\begin{aligned} R(p_0) &= \int_0^T \sum_i \mu_i(\cdot) X_i(\tau) d\tau \\ &= \int_0^T \sum_i \dot{X}_i(\tau) d\tau = \sum_i (X_i(T) - X_i(0)) \end{aligned} \quad (5)$$

From equations (1), one can write:

$$\begin{aligned} \dot{S}(t) + \sum_{i=1}^n \frac{\dot{X}_i(t)}{Y_i} &= S(0) + \sum_{i=1}^n \frac{X_i(0)}{Y_i} \\ &= S(T) + \sum_{i=1}^n \frac{X_i(T)}{Y_i} \end{aligned} \quad (6)$$

Under Hypothesis 1,  $S(t) \rightarrow 0$  when  $t \rightarrow +\infty$ . If  $T$  is large enough, one can consider  $S(T) \simeq 0$ . Thus, from (6) one has

$$\sum_i^n \left( \frac{X_i(T) - X_i(0)}{Y_i} \right) = S(0). \quad (7)$$

Let us introduce the numbers

$$p_i = \frac{X_i(T) - X_i(0)}{Y_i S(0)} \in [0, 1]. \quad (8)$$

Then, from (5), one has

$$\begin{aligned} R(p_0) &= S(0) \sum_i p_i Y_i \leq S(0) \sum_i p_i \max_i Y_i \\ &= S(0) Y_i^* \sum_i p_i = S(0) Y_i^* \end{aligned} \quad (9)$$

where  $Y_i^*$  is the largest  $Y_i$  for  $i = 1 \dots n$ .

From this result, it may be concluded that

- i) for a constant initial substrate concentration  $S(0)$ , the net biomass production  $R(p_0)$  only depends on this initial concentration and on the biomass yields  $Y_i$ ,
- ii) this net biomass production cannot exceed the biomass produced by the best species, that is the species having the largest yield  $Y_i^*$ .

In other words, whatever  $n$ , with this classical model under Hypothesis 1, there does not exist any combination of initial biomass concentrations allowing to produce more biomass than with using only the best species. Thus, this model does not exhibit biomass overyielding.

*Remark 3.* This result remains valid whatever the expressions of  $\mu_i(\cdot)$  are. The only condition is that these functions are positive when  $S$  is positive. The only condition for the result to hold is that the terms  $\mu_i(\cdot)$  in the dynamics of  $X_i$  are the same than the ones appearing negatively in the dynamics of  $S_i$ , whatever are the growth rates under the condition that  $S_\infty = 0$ . Their expressions can involve any other state of the system (such as for instance the Contois function  $\mu(S, X) = \mu_{max} S / (S + KX)$  where the parameter  $K$  measures the density effect) or any external ‘inputs’ or environmental variables like the pH, temperature or the oxygen concentration, or even include direct interaction terms under the condition that such inputs do affect all growth rates in the same manner. In particular, it should not cancel only one kinetics while the others would not

be affected since in such a case, as it will be underlined here below, overyielding is possible. From a chemical engineering viewpoint, this result is easily understandable: since the performance index - the biomass production - is essentially related to the yield of the biomass, the final state does not depend on the transitory but only on the initial available resource.

### 3. MODELS OF OVERYIELDING

In this section, we study different mechanisms that could explain overyielding in batch processes, derived from the classical competition model of Section 2.1.

#### 3.1 Constant yields and growth thresholds

Model 1 is unchanged but the Hypothesis 1 is relaxed in the following way:

*Hypothesis 4.* The functions  $\mu_i(\cdot)$  are Lipschitz continuous from  $\mathbb{R}_+$  to  $\mathbb{R}_+$  and there exist growth thresholds  $\underline{S}_i > 0$  ( $i = 1 \dots n$ ) such that  $\mu_i(S) = 0$ ,  $S \in [0, \underline{S}_i]$  and  $\mu_i(S) > 0$ ,  $S > \underline{S}_i$

The threshold  $\underline{S}_i$  represents the minimal substrate concentration under which a growth cannot occur (see Van Uden (1967)). This value is often imposed to be null, as in the Monod model. However, in practice it is rare to have observations for low values of the substrate concentration to identify such threshold. Nevertheless, it has been observed that for some strains, this threshold is not negligible (see e.g. Van Uden (1967b); Tros *et al.* (1996)).

