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Biodiversity, evolution and adaptation of fungi in extreme environments

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pages 237-246

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Abstract

Fungi play irreplaceable roles for ecosystem functioning. They may adopt different lifestyles, for example saprotrophs, symbionts or parasites: some species are cosmopolitan with a wide distribution and others, thanks to their ecological plasticity, may adapt to harsh environments precluded to most of life forms. In stressing conditions, their role is even more crucial for the recycling of organic matter or favoring nutrients uptake. When the conditions become really extreme and competition is low, fungi focus on extremotolerance and evolve peculiar competences to exploit natural or xenobiotic resources in the particular constrains imposed by the environment. This paper focuses on three different cases of fungal life in the extremes: hydrocarbon-polluted sites, extremely acidic substrates, and littoral dunes, aiming to give few but significant examples of the role of these fascinating organisms in peculiar habitats and the valuable biotechnological potentialities of the abilities they have evolved in response to such constrains.

Keywords

- [Acidophilic fungi](#),
- [alkalophilic fungi](#),
- [antioxidants](#),
- [polluted sites](#),
- [sand fungi](#)

Abstract

Jump to section

- [Fungi from polluted environments: A rich...](#)
- [Acidomyces acidophilus \(Sigler & J.W. Carmich...](#)
- [Macrofungi colonizing littoral dunes in Sicily](#)

Fungi play irreplaceable roles for ecosystem functioning. They may adopt different lifestyles, for example saprotrophs, symbionts or parasites: some species are cosmopolitan with a wide distribution and others, thanks to their ecological plasticity, may adapt to harsh environments

precluded to most of life forms. In stressing conditions, their role is even more crucial for the recycling of organic matter or favoring nutrients uptake. When the conditions become really extreme and competition is low, fungi focus on extremotolerance and evolve peculiar competences to exploit natural or xenobiotic resources in the particular constrains imposed by the environment. This paper focuses on three different cases of fungal life in the extremes: hydrocarbon-polluted sites, extremely acidic substrates, and littoral dunes, aiming to give few but significant examples of the role of these fascinating organisms in peculiar habitats and the valuable biotechnological potentialities of the abilities they have evolved in response to such constrains.

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There is no general consensus on the definition for an extreme environment. From an anthropocentric point of view, conditions deviating from the physicochemical parameters supporting mammalian life are considered as extreme. However, what is “extreme” and what is “normal” for microbes remains debatable, and the concept “extreme” may not be appropriate for microorganisms (Gorbushina & Krumbein [1999](#)). Search for life in extreme environments focused for long time almost exclusively on prokaryotes, although, more recently, many eukaryotes have been found to do extremely well under different stressing conditions. Fungi are particularly skilled in colonizing and they persist in novel environments, use novel resources, or form novel associations, taking advantage of the suites of traits that they carry at the time of encountering the new condition. This process, known as ecological fitting (Agosta & Klemens [2008](#)), works very well with fungi due to their uncommon ecological, biological, and morphological plasticity. Fungi may, for instance, promptly shift from one growth form to another according to the variation of physic or chemical conditions. They adopt unicellular growth when immersed in rapidly fermentable sugar or when they are in their infective phase, as for most human pathogens or during vascular plant invasion; alternatively they may grow as filamentous, the “search for food” growth form, allowing them to inspect the surroundings, or may shift to meristematic growth when exposed to stressing conditions to optimize surface/volume ratio.

Therefore, fungi dwell in virtually all types of habitat including the extremes. They may thrive in unusual environments (Onofri et al. [2011](#)) which range from extremely dry and cold deserts in the Antarctic and other very cold areas worldwide (Selbmann et al. [2005](#); [Maggi et al., this issue](#)), highest mountain peaks (Selbmann et al. [2008](#)) to deep permafrost soils (Gilichinsky et al. [2007](#); Zucconi et al. [2011](#)), geothermal and humid soils in volcanic areas (Appoloni et al. [2008](#)), acid mine drainages with sulfuric acid (Baker et al. [2004](#); Selbmann et al. [2008](#)), or in highly alkaline sites (Nagai et al. [1998](#)). Life is primarily determined by the presence of water, but some fungi can also reproduce at high salt concentration (Gunde-Cimerman et al. [2000](#), [2009](#); Gostinčar et al. [2010](#)), under extremely low water activity.

Fungi evolved in the extremes may even tolerate stresses, overcoming the conditions of their natural environments: black meristematic fungi are the best example for stress tolerance among eukaryotes. Even if psychrophiles, the growth of some black fungi of the Antarctic desert is not affected after 1 h exposure 90°C (Onofri et al. [2008](#)). Some black fungi may also survive Ultra-Violet rays (UV-B) exposure at lethal doses, for example yeasts (Selbmann et al. [2011](#)) or even at space conditions (Onofri et al. [2012](#)).

