



# Lipid metabolism and benzo[a]pyrene degradation by *Fusarium solani*: an unexplored potential

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## Abstract

In a search for indigenous soil saprotrophic fungi for bioremediation purposes, *Fusarium solani*, a saprotrophic fungus belonging to the phylum Ascomycota, was isolated from a fossil carbon contaminated soil. The effect of the carbon source, glucose or olive oil, was investigated in vitro on the biomass produced by *F. solani* and on the degradation of benzo[a]pyrene (BaP) in mineral medium. After only 12 days of incubation, BaP degradation by *F. solani* was higher (37.4%) with olive oil used as the carbon source than the one obtained with glucose (4.2%). Catalase activity increased in the presence of olive oil (3.4  $\mu\text{kat mg}^{-1}$  protein) in comparison with glucose (2.1  $\mu\text{kat mg}^{-1}$  protein). When olive oil was used as the carbon source, BaP degradation increased up to 76.0% in the presence of a specific catalase inhibitor, 3-Amino-1,2,4-triazole (2 mM). This metabolic engineering strategy based both on the use of olive oil as carbon source (cultivation strategy) and on the blocking of the catalase activity could be an innovative and promising approach for fungal biodegradation of BaP and consequently for bioremediation of soil contaminated with polycyclic aromatic hydrocarbons.

**Keywords** 3-Amino-1,2,4-triazole · Benzo[a]pyrene · Biodegradation · Carbon source · *Fusarium solani* · Olive oil · Peroxisome

## Introduction

Benzo[a]pyrene (BaP), a widespread pollutant with potential mutagenic and carcinogenic properties, is a priority pollutant throughout the world. Among the processes that remove BaP from the environment, the fungal degradation appears to play a major role in the remediation of contaminated sites (Aranda 2016). In a search for indigenous soil filamentous fungi with the potential to degrade high-molecular-weight polycyclic aromatic hydrocarbons (PAH), our laboratory isolated numerous telluric saprotrophic fungi from PAH-contaminated soil (Potin et al. 2004; Rafin et al. 2013) deposited at our working collection (UCEIV mycology collection, Dunkerque, France). We focused our attention on *Fusarium solani* ([Mart.] Sacc.,

1881; teleomorph *Haematonectria haematococca* [Berk. and Broome] Samuels and Rossman, Ascomycota, Hypocreales, Nectriaceae) which was able to metabolize BaP in mineral medium (MM). Recently, Fayeulle et al. (2014) demonstrated that the mycelium of *F. solani* was able to actively uptake and transport PAH into lipid bodies. We therefore wonder if lipids and PAH degradation could be closely associated within the same fungal cellular compartment. However, almost all studies on fungal PAH degradation were conducted using carbohydrates as the energy and carbon source. In the present research, the effect of the carbon source, either glucose or olive oil, was investigated on the biomass produced by *F. solani* and on its BaP degradation in MM. Moreover, our previous studies demonstrated that *F. solani* used an intracellular Fenton-like system to generate hydroxyl radicals ( $\text{OH}^\bullet$ ) known as powerful oxidants involved in BaP biodegradation (Veignie et al. 2004). We explored a complementary approach for enhancing the intracellular  $\text{H}_2\text{O}_2$  flux by using a specific catalase inhibitor (3-Amino-1,2,4-triazole: 3AT), well known in eukaryote cells (Donaldson 2002). The catalase activity of *F. solani* was assessed in all treatments. Finally, we discussed this unexplored metabolic pathway linking lipid metabolism and BaP degradation in *F. solani* used as a fungal model.

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## Materials and methods

### Chemicals and media

BaP with 96% HPLC purity, 3AT, olive oil, standard reagent hydrogen peroxide (H<sub>2</sub>O<sub>2</sub> 30%), bovine serum albumin (BSA), and phenylmethanesulfonyl fluoride (PMSF) were purchased from Acros Organics. Reagent-grade dichloromethane (DCM) and methanol (MeOH) of the highest purity were purchased from Merck. Malt yeast extract agar (MYEA) medium was used for routine fungal growth. The standard basal medium used for the BaP degradation studies was the MM at pH 7 (Veignie et al. 2004).