For such a model, one can easily verify that the property

$$R(\sigma_i) = Y_i \max(0, S(0) - \underline{S}_i), \quad i = 1 \dots n \quad (10)$$

is fulfilled. Then, we have obtained the following result (the proof is given in Rapaport *et al.* (2019)):

*Proposition 5.* Fix  $X_0, S_0$  two positive numbers. Let  $j \in \{1, \dots, n\}$  be such that

$$R(\sigma_j) = \max_{i \in \{1 \dots n\}} R(\sigma_i) > 0. \quad (11)$$

If there exists  $k \in \{1, \dots, n\} \setminus \{j\}$  such that  $Y_k > Y_j$ , then for  $S_0 > \underline{S}_k$ , the model 1 presents an overyielding.

The key point is to notice first that one has the following property

$$\lim_{t \rightarrow +\infty} S(t) = \min \left( S_0, \min_{i=1 \dots n} \{ \underline{S}_i \text{ s.t. } X_i(0) > 0 \} \right). \quad (12)$$

This allows to play with a *complementary effect* when a first species has the best biomass production when cultivated alone, while another species has a better conversion factor but suffers from a large growth threshold. The presence of this later one boosts the performances of the ecosystem due to its better conversion factor while the first carries on alone the conversion of the resource. This is illustrated in Section 4 with explicit growth functions.

#### 3.2 Constant yields and mortality terms

Biomass mortality is often observed in microbial ecosystems. While usually assumed to be negligible in continuous processes with respect to the dilution rate, it can be

relevant to take it into account in batch processes. In such a case one has to extend model (1) as follows

$$\begin{cases} \dot{X}_i = (\mu_i(\cdot) - k_i) X_i \\ \dot{S} = - \sum_{i=1}^n \frac{\mu_i(S)}{Y_i} X_i \end{cases} \quad (13)$$

where the functions  $\mu_i(\cdot)$  fulfill Hypothesis 1. It can be easily checked that when a species  $i$  is cultivated alone,

$$\lim_{t \rightarrow +\infty} S(t) = \underline{S}_i \text{ s.t. } \int_{\underline{S}_i}^{S_0} \left( \frac{k_i}{\mu_i(\sigma)} - 1 \right) d\sigma = \frac{B_0}{Y_i} \quad (14)$$

where  $\underline{S}_i > 0$ . There is a similitude with the growth threshold model, but here the biomass systematically tends asymptotically to 0 due to the mortality terms. Therefore, one has to consider the maximal value of the biomass over the time instead of its asymptotic value to define its production, which makes the mathematical analysis more difficult. Nevertheless, one can identify the following situations which exhibit overyielding:

- a species  $i$  has a high conversion rate  $Y_i$  but its growth function  $\mu_i$  is non-monotonic with  $\mu_i(S_0) < k_i$ . When the initial condition  $(B_0, S_0)$  is such that  $\mu_i(\underline{S}_i) < k_i$ , where the number  $\underline{S}_i$  is defined in (14), the species goes down directly to extinction when cultivated alone. It cannot produce biomass.
- another species  $j$  has a lower conversion rate but its growth function is monotonic with  $\mu_j(S_0) > k_j$ .
- if the species  $j$  conducts the resource concentration  $S$  at values for which  $\mu_i(S) > k_i$ , then the species  $i$  will produce biomass and the ecosystem will take advantage of its high conversion rate.

This will be illustrated on a concrete example in Section 4. The fact that the growth kinetics of a species is no longer proportionate to the kinetics of its substrate consumption (as it was the case for the former model) amounts formally to have a variable yield conversion. This has led us to consider the general framework of variable yields which is studied in the next section.

