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Review

Fungi in acidic fire: A potential source of industrially important enzymes

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ABSTRACT

The microbial life that exists in harsh habitats of low pH possess several unique characteristics, which assign interesting qualities to these microorganisms and enable them to thrive in such a harsh environment. Among microorganisms inhabiting low pH environments, fungi are the second largest reported organisms. These acidophilic fungi are the main source of acid–stable enzymes that could be utilized in many industries including paper, leather making, food and feed industries, where the efficacy of commonly available enzymes is limited by challenges like stability and functional kinetics. The current review discusses the acidophilic fungi with emphasis on their diversity and pH homeostasis mechanisms adopted against low pH environments. In addition, an overview about the acid–stable enzymes obtained from these acidophilic fungi, their main sources and potential applications have also been discussed.

1. Introduction

Life exists at various extremes, including organisms inhabiting low pH environments with a growth optimism of less than pH 3, which are termed Acidophiles (Baker-Austin and Dopson, 2007). Acidophilic environments on earth are comprised of both natural and anthropogenic origin, with varying range of acidity. These localities include geothermal

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and volcanic areas, acidic geothermal springs, acidic lakes, acid rock drainage (ARD) and acid mine drainage (AMD) (Zettler et al., 2002; Baker et al., 2003; Brown and Wolfe, 2006; Aguilera et al., 2010). Baker et al. (2003) and Brake and Hasiotis (2010) categorized such environments as extreme acidic, also accompanied with elevated levels of toxic metals, sulfate, and high temperature, yet diverse range of microbes inhabit these extreme environments. These microbes derive electrons from sulfide minerals and establish a chemoautotrophic based ecosystem. The activity of acidophilic microbes contributes to enhance the AMD formation.

Conventional and molecular studies of microorganisms inhabiting acidic environments provided insights into the acidophilic as well as metal–tolerant microbial diversity (Silverman et al., 1964). Eukaryotic microbial communities are thought to be important players in such low pH environments, but this needs further study (Baker et al., 2003). In one particular subsurface mine situated in the iron mountains, California, Fungal hyphae accounted for the majority of biomass in biofilm communities, especially in running solutions (Baker et al. 2003) These fungal hyphae fasten the biofilm to the pyrite rocks and accord structure, particularly to the slime streamer (Baker et al., 2003). They serve as the attachment site for prokaryotes by providing a large surface area. Furthermore, fungi regulate the level of organic carbon and maintain it at a lower level by production of carbonate ions that results in the enhanced proliferation of chemolithoautotrophic acidophilic microbial organisms, especially prokaryotes (Baker et al., 2004).

Microbe minerals interaction is of great significance as it causes AMD generation in acidic environments (Fig. 1). Desulphurization of coal, industrial toxic wastes treatment and metals bioaccumulation, are some of important applications of acidophiles (Rossi and Torma, 1983; Rawlings, 1997), also acidophiles are globally used for bioleaching to extract metals from their respective low-grade ores and industrial wastes. These microorganisms provide propitious source of novel acid–tolerant enzymes and such extremozymes may meet the need of current industrial processes. Here we reviewed the characteristics of acidophilic fungi including their diversity and adaptation to extreme acidic environments. Most importantly, this review highlighted the acid–tolerant enzymes from the acidophilic fungi, their main sources and potential applications.

2. Diversity of acidophilic fungi

The estimated fungal diversity around the globe ranges between 0.7 and 9.9 million species (Hawksworth, 1991; Schmit and Mueller, 2007), nevertheless, only 80,000 species have yet been reported (Schmit and Mueller, 2007). Several of uncharted environments have proven to be promising source of novel and specialized fungi. The extreme acidic water and saline soil with pH < 3 are also placed in this division along with tropical forests (Suryanarayanan and Hawksworth, 2005). Despite the extreme conditions such as low pH (<3) and saline soils, these environments present several fungi and the most appropriate biotopes for numerous other microbes. Recently, scientists are now focusing in studying such harsh environments to explore and understand the novel and unique life existing in these environments (Baker and Banfield, 2003; Gunde–Cimerman et al., 2005).

Among microorganisms, bacteria followed by fungi are predominantly reported from acidic environments (Ingledew, 1990). Fungi along with protozoa and algae, are