### Fungal and inoculum preparation

*F. solani*, previously isolated from petroleum-contaminated soil, was supplied from our working collection of the UCEIV mycology collection (Dunkerque, France). This isolate was investigated in previous studies by Rafin et al. (2013), Fayeulle et al. (2014), and Veignie et al. (2004). This strain was identified by the CBS-KNAW Fungal Biodiversity Centre, Utrecht (The Netherlands). It was grown on MYEA at 22 °C under a 12/12-h photoperiod. For cultures in MM, Erlenmeyer flasks were inoculated by adding a spore suspension that was prepared by washing a 10-day-old culture of *F. solani* on MYEA with 4 ml of sterile deionized water. The final concentration of the fungal suspension was 10<sup>4</sup> spores ml<sup>-1</sup> of MM.

### Determination of *F. solani* dry biomass in the presence of glucose or olive oil as carbon source

Cultures were conducted in 250-ml Erlenmeyer flasks with 25 ml MM containing 10 g l<sup>-1</sup> of glucose or 5.4 g l<sup>-1</sup> of olive oil, corresponding to the same carbon concentration (4 g l<sup>-1</sup>). The amount of carbon in olive oil was predetermined using the CHNS elemental analyzer (Thermo Fisher Scientific, Milan, Italy). Samples were inoculated by adding a spore suspension of *F. solani* as a final concentration of 10<sup>4</sup> spores ml<sup>-1</sup> of MM. Three replicates were run for each carbon source. The fungal growth was estimated by determining the dry biomass produced over a period of 7 days after incubation at room temperature (18–22 °C) on a reciprocal shaking incubator (Infors, 175 rpm). The mycelium was filtered through pre-dried cellulose filters (55 mm diameter, 25 μm porosity) in a vacuum filtration apparatus and weighed after complete drying in an oven (3 days). The results were expressed as the mean value ± standard error of three replicates.

### BaP degradation with glucose or olive oil used as carbon source

The BaP degradation experiment was performed for 12 days. Our previous studies indicated that such an incubation period was required for obtaining a maximal BaP degradation rate. An appropriate volume of BaP stock solution initially dissolved in DCM (4 mM) was transferred into each 250-ml Erlenmeyer flask. After solvent evaporation, 25 ml of MM containing 10 g l<sup>-1</sup> of glucose or 5.4 g l<sup>-1</sup> of olive oil corresponding to the same carbon concentration (4 g l<sup>-1</sup>) was added to each flask. The final dose of BaP was 2 mg per flask (i.e., 317 mM). Flasks were sterilized at 121 °C for 20 min. Inoculation was performed by adding a spore suspension of *F. solani* aged 10 days (final concentration of 10<sup>4</sup> spores ml<sup>-1</sup>). In order to evaluate adsorbed BaP on fungal hyphae and abiotic degradation (extraction controls), flasks containing 15 ml MM containing the same carbon concentration (4 g l<sup>-1</sup>) without BaP were inoculated with *F. solani*. At the end of the experiment, the obtained cultures (mycelia + filtrate) were suspended in 10 ml MM with BaP (2 mg per Erlenmeyer) and stirred for 4 h on a reciprocal shaking incubator at 4 °C (Potin et al. 2004). This treatment allowed us to determine the adsorption processes on hyphae and abiotic degradation used for further calculations of BaP degradation. To detect abiotic BaP degradation, a treatment was prepared with BaP and without the fungus. All the treatments were undertaken in triplicates and incubated at 25 °C on a reciprocal shaking incubator at 175 rpm for 12 days. After incubation, the cultures were lyophilized for 3 days. Flasks containing total lyophilized cultures were introduced into a Soxhlet apparatus and extracted for 16 h with DCM. Organic fractions were concentrated in 20 ml of DCM/MeOH (50:50, v/v). With this extraction method, 98% of BaP initially present in MM was recovered. BaP concentrations were determined using the HPLC method described by Rafin et al. (2013). The percentage of BaP degradation was given by the formula  $[m_{Ec} - m_T / m_{Ec}] \times 100$ , in which  $m_{Ec}$  was the quantity of BaP recovered in extraction controls (conducted to detect adsorbed BaP on fungal hyphae) and  $m_T$  was the quantity of BaP obtained in each treatment. The results were expressed as the mean value ± standard error of three replicates (Table 1).