#### 3.3 Variable yields with no growth threshold or mortality

In this section, we investigate how variable yields could produce overyielding as a mechanism on its own (i.e. without growth threshold or mortality). To properly separate this mechanism from the one induced by growth thresholds that has been presented previously, we do not consider here growth threshold nor mortality terms but rather the following extension of model (1)

$$\begin{cases} \dot{X}_i = \mu_i(S_i) X_i \quad (i = 1 \dots n) \\ \dot{S} = - \sum_{i=1}^n \frac{1}{Y_i} (\mu_i(S) + m_i(S)) X_i \end{cases} \quad (15)$$

where  $m_i(\cdot)$  can be interpreted as maintenance terms (consumption of substrate not associated to biomass growth), with the following assumption:

*Assumption 6.* The function  $m_i(\cdot)$  are Lipschitz continuous from  $\mathbb{R}_+$  to  $\mathbb{R}_+$  with  $m_i(0) = 0$  and  $m_i(S) > 0$  for  $S > 0$ . Moreover, for each  $i \in \{1, \dots, n\}$ , one has

$$\exists \lim_{S > 0, S \rightarrow 0} \frac{m_i(S)}{\mu_i(S)} < +\infty \quad (16)$$

Typically, we expect the functions  $\mu_i$  and  $m_i$  to be linear about  $S = 0$ , which justify this condition. Under this assumption, one can define for each  $i \in \{1 \dots n\}$ , the function

$$\alpha_i(S) := \frac{m_i(S)}{\mu_i(S)}, \quad S \geq 0 \quad (17)$$

and consider functions  $y_i(\cdot)$  defined as follows

$$y_i(S) := \frac{Y_i}{1 + \alpha_i(S)Y_i}, \quad S \geq 0 \quad (18)$$

Then, formally, one can check that system (15) is equivalent to the following model:

$$\begin{cases} \dot{X}_i = \mu_i(S)X_i & i = 1 \dots n \\ \dot{S} = -\sum_{i=1}^n \frac{\mu_i(S)}{y_i(S)} X_i \end{cases} \quad (19)$$

where the function  $y_i(\cdot)$  are positive Lipschitz continuous functions. This model amounts to consider the classical model (1) where the yield coefficients  $Y_i$  are replaced by *variable yields*  $y_i(\cdot)$ .

Then, one can check that the following property is fulfilled.

$$R(\sigma_i) = \int_0^{S_0} y_i(s) ds, \quad i = 1 \dots n \quad (20)$$

We have obtained the following result (the proof is given in Rapaport *et al.* (2019)).

*Proposition 7.* Fix  $B_0, S_0$  two positive numbers. Assume there exist  $j, k$  in  $\{1, \dots, n\}$  such that

- (i)  $R(\sigma^k) = \max_{i \in \{1 \dots n\}} R(\sigma^i)$
- (ii) there exist  $\tilde{S}, S^*$  with  $0 < \tilde{S} < S^* < S_0$  such that
  - (a)  $(y_j(S) - y_k(S))(S^* - S) > 0, \forall S \neq S^*$
  - (b)  $\exists \alpha, \beta > 0$  s.t.  $\mu_k(S) < \alpha \mu_j(S) S^{1+\beta}, \forall S \in (0, \tilde{S})$

then, the model (15) presents an overyielding when the initial proportion of species  $j$  is sufficiently small.

Here, the consideration of variable yields requires kinetics conditions for small values of  $S$ , differently to the growth thresholds model. Although different thresholds or different variable yields both reflect complementary relationships between species, the underlying mechanisms in the transient are quite different.

## 4. NUMERICAL SIMULATIONS

In this section, we first give one instance for each model presented above. Each model has been simulated for parameter values realistic w.r.t. to the literature. Depending on the operating conditions and the species, one model could be more realistic than another one. Our objective here is not to determine which model is the most realistic but to analyze which mechanism could produce overyielding. Then, we investigate the robustness of the results with respect to model parameters, that is whether models exhibit overyielding while their parameter values vary.

### 4.1 Constant yields and growth thresholds

For this first example, we consider two species with growth function of Moser type with thresholds:

$$\mu_i(S) = \begin{cases} 0, & S < \underline{S}_i \\ \frac{\mu_{max,i} S^{\alpha_i}}{K^{\alpha_i} + S^{\alpha_i}}, & S \geq \underline{S}_i \quad (\alpha_i > 1) \end{cases}$$

whose graphs are depicted in Fig. 2 and parameter values are given in Table 1.

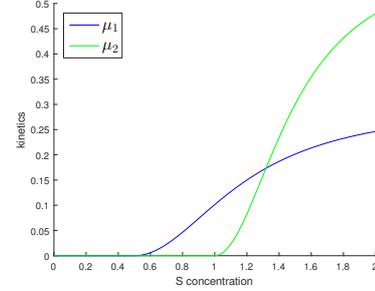


Fig. 2. Graphs of the two growth rate functions.