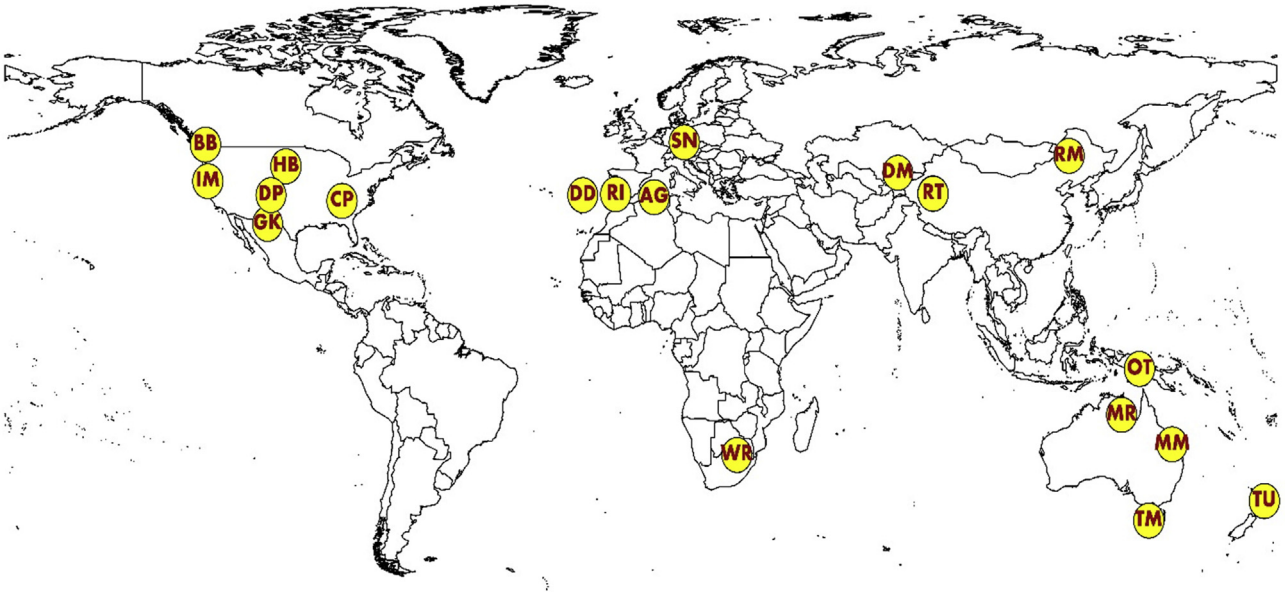

Fig. 1 – Worldwide distribution of Acid Mine Drainage (AMD). BB (Britannia Beach), IM (Iron Mountain Mine), HB (The Hughes Borehole), DP (Davis Pyrite Mine), GK (The Gold King Mine), CP (Clinch-Powell River System), SN (The Soos National Natural Reserve), DD (The Donana Disaster), RI (The Rio Tinto), AG (Anabel's Garden, Rio Tinto, Nerva), WR (West Rand Goldfield), DM (Davis Mine, Rowe MA), RT (Rough and Tough Creek), RM (Richmond Mine), OT (The Ok Tedi environmental Disaster), MR (The McArthur River mine), MM (Mount Morgan Mine), TM (West Coast Tasmania Mines), TU (The Tui mine).

Table 1 – Distribution of acidophilic fungi in various acidophilic habitats throughout world.

Acidic habitats	Isolation pH	Fungal genera/species	References
Acidic soil (Czech Republic and Iceland)	2.0	*Acidiella bohemica* and *Acidomyces* spp.	(Hujslova et al. 2013)
Acidic and high temperature hot spring	2.0	*Teratosphaeria acidotherma*	Isobe et al. (2013)
Soil (Pindari glacier, Indian Himalayan Region)	4.5–5.1	*Trametes hirsute*	Dhakar and Pandey (2013)
Decayed wood (Yucatan, Mexico)	6.0	*Trametes hirsute*	Zapata–Castillo et al. (2012)
Acidic wastewater (tin mine Yunnan province, China)	3.0	*Penicillium pinophilum*	Cai et al. (2011)
Acidic wastewater (tin mine, Yunnan Province, China)	3.0	*Phialophora sp.*	Zhao et al. (2010)
Sainokawara hot spring (Agatsuma gun, Gunma Prefecture, Japan)	1.0	*Teratosphaeria acidotherma*	Yamazkai et al. (2010)
Rock samples (Northern and Southern Victoria Land, Antarctica)	1.0	*Recurvomyces mirabilis* and *Elasticomyces elasticus*	Selbmann et al. (2008)
Plant Pathology Unit, National Research Center, Cairo, Egypt	5.0	*Trichoderma harziunum*	Mohamed et al. (2006)
Decaying leaves, mangrove plants	5.0	*Fusarium moniliforme*	Niture and Pant (2004)
Lignite (Brown coal)	4.8	*Hortaea acidophila*	Holker et al. (2004)
Acidic Tinto River (southwestern Spain)	3.0	*Rhodotorula*, *Cryptococcus*, *Tremella*, *Holtermannia*, *Leucosporidium*, *Mrakia*, *Candida* and *Williopsis*, *Penicillium*, *Scytalidium*, *Bahusakala*, *Phoma*, *Heteroconium*, *Lecythophora Acremonium* and *Mortierella*,	Lopez Archilla et al. (2004)
Egyptian soil	4.5	*Aspergillus carbonarius*	El–Gindy (2003)
Nonsterile cultures of the unicellular acidophilic green alga *DunaIieIla acidophila*	1.0	*Bispora* spp.	Gimmler et al. (2001)

key players in the fabrication of microbial mats in acidic spring/lakes (Baker and Banfield, 2003). In addition, fungi are the main contributors of water biomass in Rio Tinto river Spain having pH 2 and 30 °C (Amaral Zettler et al. 2002). Attachment of several microorganisms is facilitated by the fungal hyphae that make biofilms in AMD (Johnson, 1998; Baker et al., 2004). A Number of studies reported filamentous fungi and yeast having optimal growth at very low pH and some of their species are extremely acidophilic (Nordstrom and Southam, 1997; Robbins et al., 1999; Gimmler et al., 2001).

The fungal communities inhabiting low pH environments are not only acidophiles, but some of them are acid–tolerant i.e. they can grow in acidic condition but are also capable of optimal growth at neutral and even alkaline pH. The natural acidic habitats like lakes, peat bogs, soil and swamp often possess a pH range of 3–4. Several studies have been carried out to find fungi in acidic environments (Table 1) like acid waste waters, sulfide–rich habitats and underground mines (Stokes and Lindsey, 1979; Ehrlich, 1996; Nordstrom and Southam, 1997; Robbins et al., 1999; Gimmler et al., 2001). Apart from these natural acid environments, several fungi from extremely low harsh pH environments, have been isolated.

Starkey and Waksman (1943) have isolated extreme acidophilic fungus, *Acontium velatum*, from 4% $CuSO_4$ mixture with pH < 0.7. Additionally, Sletten and Skinner (1948) have reported *Trichosporon cerebriae* with propagating abilities in 2N solution of sulfuric acid having peptone and glucose as a source of nitrogen and carbon respectively. *Capnodialean* (an acidic anamorphic fungus), has been reported from such a harsh environmental condition of low pH. Moreover, some species of acidophilic fungi were reported from AMD (pH 0.8–1.38) (Sigler and Carmichael, 1974) and sulphur pile field (pH 1.4–3.5) (Baker et al., 2004). Holker et al. (2004) has isolated Hortaea acidophila (known as strict acidophilic fungi), from a brown coal (containing fulvic and humic acids) with pH 0.6.