Due to their uncommon adaptability, fungi may also easily colonize in new extreme and stressful environments created by anthropogenic activities, such as those polluted with heavy metals (Ceci et

al. [2012](#)), radionuclides, and high concentrations of toxic xenobiotic compounds. Dadachova et al. ([2007](#)) stretched considerably our imagination and isolated fungi from the highly damaged radioactive reactor at Chernobyl, feeding on radionuclides.

Therefore, fungi not simply tolerate and survive the extremes, but, by adopting different mechanisms, they also actively reproduce.

The contributions here reported are remarkable examples of fungal adaptation to the extremes, highlighting the uncommon ability of these fascinating organisms looking for and exploiting new environments, thanks to their ecological plasticity. In the long run, this process leads to the selection of extremotolerant/extremophilic strains. Fungi evolved in natural extreme environments or in polluted sites may be of valuable biotechnological potential for the production of extremozymes, specific metabolites, or for their exploitation in bioremediations programs, respectively.

Fungi from polluted environments: A rich source for bioexploitation

Jump to section

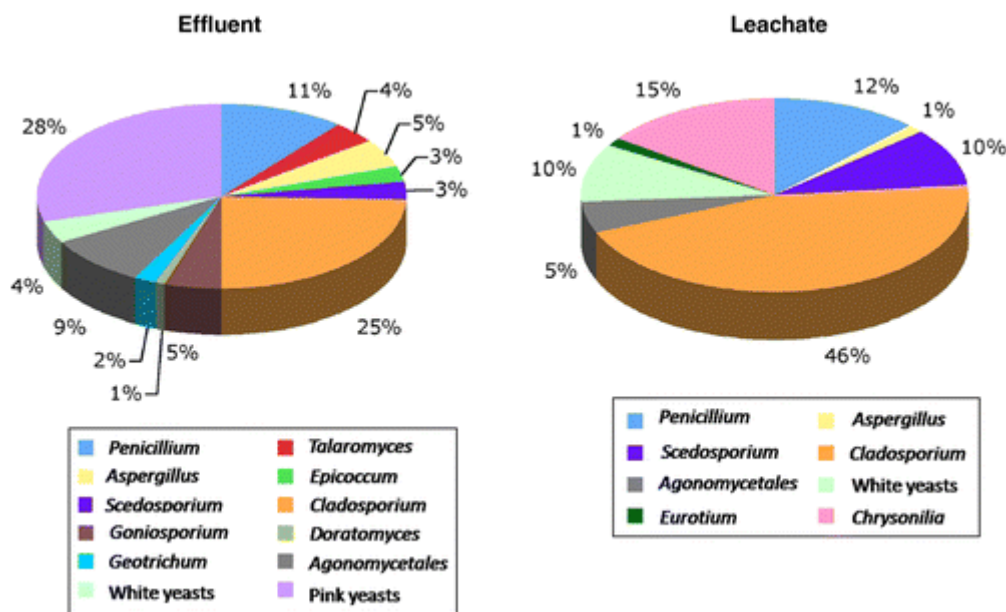
- [Fungi from polluted environments: A rich...](#)
- [Acidomyces acidophilus \(Sigler & J.W. Carmich...](#)
- [Macrofungi colonizing littoral dunes in Sicily](#)

Polluted sites are very selective environments, characterized by extreme conditions often hostile to life. There, autochthonous saprotrophic mycoflora is generally poor in terms of biodiversity, but fungal strains isolated from these environments are strongly adapted to high toxicity and extreme physical parameters (i.e. high salt concentration and high pH). These strains are potentially useful in biotechnological applications such as biodegradation of the pollutants themselves (Gomes & Steiner [2004](#); Rustler et al. [2008](#); Varese et al. [2011](#)), or they can be considered as sources of important bioactive compounds, such as specific enzymes, biosurfactants, and antioxidants, useful for applications in medicine or food, cosmetics, and chemical industry (Adrio & Demain [2003](#); Hofrichter [2010](#)). Sources of pollution have rapidly increased with urbanization and economic development; municipal and industrial landfills, energy power plants, refineries, and deserted mines are some significant examples. Mixtures of hydrocarbon compounds are known to possess a measurable toxicity toward living systems depending on their composition, concentration, and on environmental factors. In heavily polluted areas, there is an immediate detrimental effect on life (Steinhart & Steinhart [1972](#); Sikkema et al. [1995](#)).