	$Y_i$	$\underline{S}_i$	$\mu_{max,i}$	$K_i$	$\alpha_i$
$i = 1$	1	0.5	0.3	0.7	2
$i = 2$	1.4	1	0.6	0.5	2

Table 1. Parameter values of the two species.

With such parameters, one may verify that conditions of Proposition 5 are verified. Fig. 5 allows us to see a significant overyielding (21.62%) with the initial proportion  $p_0 = 0.4$ .

### 4.2 Constant yields and mortality terms

In accordance with Section 3.2, we have considered monotonic (Monod) and non-monotonic (Haldane) growth functions:

$$\mu_1(S) = \frac{2S}{0.05 + S}, \quad \mu_2(S) = \frac{4S}{0.001 + S + 300S^2}$$

along with the following parameter values

	$Y_i$	$k_i$
$i = 1$	5	1
$i = 2$	8	0.2

Graphs of functions  $\mu_i$  and values of  $k_i$  are depicted in Fig. 3. For initial condition  $(B_0, S_0) = (0.1, 0.1)$ , Fig. 7 shows that species 2 cannot produce biomass when alone. There is a *facilitation* phenomenon when mixed with species 1 (as it also happens in continuous culture, see Rapaport and Harmand (2008)), and an overyielding is then observed (33.81% for these parameters and initial proportion  $p_0 = 0.4$ ).

### 4.3 Variable yields and no growth thresholds

We have considered here a first species with a Monod law and a decreasing yield against a second species with a Moser law and a constant yield. Decreasing variable yields are typically met in alcohol fermentation Goma *et al.* (1979); ElAidar (2018). The expressions of the growth

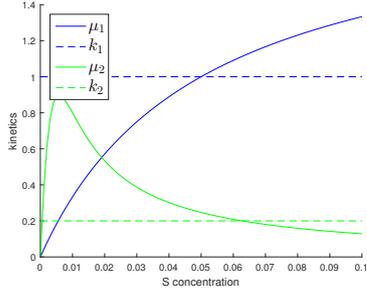


Fig. 3. Graphs of the growth rate functions and mortality levels.

	$\mu_i(S)$	$y_i(S)$
$i = 1$	$\frac{0.5 S}{0.1 + S}$	$1.8 e^{-0.2 S}$
$i = 2$	$\frac{0.8 S^4}{625 + S^4}$	0.8

Table 2. The growth and yield functions considered for the simulations.

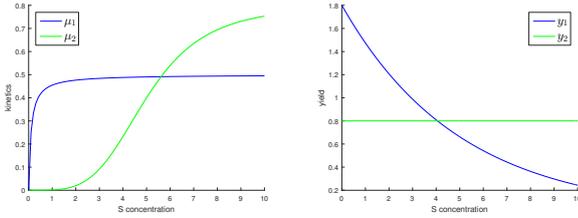


Fig. 4. Graphs of the growth rate functions (on the left) and yield functions (right).

and yield functions are given in Table 4.3 and their graphs are depicted in Fig. 4.

With such parameters, one may verify that conditions of Proposition 7 are verified. A significant overyielding may appear (13.14%), as can be seen in Fig. 9 for the initial proportion  $p_0 = 0.3$ .

#### 4.4 Robustness analysis

One may wonder if significant overyielding occurs for narrow intervals of the parameter values or not. To test the robustness of overyielding, we have generated random variations of all model parameters, including initial conditions, of magnitude up to 10% of the values given above, for each of the three models. The results are presented in Fig. 6, 8 and 10. One can observe that overyielding has the highest sensitivity for the model with mortality. This can be explained by the sensitivity of the condition  $\mu_i(\underline{S}_i) < k_i$ , where  $\underline{S}_i$  depends on all the parameters and the initial conditions (see Section 3.2).

