

Fungal cellulases from mangrove forests – a short review

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Abstract

Cellulases are enzymes that catalyze the hydrolysis of cellulose into simple sugars - a pre-requisite step for biofuel production. However, their deployment in large scale is not yet economically feasible due to limitations of enzyme efficiencies and inherent cellulose recalcitrance. One solution is to bioprospect for more efficient/novel cellulases from organisms and/or environments suspected to exhibit cellulose degradation. Soilborne filamentous fungi, in particular, are known for their role in decomposing and recycling cellulosic biomass and are attractive prospects for identifying novel enzymes. Furthermore, an environment suitable for cellulase exploration is the sediment of mangrove forests because of continuous input of cellulosic carbon in the form of litter which then acts as a substrate for decomposition by fungi. Reports describing the isolation and screening of cellulolytic fungi from mangroves around the world are scattered. This motivated the conception of this short review to provide readers with an overview of mangrove fungi and their described cellulolytic activities. World mangroves are a potential reservoir of novel cellulases that have application in industry and in the generation of renewable energy.

Keywords: Bioenergy, Biomass, Cellulose, Enzyme, Halophyte, Renewable energy

Introduction

Cellulose (β -1,4-linked glucose molecules) is a component of plant cell walls, and is the most abundant renewable resource present on earth (Malhi 2002; Shallom and Shoham 2003). Development of technologies that effectively convert agricultural material composed of cellulose to fermentable sugars for biofuel production provides a sustainable energy resource supply (Sheehan and Himmel 1999). A sustainable method is to employ a sweep of hydrolytic enzymes named cellulases, which synergistically act together to hydrolyze the

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β -1,4-glucose linkages that are present in the biopolymer (Béguin and Aubert 1994; Henrissat 1994). The cellulase enzymes are broadly categorized into exoglucanase (EXG), endoglucanase (EG) and β -glucosidase (BGL) (Béguin 1990; Eaton and Hale 1993; Li et al. 2006; Gao et al. 2008). The EG cleaves β -linkages at random, commonly in the amorphous parts of cellulose. EXG, on the other hand, releases cellobiose from non-reducing or reducing end, generally from the crystalline parts of cellulose, whereas BGL releases glucose molecules from cellobiose (Bhat et al. 1997) (Fig 1).

Microorganisms such as bacteria and fungi can produce all or individual types of cellulases— a range of which are available commercially and are widely used in industrial applications (Gilbert and Hazlewood 1991; Hanif et al. 2004; Kang et al. 2004). The majority of cellulases used commercially are secreted enzymes produced by culturable filamentous fungi belonging to the genera *Trichoderma*, *Aspergillus*, *Fusarium*, and *Penicillium* (Panagiotou et al. 2003; Kang et al. 2004; Jørgensen et al. 2005; Ahamed and Vermette 2008). However, some cellulases also exist as high molecular weight, cell attached complexes named cellulosomes, but those are more prevalent in certain anaerobic fungi belonging to the genera *Piromyces*, *Neocallimastix* (Wilson and Wood 1992; Fanutti et al. 1995; Fillingham et al. 1999), and anaerobic bacteria belonging to the *Clostridium* (Lamed et al. 1983; Felix and Ljungdahl 1993).

The secreted (free form) cellulases are well characterized and their production has been optimized for larger volumes, but little improvements have been made towards enhancing their efficiency. Specifically, one of the most difficult technological challenges to overcome is the recalcitrance of cellulosic material to enzymatic hydrolysis because of cellulose insolubility in solution and the presence of crystalline regions formed by hydrophobic interactions and hydrogen bonding between neighboring cellulose fibrils (Lynd et al. 2002; Wilson 2008). Cellulase-based strategies that can improve the biomass deconstruction process include: increasing input volumes of cellulases, producing cellulase cocktails with greater stability, and engineering cellulases with higher specific activity on solid substrates (Gilbert and Hazlewood 1993; Sun and Cheng

2002; Ravindran et al. 2010). An alternative to these strategies is to screen for, identify and characterize novel free form cellulases from environments which are suspected to harbor cellulose degrading microorganisms (Duan and Feng 2010; Hess et al. 2011; Arfi et al. 2013). The free form of cellulases are more favored candidates for industrial applications – particularly cellulases produced by filamentous fungi of the genera *Trichoderma* and *Aspergillus* (Esterbauer et al. 1991; Uhlig and Linsmaier-Bednar 1998; Takashima et al. 1999; Hanif et al. 2004; Kang et al. 2004; Ahamed and Vermette 2008). Filamentous fungi are often used in industry because they have an efficient secretory system and tend to produce the entire range of non-complexed cellulases (Mathew et al. 2008; de Siqueira et al. 2010; Lo et al. 2010). A system is available for recombinant protein expression and engineering in fungi, and promoters that drive cellulase production are also inducible by inexpensive carbon products such as lactose – a major waste product in dairy production (Esterbauer et al. 1991; Devanathan et al. 2007).