Several strict acidophilic fungi like *Hortaea acidophila* (Holker et al., 2004), *Acidomyces acidophilus* (Selbmann et al., 2008), *Acidiella bohemica* (Hujslova et al., 2013), *Acidomyces acidothermus* (Yamazaki et al., 2010; Hujslova et al., 2013), have taxonomically placed in the Teratosphaeriaceae (Dothideomycetes, Ascomycota and Capnodiales) family. These black meristematic fungi are commonly reported from extreme acidic soil. Furthermore, fungi with abilities to tolerate pH 1.0, from subclass Dothideomycetidae were isolated from Victoria Land (Selbmann et al., 2008). In addition, *Teratosphaeria acidotherma* has categorized with optimum pH below 2.5 by Isobe et al. (2013). Hujslova et al. (2013) isolated fungi from acidic soil with pH < 3 which belong to class Leotiomycetes and Sordariomycetes.

3. Adaptability mechanisms of acidophilic fungi

Eukaryotes that propagate in acidic environments confront not only very high concentration of hydrogen ions from the surrounding but also elevated levels of noxious metals, oligotrophic conditions and temperature extremes (Whitton, 1970; Brock, 1978; Brake and Hasiotis, 2010). Moreover, the extreme acidic pH irreversibly disrupts the primary and secondary configuration of proteins (Kapfer, 1998; Nixdorf and Kapfer, 1998). Acidic environments greatly influence the microbiota and its diversity, however, a wide range of microbiota do exist in such habitats including prokaryotes (both Archaea and Bacteria) (Verb and Vis, 2000; Hallberg and Johnson, 2003; Coupland and Johnson, 2004; Bruneel et al., 2006) and

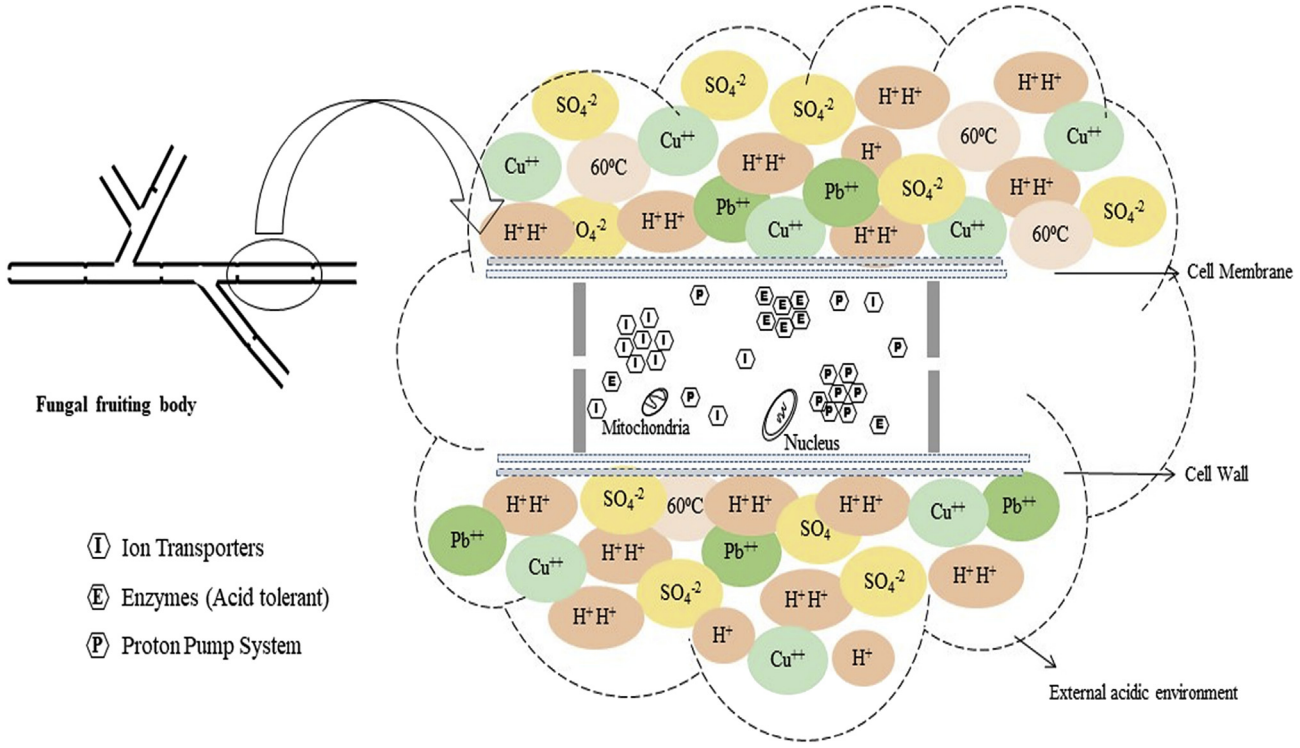

Fig. 2 – An outline of adaptability mechanisms of acidophilic fungi to internal and external acidic environment.

eukaryotic fungi, algae and protozoa (Bennett, 1969; Cooke, 1976; Albertano, 1995; DeNicola, 2000).

Studies reported by Roberts (1999), Rothschild and Mancinelli (2001), have proven that fungi, algae, and protozoa are mostly found in extreme acidic habitats, where a significantly lower concentration of energy is available in combination with extreme higher temperature that may exceed even 60 °C. In order to thrive in such a harsh environmental setting, organisms have developed several adaptation mechanisms both genetically and physically to cope with the adverse effects of these conditions (Gadd, 1993, 2007; Pick, 1999; Gross, 2000). The microbial cells in extreme acidic habitats, have to deal first with rapid acidification of cytosol due to high concentration of hydrogen ions present in surroundings (Gross, 2000). To cope with high concentration of dissolved metals, low nutrient in acidic environments, microbes also evolve various approaches or strategies to shield against their inimical effects (Olaveson and Stokes, 1989). In addition, finite or negligible amount of carbon dioxide exists in acidic habitats for photosynthetic microbes because of the lack of a bicarbonate pool (Olaveson and Stokes, 1989; Gross, 2000).