## 5. CONCLUSION

The present work has explored several biological mechanisms that could produce overyielding in microbial ecosystems operated in batch conditions. These mechanisms correspond to different modeling hypotheses, and it is

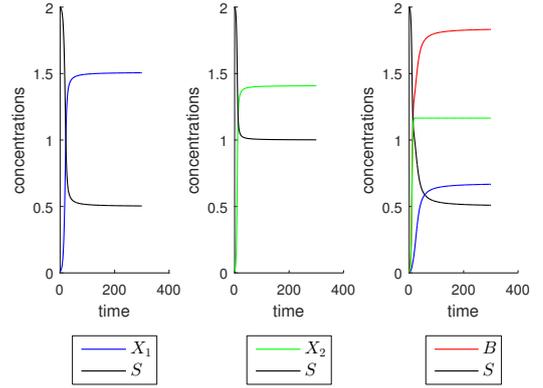


Fig. 5. Model with growth thresholds for  $(B_0, S_0) = (0.01, 2)$ . Time evolution of species 1 alone (left), species 2 alone (middle) and both species with  $p_0 = 0.4$  (right).

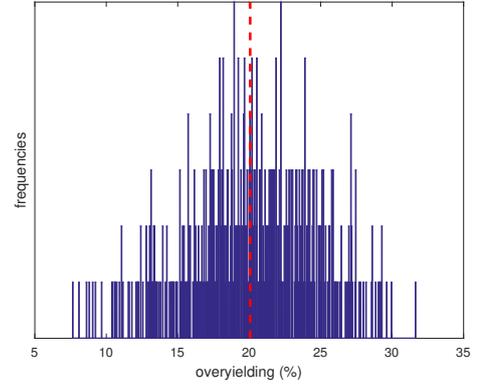


Fig. 6. Model with growth thresholds. Histogram of the overyielding (in %) obtained for 500 random variations of the parameters (average value in dotted line).

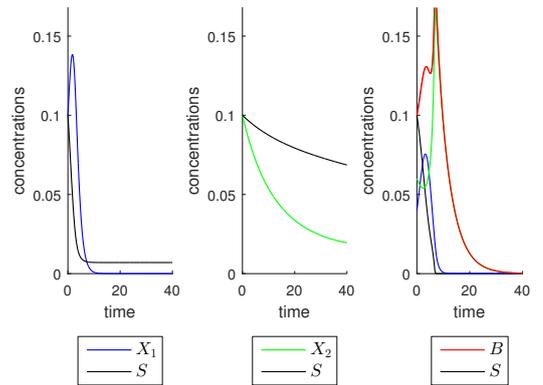


Fig. 7. Model with mortality for  $(B_0, S_0) = (0.1, 0.1)$ . Time evolution of species 1 alone (left), species 2 alone (middle) and both species with  $p_0 = 0.4$  (right).

shown that introducing thresholds in growth rates, mortality terms or variable yields can all independently explain

## ACKNOWLEDGEMENTS

This work was supported by the LabEx NUMEV incorporated into the I-Site MUSE.