Environments that are suspected to exhibit high cellulose degrading profiles receive a large input of cellulosic substrates for microbial activity. Microorganisms in these environments would have the necessary enzymes, including cellulases, to breakdown the biopolymer into simple sugars for glycolysis and respiration. High cellulose input and consequent degradation by microbes occur in various environments such as soils (forests, and agricultural lands), sediments and aquatic environments. Mangroves are one particular forest ecosystem in which it transitions between terrestrial and aquatic environments. They are typically distributed in intertidal zones with fluctuating temperatures, salinity and tides (Kathiresan and Bingham 2001). Mangroves fix carbon in excess of ecosystem requirements and up to 40% of the carbon fixed in the form of leaves and roots is decomposed and recycled back into the ecosystem (Duarte and Cebrian 1996). Mangrove decomposition is mediated by microfauna present in mangrove sediments which produce hydrolytic enzymes that deconstruct plant cell walls composed of polysaccharides into simple sugars for assimilation and energy. Cellulolytic fungi in particular, are largely diverse (Sarma et al. 2001) and their role in decomposing mangrove plant material (leaves and wood) has been reported in several studies (Fell and Newell 1984; Findlay et al. 1986; Bremer 1995), and they have been described to be more efficient biomass degraders than bacteria (Kathiresan et al. 2011).

This review provides a general overview of cellulosic fungi and cellulases described in mangrove ecosystems in perspective of bioprospecting for novel cellulases. The role of other microbes (e.g. bacteria), cellulosomes, regulation of cellulase genes, and other biomass deconstruction enzymes (e.g. xylanase and ligninases) is outside the scope of this review, but there is a great deal of literature available on these subject areas (Wood et al. 1988; Raghukumar et al. 1994; Bayer et al. 1998; Pointing et al. 1998; Beg et al. 2001; Sá-Pereira et al. 2003; Bucher et al. 2004; Raghukumar et al. 2004; Polizeli et al. 2005; Muthuvelayudham and Viruthagiri 2006; Daroit et al. 2007; Muthezhilan et al. 2007; Gao et al. 2008; Baker et al. 2010; Gao et al. 2010; Ravindran et al. 2010; Kathiresan et al. 2011; Meera et al. 2011; Wipusaree et al. 2011; Wiwat and Sillapee 2011; Deepthi et al. 2012; Mtui 2012; Torres and dela Cruz 2012; Gao et al. 2013)

Overview of fungal cellulases

Cellulolytic enzymes (e.g. cellulases, mannanase, and xylanase) refer to a group of biomass hydrolyzing enzymes produced by a

wide range of fungi, and other microbes (Rabinovich et al. 2002; Reddy et al. 2003). Cellulases play a significant role in the global carbon cycle and provide fundamental benefits for biomass utilization (e.g. agricultural waste turnover). Cellulose

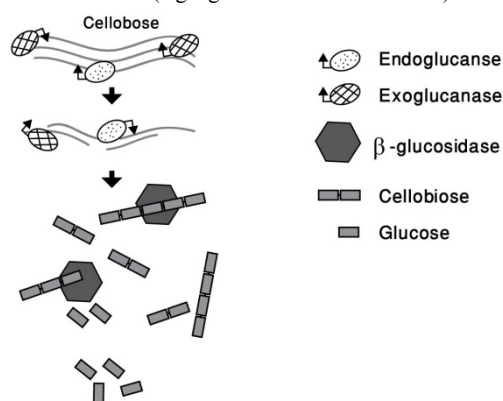


Figure 1: Mechanism of cellulases in degrading cellulose molecules. Endoglucanase cleaves β -linkages at random, commonly in the amorphous parts of cellulose. Endoglucanase, on the other hand, releases cellobiose from non-reducing or reducing end, generally from the crystalline parts of cellulose, whereas β -glucosidase releases glucose molecules from cellobiose.