Extreme acidophiles maintain their cytoplasmic pH near to neutral by employing certain adaptation mechanisms. Although, the knowledge about adaptability mechanism in fungi against low pH is scarce, fungi are well–endowed with efficient mechanisms for pH regulation that make them comparatively more suited to acidic environments (Fig. 2). Many studies (Nicolay et al., 1987; Pick, 1999; Gross, 2000; Messerli et al., 2005) have reported that fungus has the potential to develop effective intracellular pH regulatory system that aids in keeping the cytoplasmic pH to near neutral, through actively pumping out the hydrogen ion to the extracellular medium. Therefore, the important adaptation of fungi in acidic conditions is to modify plasma membrane permeability to hydrogen ion, and to overexpress membrane proteins (ion transporters) (Pick, 1999). These traits enable fungi to thrive in extremely low pH habitats (Longworthy, 1978).

4. Industrially important enzymes

Extremozymes, derived from extremophiles, (similarly, acidozymes derived from acidophiles) are known for their abilities to work efficiently in harsh conditions (that were not considered favorable for enzymes functions) of several important industrial processes. Extremozymes offer finest activities and constancy in extreme conditions alternative to the conventionally used catalytic processes (Table 2). Most important, these enzymes are efficient, environmental friendly and represent foundation for the sustainable industrial technologies. They have gained much importance owing to their inordinate potential of applications.

The current paper is targeted towards acidic fungal enzymes, and recent studies are limited to few enzymes like polygalacturonase (Yang et al., 2011), xylanase and mannanase (Luo et al., 2009a, 2009b), laccase (Tetsch et al., 2005) and D–galactosidase.

β–mannanases

Mannan (with straight β–1,4–linked D–mannopyranose units), is the main constituent of hemicellulose in plants (Ademark et al., 1998; Handford et al., 2003). β–1,4–linked backbone

Table 2 – An overview of applications of acidophilic fungal enzymes in various industries.

Enzymes	Optimum pH	Optimum Temp (°C)	Acidophilic fungal source	Applications	References
Endo–polygalacturonases	3.5	40	*Penicillium sp.* CGMCC 1669	1. Clarification of fruit, vegetable juices and wines. 2. Animal feed 3. Paper and textile industries 4. Treatment of pectic waste water 5. Fermentation of coffee and tea 6. Production of baby foods	Yuan et al. (2001)
	3.5	50	*Bispora sp.* MEY–1		Yang et al., (2011)
	2.0–3.0	37	*Aspergillus kawachii*		(Esquivel and Voget, 2004)
	4.0	25	*Saccharomyces cerevisiae*		Ginvors et al. (2002)
	4.2	30	*Aspergillus niger*		Benen et al. (1999)
	4.3	50	*Aspergillus carbonarius*		Devi and Rao (1996)
	5.0	45	*Sclerotinia sclerotiorum*		Li et al. (2004)
	5.0	30	*Aspergillus niger*		Behere et al. (1993)
Exo–polygalacturonases	4.5	30	*Rhizoctonia solani* Kühn (AG2–2)		Al–Rajhi (2013)
	4.0	65	*Paecilomyces variotii*		De Lima Damasio et al. (2010)
	5.0	40	*Trichoderma harziunum*		Mohamed et al. (2006)
	5.3	40	*Fusarium moniliforme*		Niture and Pant, (2004)
	3.4–4.2	60	*Aspergillus niger*		Sakamoto et al. (2002)
β–galactosidases	4.5	40	*Aspergillus carbonarius*	1. Production of cheese whey in food industry 2. Digestive supplement in dairy product 3. Nutrition and medicine 4. Production of sweet yoghurt and fresh cheese without sugar additives	El–Gindy, (2003)
	4.0	60	*Aspergillus niger*		Widmer and Leuba (1979)
	1.5–5.5	37	*Teratosphaeria acidotherma* AIU BGA–1		Isobe et al. (2013)
	1.5	37	*Bispora sp.* MEY–1		Wang et al. (2009)
	3.5	65	*Aspergillus niger*		Hatzinikolaou et al. (2005)
	4.0	30	*Penicillium chrysogenum*		Nagy et al. (2001)
	7.0	25	*Saccharomyces lactis*		Mbuyi–kalala et al. (1988)
Laccases	5.5–7.5	35	*Trametes hirsute* (MTC 11397)	1. Dye and effluent decolorization 2. Colour and phenolic removal of olive mill wastewater 3. Removal of phenolic compounds from wine, and in beer stabilization 4. Paper pulp deliginification 5. Development of fuel cells and biosensors	Dhakar and Pandey (2013)
	4–4.5	40–60	*Trametes hirsute* Bm 2		Zapata–Castillo et al. (2012)
	3.0	70	*Fomitella fraxinea*		Mi and Park (2008)
	4.5	37	*Pleurotus sajorcaju* MTCC 141		Sahay et al. (2008)
	4.0–5.0	40	*Trametes versicolor*		Minussi et al. (2007)
	4.0–5.0	22–25	*Perenniporia tephropora*		Ben Younes et al. (2007)
	1.5–2.0	37	*Hortaea acidophila*		Tetsch et al. (2005)
	2.4	62	*Sclerotium rolfsii*		Ryan et al. (2003)
	4.0–6.0	65	*Phellinus ribis*		Min et al. (2001)
	3.5	20	*Ganoderma lucidum*		Ko et al. (2001)
Xylanases	3.5–5.0	55–75	*Penicillium citrinum* HZN13	1. Animal feed 2. Pulp and paper 3. Textile, food industries 4. Agriculture	Bagewadi et al. (2016)
	4.0	50–60	*Penicillium oxalicum* GZ–2		Liao et al. (2014)
	4.0	50	*Penicillium oxalicum* GZ–2		Liao et al. (2012)
	2.6	65	*Bispora* sp. MEY–1		Luo et al. (2009a)
	5.0	60	*Aspergillus terreus* (BCC129)		Chantasingh et al. (2006)
	2.0	45	*Aureobasidium pullulans*		Tanaka et al. (2004)
	6.0	60	*Streptomyces* sp. Abl06		Techapun et al. (2002)
	2.0	50	*Aureobasidium pullulans* var. *melanigenum*		Ohta et al. (2001)
	2.0	50	*Penicillium* sp. 40		Kimura et al. (2000)
	4.8	54	*Aureobasidium pullulans*		Li et al. (1993)
β–mannanases	4.0	80	*Penicillium oxalicum* GZ–2	1. Paper and pulp industries 2. Animal feed 3. Food and oil drilling industries	Liao et al. (2014)
	3.0	70	*Bispora antennata*		Liao et al. (2012)
	3.5	70	*Aspergillus niger* LW–1		Li et al. (2004)
	4.0	70	*Penicillium pinophilum* C1		Cai et al. (2011)
	1.5	60	*Phialophora sp.* P13		Zhao et al. (2010)
	4.0	40	*Penicillium occitanis* Pol6		Blibech et al. (2010)
	2.4	50	*Aspergillus sulphureus*		Chen et al. (2007)
	5.0	60	*Penicillium oxalicum*		Kurakake et al. (2006)