The autochthonous mycofloras from different polluted sites were investigated and their potential applications for bioremediation and for bioactive compounds exploitation were analyzed. Biological material was isolated from two polluted substrata: Italian landfill leachate in methanogenic phase (more than 10 years old) and a hydrocarbon-polluted site. The percolation of rainwater during the decomposition of wastes generates leachates which are among the most polluting and difficult to treat wastewaters. Their dark color in particular remains after treatment by biological oxidation in traditional treatment plants (Stegmann et al. [2005](#)). The autochthonous mycoflora from a sample of crude leachate and from an effluent originating from the biological oxidation treatment of leachates was isolated by filtration of 100 ml sample on sterile membrane (pore size of 0.45 μm) and cultured on Malt Extract Agar (MEA) with antibiotics in 10 replicates. Then, the fungal isolates were identified and tested in the bioremediation of wastewaters, in the presence or absence of an additional carbon source. The occurrence of fungal propagules of crude leachate was very low (73 CFUs l^{-1}) and only 11 fungal taxa were isolated. The indigenous mycoflora increased both quantitatively and qualitatively during the biological oxidation treatment, reaching 102 CFUs l^{-1} , which corresponded to 16 taxa. For each taxon, at least one fungal strain was isolated. In addition,

all the undifferentiated colonies near a fast growing fungus were isolated before the overgrowth occurred. A total of 51 strains were isolated. They were ascribable to 11 genera, some to Agonomycetales and yeasts (Figure 1).

Figure 1 Relative abundance of different fungal taxa in leachate and effluent.



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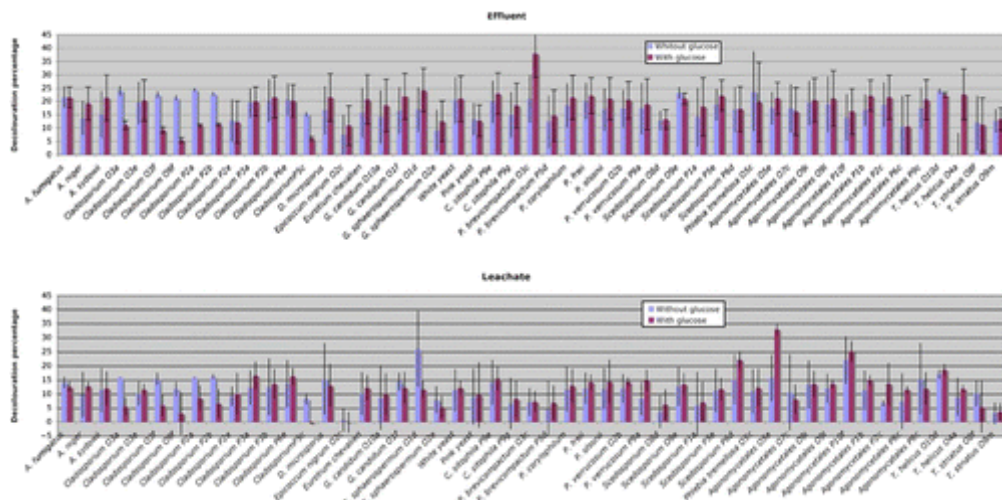
Both samples were dominated by mitosporic fungi; they all are adaptive extremophiles. Many extremophilic fungal species have a mainly mitotic lifestyle, although even in species with sexual cycles, small isolated populations can diversify independently (i.e. *Eurotium*). This is partially due to the progressing genetic drift that rapidly fixes alleles in small populations which have managed to adapt to extreme habitats, thanks to the absence of sexuality and/or gene flow (Gostinčar et al. 2010).

Some of the isolated fungal species were potentially pathogenic. The human pathogenicity of fungi is associated with moderate osmotolerance at the order level (de Hoog et al. 2005). Actually, warm-blooded animal body and skin represent an extreme environment for microorganisms, with elevated temperatures and salt levels, as well as mechanic stress. Thus, fungi with suitable preadaptation, as those characterizing leachates, might represent a pool of potential medically important fungi, which might readily switch from environmental niches to human bodies (Gostinčar et al. 2010). Prenafeta-Boldú et al. (2006) referred to this preference of different habitats as “dual ecology”. Opportunistic pathogenic fungi, such as *Geomyces pannorum* (Link) Sigler & J.W. Carmich., *Candida* spp. Cif. & Redaelli, *Cladophialophora* spp. Borelli, *Exophiala* spp. J.W. Carmich., *Geotrichum candidum* Link, *Microsporum canis* E. Bodin ex Guég., *Scedosporium* spp. Sacc. ex Castell. & Chalm., and *Aspergillus fumigatus* Fresen, were often isolated from both water and soil of polluted and human-impacted environments (Ulfig 1994; Tigini et al. 2009). Many of these species are able to use hydrocarbons, aromatic compounds, and natural gas as carbon source; they also grow at very low oxygen partial pressure and in the presence of high ammonium and salt concentrations (Kaltseis et al. 2009; Badali et al. 2011).