de-polymerization to glucose for fermentation into ethanol as a biofuel is considered a major alternative to fossil fuels (Duff and Murray 1996). If ethanol become a major transportation fuel, it is estimated that the demand for cellulases will rise and will become the largest volume of industrial enzymes sold as a response to this shift toward renewable energy (Wilson 2009). In addition to being a fundamental asset for bio-ethanol (biofuel) production, cellulases also have several other common industrial and agricultural applications (Gilbert and Hazlewood 1991; Hanif et al. 2004; Kang et al. 2004). For example, they are being used commercially in industries of starch processing, malting and brewing, grain alcohol fermentation, pulp and paper industry, extraction of fruit and vegetable juices, and textile (Eriksson 1993; Gao et al. 2008; Zhou et al. 2008).

Fungal cellulases are usually secreted out of the cell. However, on rare occasions and mostly in anaerobic fungi, cellulases are attached to cell membranes and are produced as multi-enzyme complexes known as cellulosomes (Bayer et al. 1994; Leschine 1995; Bayer et al. 1998; Doi et al. 1998; Schwarz 2001; Tamaru and Doi 2001; Doi and Kosugi 2004; Demain et al. 2005). Examples of anaerobic fungi that uses cellulosomes include *Orpinomyces* sp. and *Piromyces* sp. (Steenbakkens et al. 2001). In contrast, aerobic fungi produce their cellulase components as free, non-complexed enzymes. The non-complexed cellulase systems are more studied and exploited for biotechnological applications and are largely understood in the fungal genera; *Trichoderma*, *Fusarium*, *Penicillium*, *Phanerochaete*, and *Hemicola* (Esterbauer et al. 1991; Takashima et al. 1999; Hanif et al. 2004; Kang et al. 2004; Aro et al. 2005; Ahamed and Vermette 2008). The fungus, *T. reesei* is the most studied for cellulases production (Kubicek 1992). The genome of *T. reesei* has been sequenced by Martinez et al. (Martinez et al. 2008) and it contains fewer cellulases than anticipated - relative to its current popularity. According to a case study done by Aro et al. (2005), *T. reesei* release 8 EG, 2 EXG, and 7 BGL to degrade cellulosic substrates. For *T. reesei*, the regulation of cellulase production is susceptible to activation and repression

mechanisms (Ilmen et al. 1997). For instance, lactose is one known inducer for cellulase activity, while glucose is a repressor (Xiao et al. 2004; Sehnem et al. 2006). Nonetheless, recent studies showed that cellulolytic fungi secrete biomass degrading enzymes with or without inducers (Mtui and Nakamura 2007; Patrick et al. 2011).

Overview of Mangrove Ecosystems

Mangroves traditionally were intensely used by humans for food, wood, fuel and medicine (Kathiresan and Bingham 2001). The positioning of mangroves on the coasts offers an ecosystem service by protection against coastal erosion and reduction in the impact of natural disasters such as tsunamis (Kathiresan 2000; Adams et al. 2004; Giri et al. 2010). Mangroves support biodiversity because they are habitats for various marine micro and macro fauna such as birds, fish, crustaceans, shellfish, mammals and microorganisms. Furthermore, following coral reefs, Mangroves are the second most productive ecosystems in terms of gross productivity (Qasim and Wafar 1990; Duarte and Cebrian 1996). Mangrove are woody halophytes at the intersection of land and sea in the tropical and subtropical regions of the world between 30°N and 30°S (Alongi 2002; Giri et al. 2010). They occupy about 181,000 km² of tropical and subtropical coastline distributed in about 112 countries and territories (Sahoo and Dhal 2009) with Indonesia, Australia, Brazil and Nigeria having roughly 43% of the world's mangrove forests (Spalding et al. 1997; Duke et al. 1998). It was estimated that mangrove forests in the year 2000 accounted for 0.7% of the total world tropical forests from which 75% are concentrated in 15 countries (Giri et al. 2010) (Table 1). There are about 27 genera and roughly 70 species of mangroves populating the world (Spalding et al. 1997).