with either mannan residues or combination of mannose or glucose exists in all four different sub−families of mannan includes glucomannan, galactoglucomanan, galactomannan and linear mannan (Petkowicz et al., 2001). β−mannanase (EC 3.2.1.78) randomly hydrolyze β−mannosidic bonds in mannan and carry out the major modifications in mannan of plants (Singh et al., 2003). The industries dealing with paper and pulp, oil drilling feed and food, have been extensively aided by β−mannanase (Dhawan et al., 2007). For instance, hydrolysis of mannan into its simpler constituent, requires several enzymes (Talbot et al., 1998). Hemicellulases are crucial for bioconversion of the lignocellulosic biomass, especially in detergent, food and feed industries (Kafer et al., 1977). Hemicellulases have important application in paper and pulp industry, particularly in the process of bleaching of pulp and aid to enhance the retention of newsprint (Techapun et al., 2002; Helenius and Aebi, 2004). Reid and Ricard (2002) reported the potential of mannanases for bleaching of pulp, which can reduce the use of chemicals but the effectiveness is not as good as xylanase. Mannases are effective bleaching agents only in combination with xylanases (Woodcock et al., 1989), however their combined use is limited. To consider the array of substrate specificities for the enzyme hemicellulases, it's worthier to use the combination of enzyme that will significantly impact the economic value. Therefore, much research is required to identify and characterize hemicellulases with newer functionalities to overcome the use of hazardous chemical in paper and pulp industries (Villarroya et al., 1978; Deborah et al., 2003; Barbara et al., 2004).

Many biological sources including plants, bacteria, fungi and yeast, have been used for isolation of β−mannanases (Morreira et al., 2008). The amino acid sequence of β−mannanases (http://www.cazy.org/) showed similarity with glycoside hydrolase family 5 and 26 β−mannanases from eukaryotic organisms are generally GH5 while those from bacteria are either GH5 or GH26 (Shimizu et al., 2015). Among microorganisms, fungi are promising sources of valuable enzymes because of their abilities to decompose of recalcitrant substances on biosphere. Fungi mostly produce extracellular enzymes that catalyze range of reactions to degrade lignocellulosic biomass. For example, a white−rot fungus, named *Phanerochaete chrysosporium*, is widely studied to decompose recalcitrant compounds like lignin (Gilkes et al., 1991).

The majority of fungal mannanases are acidic, their optimal pH lies in range of 2.4−6 this make them attractive option for feed industry. Trailing in search of most efficient enzyme, filamentous fungi including *Penicillium, Aspergillus* and *Trichoderma* are extensively investigated and found as ideal source of active β−mannanases production (Morreira et al., 2008). Mannanases from the *Penicillium* species have been reported with high enzyme activity over an extensive array of pH (Morreira et al., 2008; Kurakake et al., 2006; Blibech et al., 2010). A novel acidic β−mannanase production with greatest activity at pH 3 and 28 °C, has been isolated from *Penicillium pinophilum* C1 from extreme acidic wastewater from tin mine. Cloning and expression of mannanases in *Pichia pastoris* has successfully been carried and was assessed in animal feed and presented a significant source of acidic fungal β−mannanase.

Bispora antennata has been reported to produce novel β−mannanase that showd optimum activity at pH 6 and was stable over varied range of pH (Liu et al., 2012). Likewise, in another study by Liao et al. (2014), 1,4−β−mannanase (novel acidic thermostable) has been genetically engineered in *Pichia pastoris* and *Penicillium oxalicum* GZ−2 and has been employed to functionally express the efficient enzyme. In addition, *Penicillium pinophilum* C1 was used for cloning and characterization of acidic endo 1,4−β−mannanase, isolated from acidic wastewater (tin mine) (Cai et al., 2011). A recombinant mannanases from *Phialophora* sp. P13, was characterized for its stability at both acidophilic and non-acidophilic pH, shown maximum activity at pH 1.5 and its stability ranges from pH of 1.5−7 (Zhao et al., 2010). Moreover, mannanases synthesized by *Penicillium* has been isolated, purified as well as characterized and most of the studies reported their highest activity at low pH, while being stable at broad pH range (Morreira et al., 2008; Kurakake et al., 2006; Blibech et al., 2010).

D−galactosidases

D−galactosidases is a glycoside hydrolase enzyme which split lactose a disaccharide sugar into glucose and galactose monosaccharides. The applications of D−galactosidases are important due to two reasons. First, Lactose is one of the principle carbohydrates of milk with low sweetness and lactase hydrolyzes it into its simple components for efficient absorption. In most mammals, lactase enzyme is secreted by villi. After weaning the activity of lactases phlorizin hydrolase decreases and leads to lactose intolerance (Holsinger et al., 1988). Consequently, more than 70% population of the world suffers from lactose intolerance, which restricts them from consumption of dairy products. The individuals with lactase deficiency have gastrointestinal complications associated with uptake of nutrient and calcium specifically (Gregory et al., 2001). Second, whey is the remaining product of milk after curdling in the process of making cheese and other such products. It is the major waste product of dairy industry and is characterized by high Biological oxygen demand (BOD), due to the presence of high lactose concentration in the range of 4−8% w/v (Hatzinikolaou et al., 2005), which poses a major disposal challenge. Lactose is arduously degradable sugar and therefore it counts one of the major aquatic environment pollutants (Siso, 1996). In recent decades increased production of dairy products has resulted in increased whey production, so the utilization of this byproduct is the best solution to this problem. To overcome the disposal dilemma, various applications of whey are being developed. Non−lactose fermenting microorganisms hydrolyzed whey lactose in the process of hydrolysate production that utilized further as a carbon source for production of ethanol (Cote et al., 2004). But high concentrations of acid and high temperatures are the general requirements of the acid hydrolysis process. Beside production of several unwanted byproducts, glucose and galactose, are not produced at quantities equimolar to the initial lactose concentration (Ladero et al., 2003).