### Catalase activity

The catalase activity of the fungal biomass was assessed in the presence of glucose or olive oil. After 7 days of incubation, the harvested mycelia were washed twice with distilled water, frozen at -20 °C and powdered in liquid nitrogen using a mortar. A sample of 100-mg freeze-dried mycelia was solubilized in 5 ml of 50 mM sodium phosphate extraction buffer containing PMSF (1 mM pH 7.5) and centrifuged for 30 min at 5000 rpm. Catalase activity was determined

**Table 1** Effect of carbon source (glucose and olive oil) on BaP degradation and catalase activity of *Fusarium solani* in mineral medium in the absence or in the presence of 2 mM of 3-Amino-1,2,4-triazole (mean value ± standard error for triplicates)

Carbon source	Glucose		Olive oil	
	Without	With	Without	With
3AT				
BaP degradation (%)	4.2 ± 4.7		37.4 ± 10.2	76.0 ± 13.0
Catalase activity (μkat mg <sup>-1</sup> protein)	2.1 ± 0.16		3.4 ± 0.14	0

spectrophotometrically at 240 nm following the disappearance of peroxide ( $\epsilon = 43.6 \text{ mM}^{-1} \text{ cm}^{-1}$ ) for 3 min at 25 °C. To determine the specific catalase activity, the total intracellular proteins were determined using an absorbance at 280 nm and BSA as the standard. One unit (U) of catalase activity was defined as 1 μmol of H<sub>2</sub>O<sub>2</sub> consumed per minute at pH 7.4 and 25 °C. The results were expressed as the mean value ± standard error of three replicates (Table 1).

**Assessment of 3AT toxicity on *F. solani* by measurement of fungal dry biomass in the presence of olive oil**

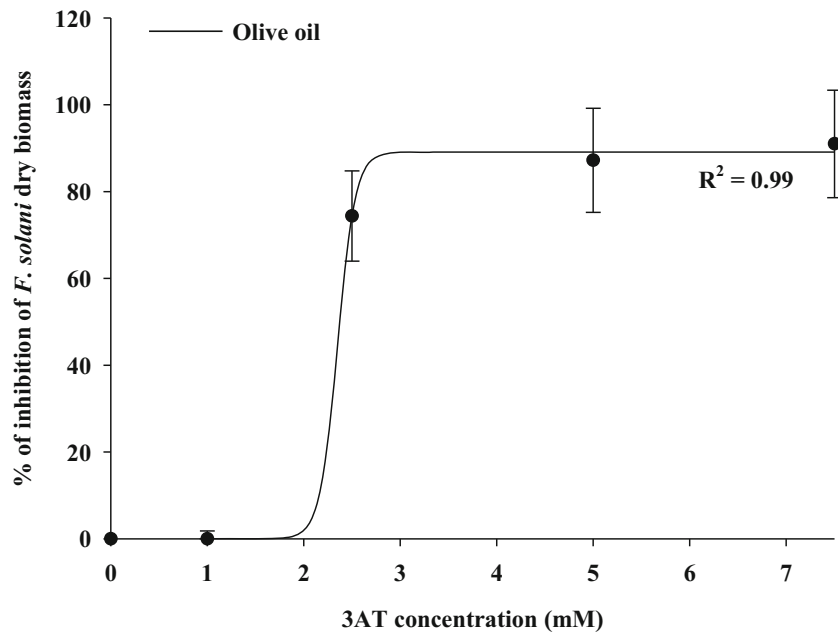
A preliminary experimentation was first conducted for determining the 3AT concentration compatible with the fungal growth with oil as carbon source. Two hundred fifty-milliliter Erlenmeyer flasks containing 25 ml MM with 5.4 g l<sup>-1</sup> olive oil were inoculated with *F. solani* as described previously. After inducing spore germination for 6 h, the 3AT concentration range tested (0, 1.0, 2.5, 5.0, and 7.5 mM) was introduced by adding a filter-sterilized 3AT solution to each flask at the desired final concentration. Three replicates were

run for each 3AT concentration. The fungal growth was estimated by determining the dry biomass produced over a period of 7 days after incubation at room temperature on a reciprocal shaking incubator as described previously. The percent of inhibition growth in the presence of 3AT at each concentration was calculated. The results were expressed as the mean value ± standard error of three replicates (Fig. 1). This experimentation allowed to determine the 3AT concentration of 2 mM used in the following experimentation.

**BaP degradation and catalase activity with olive oil in the absence or presence of 3AT**

The BaP degradation experimentation in the presence of olive oil as carbon source without (control) or with 3AT (2 mM) was then performed for 12 days as described previously. For the inhibition treatments, a filter-sterilized 3AT solution was added to MM (final concentration of 2 mM). The percentage of BaP degradation was determined in the absence (control) or in the presence of 3AT. The catalase activity of the fungal biomass was assessed in the same treatments after 7 days of

**Fig. 1** Dose–response curve of *Fusarium solani* to 3-Amino-1,2,4-triazole concentration range after 7 days of incubation in mineral medium with olive oil used as carbon source (mean value ± standard error for triplicates)



incubation. The results were expressed as the mean value  $\pm$  standard error of three replicates (Table 1).