The amount of litter fall produced by those different mangrove species varies annually depending on climate and rainfall (Gill and Tomlinson 1971; May 1999; Sharma et al. 2011). Generally, litterfall was highest in summer and lowest in winter (Kamruzzaman et al. 2012), but mangrove leaves are shown to have a falling rate of 700-1,000 g dry weight m² per year (Odum and Heald 1975; Flores-Verdugo et al. 1987; Flores-Verdugo et al. 1990; Oelze and Klein 1996). This motivated researchers to examine litterfall and mangrove biomass more closely. For example, leaves, comprising the major component of litter, account for up to 63.2% in the red mangrove *Rhizophora mucronata*, and 86.7% in the white mangrove *Avicennia marina* of total produced litter in the Pichavaram mangrove, Southeast of India (Muniyandi 1986). Bernini and Rezende (2010) found that total litter production of Southeast Brazil mangroves was higher in the *Rhizophora mangle* forest, followed by *Avicennia germinans* and *Laguncularia racemosa*. In Okinawa, Japan, Sharma et al. (2011) measured the total litterfall of *Rhizophora stylosa* while Kamruzzaman et al. (2012) looked into *R. stylosa*, *Kandelia obovata*, and *Bruguiera gymnorrhiza*. Many other studies also estimated the litterfall of different mangrove areas around the world as indicative of biomass and productivity such as in Gulf of California, Mexico (Flores-Verdugo et al. 1987; Arreola-Lizárraga et al. 2004), Bon Accord Lagoon, Tobago (Juman 2005), Middle Harbour, Sydney, Australia (Goulter and Allaway 1979; Bunt 1995), and in Southeastern Brazil (Bernini and Rezende 2010).

Mangrove Fungi

Mangrove fungi were first discovered in Australia by Cribb and Cribb (1955) from the exposed dead roots of the Grey mangrove, *Avicennia marina*. There are many different factors for fungi biodiversity in mangrove forests such as salinity (Manoharachary et al. 2005), types of substrates on which they colonize, and niche variation due to daily changes in sea level (Hughes 1974; Ananda

and Sridhar 2002; Nayak et al. 2012). Studies on mangrove fungi focused on their ecological roles, taxonomic composition, diversity, biogeography and role in decomposing leaf litter (Kohlmeyer and Kohlmeyer 1979; Hyde and Lee 1995; Schmit and Shearer 2003). It was estimated by Alongi (1988) using epifluorescence microscopy that fungi and bacteria constitute 91% of the total microbial biomass of mangrove

Table 1: Estimated distribution of world mangroves per continent. Adapted from Giri et al. (2010)

Continent	Global total (%)
Asia	37.7
Oceania	10.6
South America	7
North and Central America	8.5
Africa	11.5

ecosystems, whereas algae and protozoa only account for 7 and 2%. On a general scale, the latest estimate of world marine fungi is 1,500 (Hyde et al. 1998). There are around 269 species of higher marine fungi that inhibit mangrove roots in the world. Schmit and Shearer (2003) listed 625 fungi, including 278 ascomycetes, 277 mitosporic fungi, 30 basidiomycetes and 14 oomycetes to be associated with mangrove forests. Jones and Mitchell (1996) indicated there may be over 1000 fungal species, whereas Jones and Alias (1997) set the total number of mangrove fungi at 585. From 29 different mangrove forests, Hyde (1990) listed only 120 fungal species. Additional information on the biodiversity of mangrove fungi and other microorganisms has been recently reviewed (Thatoi et al. 2013).

Mangrove trees are believed to be the major contributor to lignocellulose biomass in the coastal marine environments and that fungi play a major role in the degradation and carbon turnover of this biomass (Raghukumar et al. 1994; Raghukumar et al. 1995; Rajendran 1997). Mangrove forests are believed to support high activity of biomass breakdown and detritus production, which thereby indicates an abundance of cellulolytic fungi. Previous studies (Kohlmeyer and Kohlmeyer 1979; Fell and Master 1980; Matondkar et al. 1981) indicate that fungi show a peak population at initial decomposition of plant material, and thereby allow secondary colonization by bacteria. The role of mangrove fungi in decomposing plants contributes to the energy flux in the food web from detritus to animal consumers *via* grazing on this highly nutritious fungal biomass (Ronald Benner 1985). Hence, this mangrove detritus serves as the base of a productive food web in tropical and subtropical coastal marine environments (Odum and Heald 1975; Rodelli et al. 1984).