D−galactosidase, also called lactase, (EC 3.2.1.23), breakdown the disaccharide sugar into monomeric counterparts i.e. glucose and galactose. Galactosidase having acidic optimal pH are commonly employed in acidic whey processing

(Takenishi et al., 1983; Gonzalez et al., 1991; Nagy et al., 2001; El–Gindy, 2003; Hatzinikolaou et al., 2005; Nakkharat et al., 2006), second major use of lactase is for lactose intolerant individuals as digestive supplements (Wang et al., 2009). β–Galactosidases are ubiquitous, and number of studies have illustrated their regulation and physiological characteristics from animals, plants, molds, yeast, and bacteria (Nagy et al., 2001). Because of its extensive applications in medicine, nutrition and food, it gained high attention among such industries (Shukla, 1975). The detailed study of different forms of galactosidase from microbes is still scant, whereas genus *Aspergillus* is known for its ability to produce multiple forms of extracellular enzyme with different pH optimums, that include *Aspergillus carbonarius* (pH 4.5) (El–Gindy, 2003), *Aspergillus niger* (pH 2.5 and 4) (Widmer and Leuba, 1979) and *Saccharomyces lactis* (Mbuyi–kalala et al., 1988). Nagy et al. (2001) isolated and purified acidic intracellular galactosidase from *P. chrysogenum* NCAIM 00237 having maximum activity at a pH of 4 at 30 °C.

Nowadays, β–galactosidases (from fungal sources) is used as digestive supplements in many products and consumed by lactose intolerant individuals. The enzymes (obtained from *Aspergillus oryzae* and *Aspergillus niger*), have been recognized as Global Recycle Standard (GRS) (Wierzbicki et al., 1973; Zhang et al., 2005; Hu et al., 2007). Such products are available in the form of soft gel capsules, caplets and chewable tablets, and increase lactose digestion while mitigating the condition resulting from lactase deficiency (Lin et al., 1993). In large scale production of penicillin by *Penicillium chrysogenum*, lactose is utilized as basic source of carbon as it induces the biosynthesis of penicillin, while other simple sugar like glucose can suppress the synthesis (Revilla et al., 1984; Christensen et al., 1995; Martin et al., 1999). Thus, lactose plays a crucial role in making *Penicillium* prepare penicillin.

Galactosidase is the key enzyme of dairy industry that hydrolyzes lactose in the whey and milk (Burgess and Shaw, 1983). It is particularly utilized in production of low lactose milk products (Neelakantan et al., 1999), fresh cheese and sweet yoghurt (Baumgartner and Hinrichs, 2000). Hatzinikolaou et al. (2005) reported the elevated production of galactosidase by wild strain of *Aspergillus niger* with increased thermal and low pH stability. Interestingly, Isobe et al. (2013) isolated *Teratosphaeria acidotherma* AIU BGA–1 from acidic hot spring and reported the production of 4 different types of β–galactosidase with varying pH optimums.

Laccases

Laccases (phenol oxidases; E.C. 1.10.3.2.) belong to oxidoreductases and are also named as multicopper blue oxidases. Laccases are glycoproteins of molecular weight of about 50–130 kDa (Mayer et al., 2002; Morozova et al., 2007; Desai et al., 2011; Shraddha et al., 2011). Phenolic and aromatic rings are the major substrate for laccases including monophenol, diphenol, metoxiphenol, polyphenol, aniline, benzenotiole, aryldiamines etc. Laccase gained considerable interest during the past decades, as they can utilize variety of substrates, thus have a wide biotechnological application. Laccases efficiently degrade lignin and are employed in paper and pulp industry for delignification (Camarero et al., 2007), and are also used in synthesis of biosensors and fuel cells (Ghindilis, 2000). These enzymes are bestowed with the strong ability to breakdown phenolic compounds, hence, are used for the removal of such compounds from wine and as stabilizers in beer (Minussi et al., 2002). In organic production, laccases transform the major functional groups of the compounds and bring about the coupling of steroids and phenolics (Ponsoni et al., 2007; Kunamneni et al., 2007), and are crucial in bioremediation processes particularly dyes and industrial effluents (Ben Younes et al. 2007).

Laccases acquire diverse biological roles, like morphogenesis and development of fungi (Leonowicz et al., 2001), the enzymes also regulate the fungal pathogenicity (Zhu et al., 2001), and actively involved in carbon cycling through efficient degradation of lignin. Ascomycetes, Basidiomycetes and Deuteromycetes are reported as best producer of laccases that have biotechnological significance (Morozova et al., 2007). Additionally, laccases also hold on some physiological fungal functions (Claus, 2004).

The degradation of recalcitrant compounds such as lignin and similar aromatic compounds results in formation of highly reactive radicals that become the major cause of environmental pollution (Evans et al., 1994; Wood, 1994). Such reactive species are catalyzed by three oxidative enzymes, namely laccases, lignin peroxidase (LiP) and manganese peroxidase (MnP) (Fahraeus and Reinhammar, 1967; Orth et al., 1993). Numerous laccases have been purified and characterized from white rot fungi. They are heterogeneous even though produced by the same species of white rot fungi and are unique in their specificity as well as structure (Baldrian, 2006). The diverse applications of laccases need identification of novel sources in terms of desired characteristics and functions for specific applications.