Bioremediation potential of autochthonous fungal strains was tested against wastewater samples by means a miniaturized screening. The addition of 1 g l^{-1} glucose as carbon source was also considered, in order to evaluate a possible co-metabolism. After 20 days of treatment, the isolates showed up to 15–17% decolorization for the leachate and up to 21–26% decolorization for the effluent (Figure 2). In general, the addition of glucose (0.1%) did not affect the decolorization of wastewaters. The most promising strains belong to *Aspergillus* P. Micheli, *Penicillium* Link and

Scedosporium genera already known to be able to degrade recalcitrant compounds (Tigini et al. 2009).

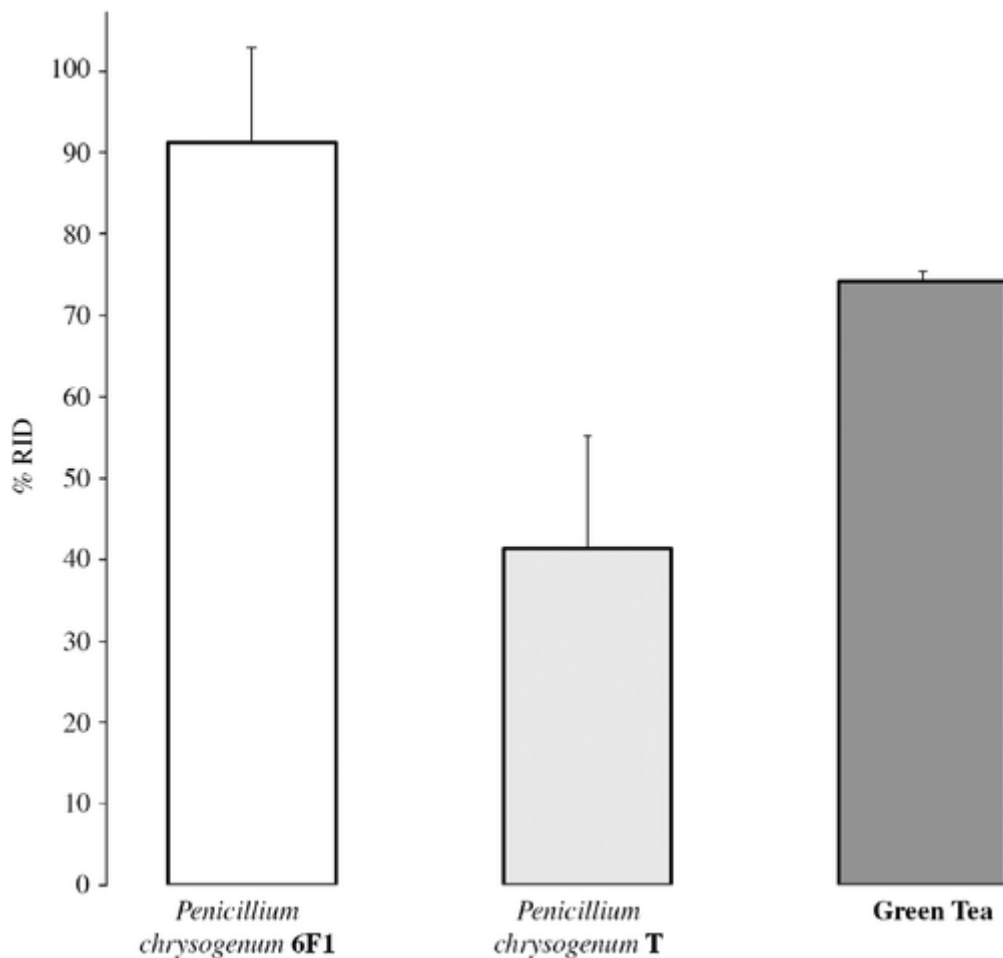
Figure 2 Decolorization percentage of the leachate and the effluent obtained by autochthonous fungi.