## Statistical treatments

Differences in BaP degradation between treatments and reference culture were identified by a two-sample *t*-test at 99% confidence.

## Results and discussion

### Influence of carbon source on *F. solani* dry biomass

In the present research, we studied firstly the effect of either glucose or olive oil, used as the carbon source and energy on the BaP degradation by *F. solani* in MM. As almost all studies on fungal PAH degradation were conducted using carbohydrates such as glucose as the energy and carbon source, the first step was to study the capacity of this fungal strain to grow on each carbon source. For this, the dry biomass of *F. solani* in MM after 7 days of incubation was assessed in the presence of each carbon source used at the same carbon concentrations ( $4 \text{ g l}^{-1}$ ). *F. solani* dry biomass was  $91.4 \text{ mg} \pm 3.5$  with glucose and  $130 \text{ mg} \pm 24.5$  with olive oil, respectively, i.e., 30% higher than with glucose. Our results clearly indicated that *F. solani* was able to use both glucose and olive oil as carbon source for growth and energy consumption.

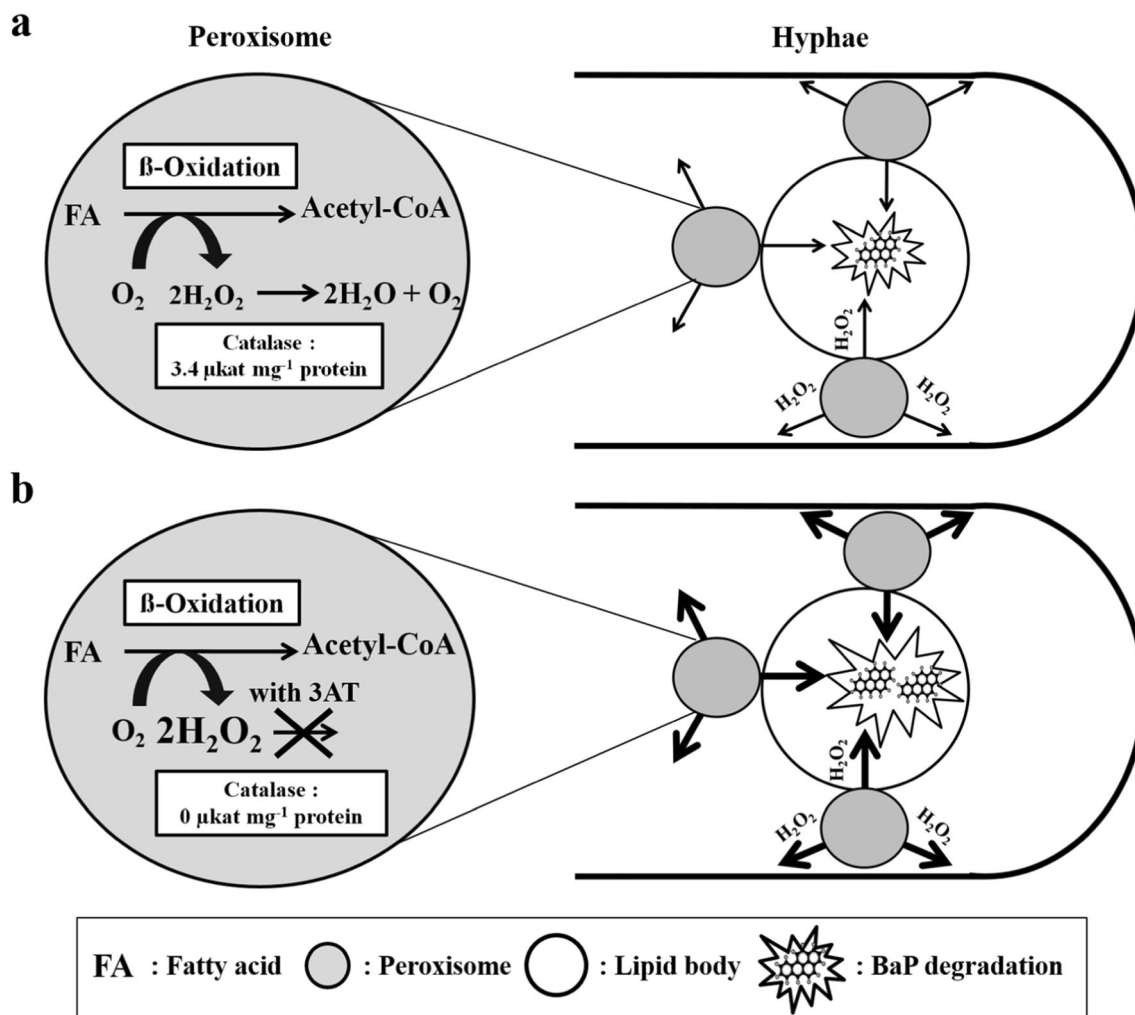
Radwan and Soliman (1988) previously showed that several species of soil fungi, in particular *Fusarium* sp., *Aspergillus* sp., or *Penicillium* sp., could use oleic acids as well as their sodium salts as sole source of carbon and energy. It is well known that lipid carbon supplies 9 kcal (kcal) per gram of carbon in comparison with 4 kcal per gram of carbon supplied by glucose, i.e., a ratio of 2.25/1 between lipids and glucose. However, the fungal biomass ratio obtained in our experiment (1.4/1) was lower than this theoretical ratio. The weak diminution of fungal biomass produced with the lipid substrate could be explained by the necessity for the fungus to develop special strategies to reach a hydrophobic substrate such as olive oil. It is known that fungi could adopt various energy-dependent mechanisms for the uptake of such compounds, i.e., by modifying cell wall structure or producing biosurfactant-like compounds (Muriel et al. 1996; Camargo-de-Morais et al. 2003; Luna-Velasco et al. 2007; Veignie et al. 2012).