Fungi can produce laccases that are active at wide range of pH, temperature, and salt concentration, which makes them suitable for applications even at extreme conditions. Dhakar and Pandey (2013) reported laccase production with optimum pH of 5–7 by using pH tolerant fungi isolated from Indian Himalayan glacier. Laccase from white rot fungus, *Trametes hirsuta* Bm–2 was purified possessing maximum activity at pH 4–4.5 and 40–60 °C temperature, the enzyme decolorizes acid blue dye 100% and the effluents of textile up to 36% (Zapata–Castillo et al., 2012). Likewise, *Trametes versicolor* CCT 4521, was also reported to produce two types of laccases of molecular weight 66 kDa with optimum temperature near 40 °C and pH 4–5 (Minussi et al., 2007).

Laccases employed in treatment of effluents must efficiently withstand the consequences of processing conditions that includes high concentrations of organic solvents, metals, acids, salts, and alkalis (Laing, 1991). In addition, another medicinal white rot fungus, *Ganoderma lucidum*, was characterized for the synthesis of laccases with best activity at pH 3.5 and 20 °C temperature (Ko et al., 2001). Mi and Park (2008) also reported laccase activity at acidic pH 3 and 70 °C from *Fomitella fraxinea*. Similarly, *Phellinus ribis*, produces laccase with maximum activity between pH 4–6 (Min et al., 2001). Ryan et al. (2003) reported different forms of laccases i.e. SRL1 and SRL2 from plant pathogen *S. rolfsii*, with molecular weights of 55 and 86 kDa respectively, optimum activity was shown at pH 2.4 by these enzymes. Sahay et al. (2008) reported

the effect of different liginolytic substrates like wheat straw, corn cob, saw dust, bagasse particles and coir dust on laccase production and activity in *Pleurotus sajorcaju* MTCC 141 and significant activity was depicted at pH 4.5. Likewise, Ben Younes et al. 2007 also characterized white–rot fungus, *Perenniporia tephropora* for the production of laccase and employed it to decolorize the synthetic dyes. The study showed interesting results, the optimum pH of the enzyme is substrate dependent and each dye has different optimum pH for the enzyme to decolorize it. For 2,6–di–methoxyphenol (DMP) optimum pH was 4 and for 2,2–azino–di(3–ethyl–benzthiazoline–6–sulfonate) (ABTS) it was 5.

Endo/exo–polygalacturonases

Pectins are heterogeneous mixture of polysaccharides consisting of straight chains of D–galacturonic acid residues. They constitute an essential part of middle lamella and one third part of plant cell wall dry weight (Jarvis and McCann, 2000) The backbone of pectin has 1,4–linked –GalpA residues, known as galacturonans. Pectinolytic enzymes naturally degrade these linkages and are categorized into two classes, namely depolymerases and pectinesterases. Depolymerases consist of exo/endo–Pectin lyase, exo/endo–Pectatelyase, exo/endo–Polygalacturonase (PG) and exo/endo–Polymethyl Galacturonase (Rexova–Benkova et al., 1976; Mohamed et al., 2006). Among these, endo–polygalacturonase is thoroughly studied and commonly employed commercial enzyme, which randomly hydrolyzes the glycosidic linkages present among the residues of non–methylated acids (Sakai et al., 1999; Lang et al., 2000). Microorganisms are the best reported sources that produce endo–polygalacturonase, which is followed by plants (Naidu et al., 1998; Markovic et al., 2001; Gognies et al., 1999).

Several studies have been conducted on endo–PGs production, purification and characterization (Niture, 2008). Most of the endo–polygalacturonase from fungal sources have demonstrated their greatest activity at low pH values (commonly pH 4–6) (Kashyap et al., 2001; Niture, 2008), whereas bacterial endo–polygalacturonase are mostly active at alkaline pH (Kashyap et al., 2001). *Aspergillus* and *Penicillium* are dominant fungi that are customarily employed in commercial production of Pectinolytic enzymes (Alkorta et al., 1998; Mohamed et al., 2006; Niture, 2008). Number of studies have been conducted that sequenced, cloned and expressed the genes of endo–polygalacturonase (Naidu et al., 1998; Markovic et al., 2001; Mertens et al., 2008). On the basis of their sequence similarity endo–polygalacturonase are placed in glycosyl hydrolase (GH) family 28 (Henrissat, 1991). In food industries, acidic polygalacturonase are widely employed for the clarification of vegetable and fruit juices and wine by degradation of pectin and decreasing the viscosity. In feed industry, it is used in combination with other hydrolases for the synthesis of animal feed (Alkorta et al., 1998; Kashyap et al., 2001). Endo–PGs have their application in fermentation of tea and coffee, pectic wastewater treatment, textile and paper industries. To date, pectinase used in commercial preparations are mostly composed of various pectin degrading enzymes or in conjugation with other enzymes in different proportions (Sieiro et al., 2009).

Benen et al. (1999) isolated three acidic endo–PGs i.e. endo–polygalacturonases I, II and C from a recombinant strain of *Aspergillus niger* and reported its greatest activity at pH 4.1. *Trichoderma harzianum* was reported to produce extracellular polygalacturonase II and purified through chromatography column employing Sephacryl S–200 and DEAE–Sepharose, the purified enzyme depicted highest activity at pH 5 (Mohamed et al., 2006). Yang et al., (2011) cloned the gene encoding endo–PGs from acidophilic, *Bispora* sp. MEY–1 and successfully expressed in *Pichia pastoris* that showed extensive stability between pH 2–7 and optimal pH 3.5 at 50 °C temperature. *Saccharomyces cerevisiae* is extensively used in food industries, some studies have been conducted regarding production of pectinase (Longo et al., 1992; Blanco et al., 1994) and has been found to produce all types of pectinases having high activity in range of pH 3–5.5 at 25 °C (Gainvors et al., 1994). Moreover, *Aspergillus carbonarius*, *Paecilomyces variotii Aspergillus niger*, *Rhizoctonia solani* and *Fusarium moniliforme* are found to produce acid stable polygalacturonases (Behere et al., 1993; Devi and Rao, 1996; Sakamoto et al., 2002; Niture et al., 2004; Damasio et al., 2010; Al–Rajhi, 2013).