## REFERENCES

- El Aida, S., Modélisation mathématique et exploration numérique de la fermentation en oenologie, MSc Thesis, Université de Pau et des Pays de l'Adour, France, 2018. <https://prodinra.inra.fr/record/442792>
- Goma, G., R. Moletta and M. Novak, title="Comments on the "Maintenance coefficient" changes during alcohol fermentation", Biotechnology Letters, 1(10), 415–420, 1979.
- Graham, J. H. and J. J. Duda, The humpbacked species richness-curve: a contingent rule for community ecology, International Journal of Ecology, Volume 2011, Article ID 868426, 15 pages, 2011.
- Hamelin, J. and K. Milferstedt, Mixing ecosystems during start-up of anaerobic digesters improves final performance, International Conference on Anaerobic Digestion, AD Technology and Microbial Ecology for Sustainable Development (ADTech2015), Feb 2015, Chiang Mai, Thailand, 2015.
- Harmand, J., C. Lobry, A. Rapaport and T. Sari, The Chemostat: mathematical theory of microorganisms cultures, ISTE Wiley, 2017.
- Jessup, C. M., R. Kassen, S.E. Forde, B. Kerr, A. Buckling, P. B. Rainey and J. M. Bohannan, Big questions, small world : microbial model systems in ecology, TRENDS in Ecology and Evolution, 19:4, 189–197, 2004.
- Langenheder, S., M. T. Bulling, M. Solan, and J. I. Prosser, Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity, PLoS ONE, 5, e10834, 2010.
- Rapaport, A. and J. Harmand, Biological control of the chemostat with non-monotonic response and different removal rates, Mathematical Biosciences and Engineering, Vol. 5, No. 3, pp. 539-547, 2008.
- Rapaport, A., T. Nidelet, S. El Aidar and J. Harmand, About biomass overyielding of mixed cultures in batch processes, 2019. Hal archive: <https://hal.archives-ouvertes.fr/hal-02010420>.
- Schmid, B. A. Hector, P. Saha and M. Loreau Biodiversity effects and transgressive overyielding, Journal of Plant Ecology, Volume 1, Issue 2, Pages 95102, 2008.
- Tros, M.E., T. N. Bosma, G. Schraa and A. J. Zehnder, Measurement of minimum substrate concentration ( $S_{min}$ ) in a recycling fermentor and its prediction from the kinetic parameters of Pseudomonas strain B13 from batch and chemostat cultures, Appl Environ Microbiol., 62:10, 3655–3661, 1996.
- Van Uden, N., Transport-limited growth in the chemostat and its competitive inhibition, A theoretical treatment, Archiv für Mikrobiologie", 58:2, 145–154, 1967.
- Van Uden, N., Transport-limited fermentation and growth of Saccharomyces cerevisiae and its competitive inhibition, A theoretical treatment, Archiv für Mikrobiologie", Archiv für Mikrobiologie", 58:2, 155–168, 1967
- Vernail, P. and M. Vives, Positive Effects of Bacterial Diversity on Ecosystem Functioning Driven by Complementarity Effects in a Bioremediation Context, PLoS ONE, 8(9):e72561, 2013.

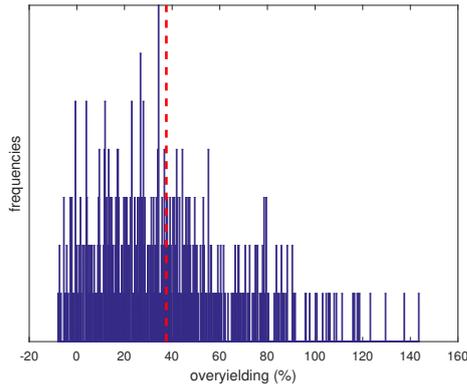


Fig. 8. Model with mortality. Histogram of the overyielding (in %) obtained for 500 random variations of the parameters (average value in dotted line).

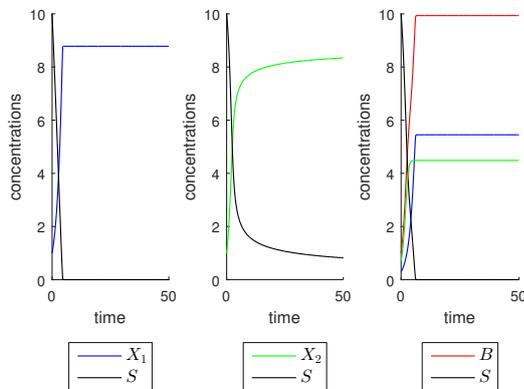


Fig. 9. Model with variable yields for  $(B_0, S_0) = (1, 10)$ . Time evolution of species 1 alone (left), species 2 alone (middle) and both species with  $p_0 = 0.3$  (right).

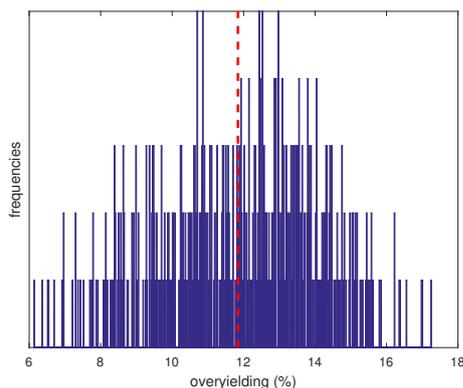


Fig. 10. Model with variable yields. Histogram of the overyielding (in %) obtained for 500 random variations of the parameters (average value in dotted line).

overyielding. Conditions for such phenomena to appear were presented and illustrated with numerical simulations. From these simulations, we established that far from being rare events, the introduced models exhibit overyielding for a large range of parameter values.