### BaP degradation with glucose or olive oil as the carbon source

Then, the effect of the carbon source, either glucose or olive oil, was investigated on the BaP degradation by *F. solani*. Table 1 presented the BaP degradation by *F. solani* in MM

with each carbon source and the catalase activity obtained in both conditions. We were over careful with the BaP absorption on *F. solani* hyphae that could account for BaP dissipation in liquid culture as demonstrated by Thion et al. (2012) with phenanthrene, pyrene, and dibenz(a,h)anthracene. The cultures were totally lyophilized and extracted into a Soxhlet apparatus for 16 h with DCM. With this method, we assumed that the remaining BaP was totally extracted whatever the place it could be present, either absorbed or strongly adsorbed to the biomass. Moreover, the method used for the calculation of BaP degradation subtracted any remaining balance of BaP adsorbed. So, the BaP degradation percent obtained is independent from the biomass. After 12 days of incubation, BaP degradation by *F. solani* was only 4.2% when glucose was used as the carbon source. A ninefold increase in BaP degradation (37.4%) was obtained with olive oil. In these culture conditions, catalase activity increased by a factor of 1.62 when olive oil was used as the carbon source ( $3.4 \text{ } \mu\text{kat mg}^{-1} \text{ protein}$ ) when compared to glucose ( $2.1 \text{ } \mu\text{kat mg}^{-1} \text{ protein}$ ).

The effect of the carbon source on the BaP degradation and the catalase activity is discussed. Fungi generally metabolize fatty acids via the peroxisomal lipid beta-oxidation pathway (Kunau et al. 1995). Indeed, the first step of fatty acid oxidation is catalyzed by acyl-CoA oxidase which produces  $\text{H}_2\text{O}_2$  during normal enzymatic activity. Moreover, our previous studies conducted on *F. solani* clearly suggested the role of  $\text{H}_2\text{O}_2$  as a BaP-oxidizing agent (Veignie et al. 2004). Here, the use of olive oil as a carbon substrate induced an increase of the intracellular  $\text{H}_2\text{O}_2$  concentration, due to the normal lipid metabolic pathway, permitting fortuitously BaP oxidation by fungal cells, as schematically summarized in Fig. 2a (control). Several important arguments have been put forth in support of this hypothesis. Firstly, the principal fatty acid present in the olive oil is the oleic acid, which is a well-known peroxisome proliferator in eukaryotic cells (van der Klei and Veenhuis 2006). In the presence of olive oil, the peroxisome proliferation could increase consequently the intracellular  $\text{H}_2\text{O}_2$  concentration. Secondly, recent studies emphasized that peroxisomes maintain a close association with other intracellular organelles (Shai et al. 2016) in particular with lipid bodies (Binns et al. 2006), which constitute the intracellular storage sites of BaP in *F. solani* as demonstrated by Fayeulle et al. (2014). We hypothesized that this spatial proximity between peroxisomes and lipid bodies involved in normal lipid metabolism pathway allows a potential diffusion of  $\text{H}_2\text{O}_2$  flux from the peroxisomes to lipid bodies, inducing fortuitously a greater BaP oxidation by fungal cells in the presence of olive oil in comparison with glucose. This cultivation strategy based on the choice of olive oil as carbon source turned out that such a metabolic engineering strategy is profitable for enhancing BaP degradation by *F. solani*. In these culture conditions,  $\text{H}_2\text{O}_2$  flux produced is rapidly neutralized by