Lignocellulosic substrates in mangrove environments, such as leaves and wood, support a wide diversity of fungi (Fell and Newell 1984; Cuomo et al. 1985; Jones and Alias 1997; Sarma et al. 2001) on which they carry out typical biomass degradation (Alongi et al. 1989; Moran and Hodson 1989). The role of fungi in decomposing mangrove litter, in addition to other functional roles, has been well reported (Fell and Master 1973; Meyers 1974; Fell et al. 1975; Boonruang 1978; Cundell et al. 1979; Fell and Master 1980; Fell and Newell 1984; Findlay et al. 1986; Robertson 1988; Raghukumar et al. 1994; Bremer 1995; Rajendran 1997; Rajendran and Kathiresan 2000; Kathiresan and Bingham 2001; Rajendran and Kathiresan 2004). Generally, fungal hyphae are usually found on and in decaying mangrove leaves and wood, as their counts

were found to outnumber those on fresh leaves, indicating a common colonization habitat. According to Newell and Fell (1995), for instance, *Halophytophthora* spp. of the fungal-like oomycetes are commonly present around leaf litter input in all mangrove environments. Another study also done by Newell and Fell (1997) showed that *Halophytophthora vesicula* is a strong competitor due to its ability to inhibit the *Halophytophthora spinosa* colonization, which can be observed from its dominant colonization on the leaves. Freshly fallen mangrove leaves are more commonly colonized by Oomycetes of the genus *Halophytophthora* (Nakagiri 2000). As for ascomycetes and Deuteromycete fungi – they are found to colonize leaves and other organic material in the sediment (Schmit and Shearer 2003). Ascomycetes also colonize decaying wood material in the intertidal zone (Hyde 1989; Kohlmeyer and Volkmann-Kohlmeyer 1991), from which a novel *Leptosphaerulina mangrovei* sp. (Pleosporaceae, Ascomycota) was isolated and described (Inderbitzin et al. 2000).

Mangrove Fungal Cellulases

Different approaches were taken by scientists to tackle the topic of cellulolytic mangrove fungi. The majority of studies focused on isolating fungi and investigating the production of cellulose degrading enzymes from mangrove environments around the world and from different reservoirs (e.g. leaves, roots, or wood) (Raghukumar et al. 1994; Luo et al. 2005; Arfi et al. 2013) – most are summarized in Table 2. Other scholars concentrated on optimizing mangrove fungal cellulases production by experimenting with different conditions (pH, temperature, substrates, etc.) (Gilna and Khaleel 2011; Sasi et al. 2012). However, as far as we are aware, a small number of studies used molecular techniques to identify or characterize cellulolytic fungal communities in mangrove environments. Arfi et al. (2013), for instance, used transcriptomic and proteomic approaches on an isolated halotolerant lignocellulolytic mangrove fungus, *Pestalotiopsis* sp. NCi6, from *Rhizophora stylosa* trees in Saint Vincent Bay, New Caledonia. They found that this fungus holds over 400 lignocellulolytic enzymes using *de novo* transcriptomic assembly. Additionally, LC-MS/MS proteomic analyses indicated that salt presence, which is ubiquitous in mangroves, increases the secretion of cellulases. The significant results found by Arfi et al. (2013) strongly highlights the potential of mangroves as a habitat of efficient halophytes saccharifying fungal-enzymes.

Many mangrove cellulolytic fungal isolation studies were carried out from the coasts of India. Raghukumar et al. (1994) showed that cellulolytic activity of several fungi (*Cladosporium herbarum*, *Fusarium moniliforme*, *Cirrenalia basiminuta*, and *Halophytophthora vesicular*) were highest on fresh litter substrate (0-21 days old). Kathiresan et al. (2011) showed that fungi belonging to *Trichosporon* sp., *Aspergillus* sp., and *Fusarium* sp. exhibited the maximum cellulases activity when leaves of mangrove leaves (*Rhizophora mucronata* and *Avicennia marina*) were used as a substrate and isolating bait. Another study, (Ravindran et al. 2010), screened for alkaline fungal cellulases from mangrove leaves (endophytes) and wood litter and identified alkaline tolerant fungi (*Chaetomium* sp. NIOCC 36) with high cellulolytic activity under a pH range (4 – 12) which are also stable up to 50°C. Immaculatejeyasanta and Panneerselvam (2011), on the other hand, looked into driftwoods from Muthupet mangrove forest from which 23 fungal species were isolated of the genera (*Aspergillus*, *Fusarium*, *Curvularia*, *Halocyphina*, *Helicascus*, *Lignicola*, *Trichoderma*, *Penicillium*, *Rhizopus*, *Neurospora* and *Alternaria*). Using plate assay method on the dominant 10 fungal species, the study found that the fungus *Helicascus kanaloanus* exhibits the highest cellulolytic activity.