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Investigation for potential producers of antioxidant compounds was carried out on the *Penicillium chrysogenum* strain 6F1 previously selected in a pool of isolates from hydrocarbon-polluted soils as best user of low-sulphur content oil (BTZ) as sole carbon source (Tosi et al. 2010). The *in vitro* fungal methanolic extracts antioxidant activities were investigated by DPPH (2,2-diphenyl-1-picrylhydrazyl)-free radical scavenging assay, according to Cheung et al. (2003), and were compared with those of an ascorbic acid standard. The strain from hydrocarbon-polluted soil (6F1) was compared with a *P. chrysogenum* isolate (T) from a Thracian tomb (Bulgaria), an undisturbed and stable site, climatically controlled. Moreover, data were compared with the antioxidant response of a sample of commercial green tea, considered as the most antioxidant natural source. *P. chrysogenum* 6F1 was the best producer of antioxidant, causing a 91.28% of DPPH reduction, with differences statistically significant ($p < 0.05$) between this strain and *P. chrysogenum* isolate (T), isolated from the tomb (41.35%) and the green tea sample (Figure 3). The activity observed highlighted the strong ability of strain 6F1 to overcome the oxidative stress.

Figure 3 Reduction of DPPH (expressed as percentage of decrease in the DPPH absorbance value) with standard deviations as a measure of free radical scavenging activity in the two strains *P. chrysogenum* analyzed: 6F1 originating from a hydrocarbon-polluted soil (white column), T originating from a climatically controlled environment (gray column), and green tea (black column).



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Polluted sites reveal to be rich sources of microorganisms of enormous biotechnological potential which are still waiting to be discovered. Zhao et al. (2010) noted that black yeasts can be enriched by the use of hydrocarbon atmospheres. A novel species, *Exophiala sideris* Seyedmousavi & de Hoog, repeatedly isolated from the environment by using this method was found by Seyedmousavi et al. (2011) from a closed arsenic mine polluted by hydrocarbons. Hence all strains available to date have been isolated in the presence of toluene.

***Acidomyces acidophilus* (Sigler & J.W. Carmich.) Selbmann, de Hoog, & De Leo as a potential source of low-pH active degradative enzymes**

Jump to section

- [Fungi from polluted environments: A rich...](#)
- [Acidomyces acidophilus \(Sigler & J.W. Carmich...](#)
- [Macrofungi colonizing littoral dunes in Sicily](#)

Acidophiles have been defined as organisms which actively grow at pH < 4.0 and are still able to grow even at pH 1.0. Extreme pH can result in irreversible damages in the primary and secondary structures of proteins. The cellular membrane may represent an osmotic barrier to the external environment: the cytoplasmic components are maintained at pH values different from that of the surrounding substrate even if the external pH reaches extreme values; this ability has enabled fungi

to become established in both extremely low-pH (close to 1) and high-pH (11) environments (Longworthy [1978](#)).

Although acidophilic microorganisms are predominantly bacteria (Ingledeu [1990](#)), fungi have also been reported from various acidic environments. In acidic water environments, fungi, among other organisms, are known to play an important role in the formation of microbial mats (Baker & Banfield [2003](#)) and, together with other eukaryotes as algae and protozoa, are reported to be the principal contributors of Tinto's River water biomass (Spain), at pH 2 and 30°C (Zettler et al. [2002](#)). In the acid mine drainages, fungal hyphae are the major components of biofilms and provide a surface for the attachment of other microorganisms (Johnson [1998](#); Baker et al. [2004](#)). A number of yeasts and filamentous fungi have been found to grow at very low pHs. Some fungal species are known to be able to grow in extremely acidic conditions. *Acontium velatum* Morgan was isolated from a solution containing 4% copper sulfate (pH 0.2–0.7; Starkey & Waksman [1943](#)); *Trichosporon cerebriae* (invalid name, Schleper et al. [1995](#)) was reported to grow in 2N sulfuric acid solution containing glucose and peptone (Sletten & Skinner [1948](#)); an acidophilic species was isolated from the soil (pH 1.4–3.5) adjacent to a sulfur pile field from a natural gas purification plant as *Scytalidium acidophilum* Sigler & J.W. Carmich. (Sigler & Carmichael [1974](#)); and acid mine drainage (pH 0.8–1.38) as “*Acidomyces richmondensis*” (invalid name, Baker et al. [2004](#)). This fungus was recently validated as *A. acidophilus* (Sigler & J.W. Carmich.) Selbmann, de Hoog, & De Leo, belonging to the order *Capnodiales* (Selbmann et al. [2008](#)); *Hortaea acidophila* Hölker et al. another capnodialean species was isolated from brown coal (pH 0.6) containing humic and fulvic acids (Hölker et al. [2004](#)). The latter two species were reported to grow even at pH 1 (Sigler & Carmichael [1974](#); Baker et al. [2004](#); Hölker et al. [2004](#); Selbmann et al. [2008](#)). All the acidophilic fungi hitherto reported are invariably anamorphic species; *Teratosphaeria acidotherma* A. Yamaz., K. Toyama, & Nakagiri is an exception and is phylogenetically related to *A. acidophilus*, recently described as a new teleomorphic species from acidic hot spring in Japan (Yamazaki et al. [2010](#)).