**Fig. 2** Scheme depicting the metabolic engineering strategy linking lipid metabolism, benzo[a]pyrene (BaP) degradation, and the involved fungal subcellular organelles. **a** Control (normal metabolism). **b** With 3-Amino-1,2,4-triazole (3 AT 2 mM)

peroxisomal catalase activity as confirmed by the enhancement of the catalase activity assessed in the presence of olive oil (Table 1 and Fig. 2a).

**Influence of 3AT (a specific catalase inhibitor) on BaP degradation with olive oil**

A preliminary experimentation allowed us to determine the 3AT concentration further used in the BaP biodegradation test (Fig. 1). The percent of *F. solani* inhibition growth with olive oil versus the concentration range of 3AT after 7 days of incubation in MM followed a typical sigmoidal dose–response curve which perfectly fitted with the five experimental data values as underlined by the  $R^2$  obtained (0.99). The concentration chosen of 2 mM (value graphically determined) was chosen as a good compromise, i.e., a concentration biologically compatible with the fungal growth in the presence of olive oil. Indeed, the dry biomass of *F. solani* was very lightly inhibited by this concentration which seemed to be sufficient for inducing a non-lethal oxidative stress.

Then, the effect of 3AT was investigated on *F. solani* BaP degradation in the presence of olive oil (Table 1). In comparison with the control (37.4%), *F. solani* culture with 3AT and olive oil dramatically increased BaP degradation up to 76.0%. Simultaneously, catalase activity decreased from 3.4  $\mu\text{kat mg}^{-1}$  protein to zero when 2 mM of 3AT was added in the culture when compared to the control. The use of 3AT, as a specific inhibitor of the catalase catalytic site, is frequently used to investigate the physiological functions of this enzyme (Ueda et al. 2003; Bagnyukova et al. 2005). It is well known that exposure to 3AT induces an oxidative stress in eukaryotic cells (Lushchak 2011). Indeed, the effect of catalase-specific inhibitor 3AT likely resulted in a significant increase of the intracellular  $\text{H}_2\text{O}_2$  concentration (Walton and Pizzitelli 2012). Under these conditions (olive oil and 3AT), the peroxisome proliferation and the catalase inhibition consequently induce a hyperoxidative state in the fungal cells permitting an important increase of the BaP degradation. It is highly likely that an increase of the intracellular  $\text{H}_2\text{O}_2$  concentration may produce reactive oxygen species (ROS), such



as hydroxyl radicals (OH<sup>•</sup>) (Aguirre et al. 2005; Bagnyukova et al. 2005) involved directly in BaP oxidation (Veignie et al. 2004) or through intermediary lipid peroxidation mechanisms (Hammel 1995). This relationship between lipid metabolism and BaP degradation is summarized in Fig. 2b. This strategy based on the blocking of the catalase activity by a specific inhibitor turned out de novo to be a profitable and promising approach for enhancing BaP degradation by *F. solani*.

## Conclusion

In the field of fungal PAH biodegradation, numerous research focused on effective enzymatic agents (i.e., peroxidases, laccases, cytochromes P450) to oxidize PAH. However, few studies have investigated the relationships between fungal nutrition and their capacities to degrade PAH. We demonstrated, for the first time to our knowledge, that lipid consumption enabled whole fungal cells to acquire fortuitously a high BaP degradation potential, likely due to a hyperoxidative state in fungal cells. A modulation of the fungal lipid metabolism could efficiently influence BaP degradation. We proposed a new metabolic engineering strategy, based both on the use of olive oil as carbon source (cultivation strategy) and on the blocking of the catalase activity for enhancing BaP degradation. The oriented fungal lipid metabolism could be a very promising approach for fungal biodegradation of BaP. This innovative concept in microbial soil ecotoxicology could permit practical applications for bioremediation of soil contaminated with PAH.

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