Aspergillus kawachii is traditionally used for brewing of *shochu–koji*, a Japanese distilled beverage of Japanese food industry (Iwano et al., 1986). *Aspergillus kawachii* secretes certain acid stable hydrolases in response to acidic pH of fermentation process that makes them more suitable than other fungal species (Mikami et al., 1987; Ito et al., 1992). Moreover, the endo–polygaacturonase isolated from *Aspergillus kawachii* IFO 4033 was found to have high activity in the pH range of pH 2–3, whereas it lost its activity at pH 5 (Esquivel et al., 2004).

Various polygalacuronases are associated with imparting pathogenicity in fungi. Pathogenic and saprophytic fungi produce number of effective enzymes that degrade meandering carbohydrates in cell walls of plants. Pectin is the most intricate and major component of middle lamella in plant cell wall (Benen et al., 1999). The invasion of damaged or weak plant tissue results in the development of primary infection that gradually spreads throughout the plant and causes tissue maceration. Throughout the period of infection, fungi synthesize cell wall degrading enzymes (CWDEs), among them pectinolytic enzymes are pectin lyase, polygalacturonases and pectin methyl esterase (Movahedi et al., 1990; Leone et al., 1990; Reignault et al., 1994).

Xylanases

Xylan is known as second utmost substantial carbohydrate in the current era. β–1,4– xylopyranol are the main structural units with substitution options with 4–O–methyl–D–glucuronic acid, D–glucuronic acid or L–arabinofuranose (Puls and Schuseil, 1993; Bhat and Hazlewood, 2001). The main component of hemicellulose of cell wall of both hard woods and monocots, is xylan. Recently, xylan degrading enzymes have gained much importance in industries dealing with agriculture, food, paper, pulp and textile (Coughlan et al., 1993). Xylanase (EC 3.2.1.8), hydrolytic enzyme breakdown the 1–4 glycosidic linkages between the units of xylopyranol. Xylanases have been reported from

microorganisms, algae, protozoans, plants and insects (Sunna et al., 1997). However, fungi are the most desirable source of the enzyme, owing to their higher efficiency even at extreme physical conditions (Moretti et al., 2012). The higher stability and efficiency of fungal xylanases make them economically valuable for industrial purposes.

Xylanase is used in pulp and paper industry during pre–bleaching steps to overcome the hazardous consequences of chlorine (Bajpai et al., 1999). These are also employed in bakeries as they aid in decreasing the viscosity of dough which helps increase the volume and shelf life of bread (Figueroa–Espinoza et al., 2004). Animal feed industries are highly benefitted by these enzymes (Silversides et al., 1999; Kung et al., 2000). Xylanases have been reported from a number of filamentous fungi, which were highly efficient in degrading xylan (Liao et al., 2012). The species of *Trichoderma* and *Aspergillus* are dominant xylanase producer fungi and are often used in industrial processes. *Penicillium oxalicum* GZ–2 has also been used for the synthesis of xylanases (Liao et al., 2014). Xylanase gene from *Aspergillus terreus* BCC129 that encode 326 amino acids from the family of glycosyl hydrolase was cloned and expressed in *Pichia pastoris*, demonstrated wide range of pH stability i.e. 4–10 (Chantasingh et al., 2006).

Bispora sp. MEY–1 was found to synthesize novel acidic xylanases (Luo et al., 2009a). Furthermore, xylanase has been purified and characterized from the *Penicillium* species, with optimum activity at pH 2–5. Four types of xylanases were produced by *Aureobasidium pullulans* Y–2311–1, which shown maximum activity at pH 4.8 (Li et al., 1993). Similarly, Ohta et al. (2001) found highly acidophilic extracellular xylanase with maximum activity at pH 2 from *A. pullulans* var. *melanigenum* strain ATCC 20524.

5. Conclusion and future prospectives

The limited stability and functional capability of enzymes in punitive conditions of an industrial processes, has long been recognized as a huge problem. A possible solution to this problem is being offered by the better activity and stability of acid–tolerant enzymes from acidophilic fungi. Here, we have reviewed the biodiversity of acidophilic fungi, their possible adaptation mechanisms to acidic environments and their potential to produce acid–tolerant enzymes. So far, very limited studies, related to the characterization of acidophilic fungi and their production of acid–tolerant enzymes and applications as biocatalysts in various unusual industrial processes, have been carried out. Industries are looking for alternatives to chemically mediated processes because of alertness toward protection of environments and necessity of sustainable biofuel substitutes, and one such alternative is enzymes catalyzed processes.

The majority of industrially used biocatalysts have driven from mesophilic fungal or bacterial source, nonetheless, usage of acidophilic source for industrial related peptides is endlessly growing. But one of the most important challenges that needed to be met, is industrial scale production of acidozymes. In addition, competent heterologous production systems related to the source of acidozymes, is still requisite, that will provide an easier and faster way of production of acidozymes in upcoming days. Moreover, obtaining of pure acid–tolerant enzymes from fungi is very difficult because of complexity of fungal growth condition, enzyme purification and quantitative production. However, due to the advancement of mew methods in biotechnology including genetic manipulation, now it is possible to produce highly pure acidozymes at lower costs that would mediate processes in very specific way. By using molecular engineering approaches (e.g. single DNA point mutation), acidozymes would be manipulated with specific desirable kinetic characteristics by making precise modifications in their structures. But it requires widespread knowledge about the sequence, structure and functions of acidozymes in order to get desirable results.

It is a fact that knowledge about structural changes related to the stability and activity of acidozymes in acidic condition, is still incomplete. Such situation limited our theoretical basis for designing an engineered enzyme with desired stability, catalytic activity and specificity in an anticipated approach and lead us toward the selection of directed evolution approach (DEA) e.g. random mutagenesis and DNA shuffling that promise an enzyme with desired properties. The DEA have been proven more efficacious than “conventional” genetic engineering approaches. This approach involves by merging mutation with selection or screening to identify improved variants. One advantage of this approach is to bring very small modification to the structure of existing enzymes. It is a hypothesis that DAE would bring more useful characteristics to acidozymes without losing its original functions.

Declaration of interest

The authors declare no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fbr.2018.08.002.

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