In general, extremozymes have attracted a great deal of interest due to their potential for practical applications. However, studies on fungal acidic enzymes still remain limited with a few exceptions including mannanase, xylanase (Luo et al. [2009a](#), [2009b](#)), and polygalacturonase (Yang et al. [2011](#)) from the acidophilic *Bispora* sp. strain MEY-1, or laccase from *H. acidophila* (Tetsch et al. [2005](#)). The aim of this study was to test the metabolic competences of *A. acidophilus* strains CCFEE 5419 (= CBS 270.74), CCFEE 5420 (= CBS 335.97), and CCFEE 5421 (= CBS 899.87), and to investigate their potential interest for application. This species belongs to the ecological group of black meristematic fungi known to be specialists in the extremes due to their morpho-physiological adaptation (de Hoog & Grube [2008](#)).

The strains were tested for the following enzymatic abilities: amylase, lipase, DNase, cellulase, and protease by using semi-quantitative tests (Hankin & Anagnostakis [1957](#), [1977](#)) and ligninase by using the Poly R-478 (Sigma) indicator (Table [I](#)). Tests were done on solid media prepared at pH 3 and pH 7 and inocula were obtained from fresh subcultures. Cultures were incubated at 25°C, which was the optimal growth temperature for all strains tested (Selbmann et al. [2008](#)). Solid media at pH 3 were prepared by sterilizing agar solution separately to avoid acidic hydrolysis. All the experiments were carried out in triplicate; plates were controlled weekly. Since some black fungi are known for their ability to degrade aromatic compounds, the potential of these fungi to use phenol (PHE), catechol (CAT; 1,2 dihydroxybenzene), 4 hydroxybenzene (4HB), protocatechuic acid (PCA; 3,4-dihydroxybenzoic acid), and phenylacetic acid (PAA) as carbon source at different pHs was tested by using Czapek medium supplemented by 500 mg/l of the tested aromatic compound as the sole carbon source. Tests were carried out in both liquid (8 ml in test tubes) and solid media at pH 3 and pH 7; the growth was measured by means of dry weight (data not shown) and colony diameter, respectively. A positive (Czapek broth) and negative control (Czapek broth without glucose) were used; tests were carried out in triplicate. Inocula were prepared as follows: the mycelium was grown for 1 week at 25°C on agar slant (Malt Agar) and then suspended in 5 ml

of saline solution (0.9% NaCl); the biomass was gently scratched and transferred into 250 ml Erlenmeyer flasks containing 50 ml of Czapek broth at 25°C in shaken culture (180 rpm) for 72 h. Biomasses were then harvested by centrifugation (15 min at 4000 rpm), washed three times with saline solution and finally resuspended in 50 ml of Czapek broth mineral solution. Two milliliters of the suspension were used as inocula for tests in liquid media and then incubated at 25°C for 2 weeks. Forty microliters of the same inoculum were used for solid media tests in which the same phenolic compounds were amended; cultures were incubated at 25°C for 2 weeks. Enzymatic activities are reported as D/d ratio (halo diameter/colony); the ability to grow using phenolic compounds as sole carbon source was recorded as dry weights compared with a negative control.

Table 1 Enzymatic activities of *A. acidophilus* strains.

[CSVPDF](#)Display Table

As shown in Table I, all strains tested provided negative results for both cellulase and protease at pH 3 and pH 7. DNase was also negative, but this activity was tested at pH 7 only, since at pH 3 nucleic acids were invariably hydrolyzed. All the strains were positive for lipase production at both pH values tested, even if the activity was invariably more intense at pH 7. The production was particularly intense for the strain CCFEE 5419.

Strains CCFEE 5419 and CCFEE 5420 were also positive for ligninase at both pH 3 and pH 7, whereas strain 5421 was positive at pH 7 only, showing a minimal growth at pH 3.

All the strains were also positive for amylolytic activity: strains CCFEE 5420 and CCFEE 5421 were active at both the pHs tested, but they were higher at pH 3. Strain CCFEE 5419 produced amylases only at pH 3.

Overall, all strains grew more rapidly at pH 3 in most of the media tested but growth was noteworthy for strain CCFEE 5419, for which the differences between colonies diameter were up to five times higher at pH 3 (in the case of cellulase). Results obtained in this study reflect the ecology of the fungi tested. The apparent stronger acidophily of the strain CCFEE 5419 may reflect an adaptation at more rigid pH constrains. Strain CCFEE 5419 was, in fact, isolated from a soil near an acidic elemental sulfur pile at pH 1.1, whereas strains CCFEE 5420 and CCFEE 5421 were isolated from pyrite ore mine drainage (pH 2) and from the acidophilic alga *Dunaliella acidophila*, respectively.

As shown in Table II, all the strains tested were able to use 4HB and PCA, both at pH 3 and pH 7, whereas PAA was efficiently metabolized only at pH 7; none of the strains were able to utilize PHE and CAT, with the exception of a slight growth recorded on CAT for strain CCFEE 5420 at pH 3. Most probably the strains tested may decarboxylate 4HB, PCA, and CAT, which are intermediate products of toluene degradation (Prenafeta-Boldú et al. 2006), but they are unable to cleave the aromatic ring.

Table 2 Phenolic compounds uptake.

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The results obtained in this study revealed that these strains may be of enormous biotechnological potential. Acid-active enzymes, such as amylase or lipase may have wide-scale applications as, for instance, in acidic effluent treatment or in detergent and leather industries, respectively. The ability of these fungi to metabolize phenolic compounds even at low pH make them good candidates for the development of bioremediation programs.

Macrofungi colonizing littoral dunes in Sicily

Jump to section

- [Fungi from polluted environments: A rich...](#)
- [Acidomyces acidophilus \(Sigler & J.W. Carmich...](#)
- [Macrofungi colonizing littoral dunes in Sicily](#)

Littoral dunes are classified by USDA Soil Taxonomy (Soil Survey Staff [1999](#)) as Dunelands-Typic xeropsamments which evolved on incoherent deposits from 10 to 20 m a.s.l. and are characterized by a coarse texture.

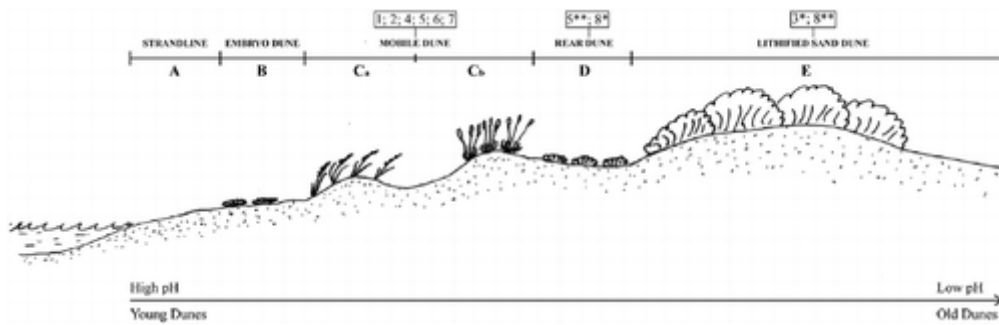
The sandy coasts are a poorly suitable habitat for the settlement of fungi that must face stressful conditions caused by marine aerosol, blowing wind, limited nutrients, and water availability, and high temperature that the sandy substrate may reach. The period of mushroom appearance in the dunes and rear dunes is mainly between late November and early February.

Despite the limiting factors mentioned above, fungal diversity in the dune system is remarkable. A group of species can be considered strictly arenicolous as reported for Italy by Contu ([1988](#)), Lantieri et al. ([2009](#), [2012](#)), Franchi et al. ([2001](#)), and Venturella and Contu ([2002](#)). Similar results have been highlighted in Finland (Eriksson [1964](#)), France (Courtecuisse [1984](#), [1986](#); Bon [1991](#)), England (Rotheroe et al. [1987](#); Rotheroe [1993](#)), Norway (Andersson [1950](#); Høiland [1975](#)), Holland (Arnolds [1983](#)), and Spain (Calonge & Telleria [1980](#); Moreno et al. [1994](#)).

Sandy coasts may constitute a refuge for cosmopolitan species and also for rare and infrequent fungi. Such species live in specific ecological niches, thanks to specific morphological and physiological adaptations. In these environments, soil fertility and the tendency to acidification depend almost exclusively on organic inputs provided by the vegetation and on the performance of the humification and mineralization processes in the soil surface horizons (Arrigoni [1990](#)).

Besides, the presence of specific fungi is closely related to the occurrence of certain plant communities (Figure [4](#)). The innermost consolidated dunes (lithified sand dunes) are the most susceptible habitats to the action of salt and wind. The vegetation of these habitats is mainly characterized by *Ammophila arenaria* (L.) Link subsp. *arundinacea* H. Lindb. fil. which favors the elevation of the dunes.

Figure 4 Distribution of sabulicolous fungi (*sensu strictu*) and plant communities of a dune transect in Sicily: (1) *A. aridicola* Geml, Geiser, & Royse; (2) *A. menieri* Bon ex Bon; (3) *H. conicoides* (P.D. Orton) P.D. Orton & Watling; (4) *P. cinctulus* (Bolton) Britzelm; (5) *P. pseudoammophila* Bon & Donadini; (6) *P. ammophila* (Durieu & Lév.) P.D. Orton; (7) *R. malençonii* Pacioni & Lalli; and (8) *X. mediterranea* (Pacioni & Lalli) Quadr. & Lunghini. (A) no plant communities; (B) *Salsolo-Cakiletum maritimae* Costa & Mansanet 1981 corr. Rivas-Martínez & al. 1992; (Ca) *Sporobolo arenarii-Agropyretum juncei* (Br.-Bl. 1933) Géhu 1984; (Cb) *Echinophoro spinosae – Ammophiletum arundinaceae* Géhu, Riv.Mart. et R.Tx. 1972 in Géhu et al. 1984; (D) *Centaureo-Ononidetum ramosissimae* Br.-Bl. & Frei in Frei 1937; and (E) *Ephedro-Juniperetum macrocarpae* Bartolo, Brullo, & Marcenò 1982. (*) Species growing only in NW-Sicily and (**) species growing only in SE Sicily.



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Field investigation on fungi growing in sandy dunes follows the standard methodology adopted by mycologists for the inventory of fungal diversity in Italy (Venturella et al. 2011). Periodical observations, from 2001 until now, were carried out in the sandy habitat of SW and SE Sicily. Target areas were selected in different protected areas of Sicily such as Oasi del Simeto (Catania), Oasi Faunistica di Vendicari (Siracusa), and Macchia Foresta Fiume Irminio (Ragusa). Besides, the following localities were also investigated: Santa Maria del Focallo and Sampieri (Ragusa), Manfria (Caltanissetta), and Balestrate, Le Macchie, Lascari, and Salinelle (Palermo).

Psathyrella ammophila (Durieu & Lév.) P.D. Orton, growing throughout the year except during summer in mobile dunes, can be observed at the base of tufts of *A. arenaria* subsp. *arundinacea*. The role of *A. arenaria* subsp. *arundinacea* is to provide the fungus with a good degree of shading and to protect it from the wind. Thanks to the capillary action of roots that allow water to rise from the deep layers, the tufts of *A. arenaria* subsp. *arundinacea* create a moist and fresh microhabitat. Some fungi which are considered exclusive of sea coasts, such as *Agaricus aridicola* Geml, Geiser, & Royse, *Agaricus menieri* Bon ex Bon, *Panaeolus cinctulus* (Bolton) Britzelm, and *Rhodocybe malençonii* Pacioni & Lalli, have been observed in the same type of habitat.

These species are characterized by long stipes embedded in the sandy substrate both to protect the sporocarps from the mechanical and drying action of wind and for absorbing moisture from substrate's deeper layers.

Peziza pseudoammophila Bon ex Donadini can be observed in the rear dune: it grows at the base of the stumps of *A. arenaria* subsp. *arundinacea* or among dried plant residues deposited on the surface of the substrate or into the deeper layers.

In eastern Sicily, erosion is responsible for the progress of the vegetation belt (characterized by *Ephedro-Juniperetum macrocarpae* Bartolo, Brullo, & Marcenò 1982) toward the seashore. There, *Xerula mediterranea* (Pacioni & Lalli) Quadr. & Lunghini is the most common species among the arenicolous and halophilic fungi. In western Sicily, *X. mediterranea* grows in rear dunes characterized by the presence of *Crucianelletalia maritimae* Sissing 1974. *X. mediterranea* is easily recognizable by the long stem deeply buried in the sand, and it is associated with *Juniperus macrocarpa* S. & S., at the base of which the number of basidiomes may be conspicuous.

Hygrocybe conicoides [(P.D. Orton) P.D. Orton & Watling], a widespread sabulicolous species, is infrequent in Sicily. The halophyte and heliophilous *H. conicoides* grows along the dune belt and in marginal areas in winter (December–January), and it is ecologically related to moss carpets in the rear dunes, a typical habitat ensuring protection from sea spray.

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