In Morib, Malaysia, a study done by Bremer (1995) confirmed that a fungal isolate (*Schizochytrium aggregatum*) produces cellulases using *Sonneratia* sp. mangrove leaves as a substrate. Twenty nine fungal isolates from mangroves (and other marine sources) in Thailand, Hong Kong and Vietnam, were screened for extracellular enzyme activity in agar media by Luo et al. (2005). Most of these fungal isolates produced endoglucanases and were mostly ascomycetes, except for a basidiomycete, *Calathella mangrovei*, and a mitosporic fungus, *Cirrenalia tropicalis*. In Singapore, Ravindran et al. (2012) isolated and characterized a new lignocellulose degrading fungus (*Coniochaeta* sp.) from rotten wood in mangroves. Interestingly, they also identified over 100 potential lignocellulose hydrolyzing enzymes when growing the fungus on corn stover. From Indian mangroves, Kamat et al. (2012) carried out a slightly different approach in which they examined the efficiency of two fungi (*Williopsis saturnus* and *Aspergillus terreus*) in co-utilizing sugarcane bagasse for the production of biodiesel.

Table 1: Cellulase activity of fungal isolates from mangroves around the world. In methodology (a) maintenance and culturing method used to cultivate fungi for cellulase assays, (b) method used to detect cellulase activity. Abbreviations in table: CMC: carboxymethyl cellulose; NS: not specified.

Fungi	Isolate source	Methodology	citation
<i>Cladosporium herbarum</i> , <i>Fusarium moniliforme</i> , <i>Cirrenalia basiminuta</i> , <i>Hyphomycete</i> XVII, <i>Halophytophthora vesicular</i>	Leaves of <i>Rhizophora apiculata</i> mangrove from Goa, India	(a) maintained in cornmeal agar / inoculated into liquid medium of similar content (b) Culture filtrate was measured for reducing sugars using standard methods (e.g. (Gessner 1980)	(Raghukumar et al. 1994)
<i>Schizochytrium aggregatum</i>	Leaves of <i>Sonneratia alba</i> and <i>Rhizophora apiculata</i> mangroves from Moib, Malaysia	(a) maintained in yeast extract and peptone agar / inoculated into liquid medium containing yeast extract, peptone, and glucose (b) Agar well plate by (Carder 1986)	(Bremer 1995)
<i>Helicascus kanaloanus</i> , <i>Julella avicenniae</i> , <i>Lignicola laevis</i> , <i>Lophiostoma mangrovei</i> , <i>Monodictys pelagica</i> , <i>Nla vibrissa</i> , <i>Penicilloid</i> sp., <i>Savoryella lignicola</i> , <i>Stagonospora</i> sp., <i>Torpedospora radiata</i> , <i>Trematosphaeria mangrovei</i> , <i>Trematosphaeria striatispora</i>	Culture Collection	(a) maintained in cornmeal agar / plate cultures with yeast extract and CMC in pH of 7.5 and at room temperature (b) Diffusing azure dye into	(Pointing et al. 1998)

		media	
<i>Aspergillus niger</i> , <i>Cladosporium cladosporoides</i> , <i>Cladosporium sphaerospermum</i> , <i>Penicillium</i> <i>chrysogenum</i> , <i>Scopulariopsis brevicaulis</i> , <i>Stachybotrys chartarum</i> , <i>Verticillium cyclosporum</i> , <i>Chaetomium</i> <i>hamadae</i>	Roots of <i>Avicennia marina</i> mangrove from the Red Sea coast, Egypt	(a) maintained in malt extract and potato-dextrose agars / culture plating in malt extract and potato-dextrose agars with cellulose at 28 °C (b) Calculating relative frequency of colonization using Canoco program (Ter Braak 1988)	(El-Morsy 2000)
<i>Marinosphaera mangrovei</i>	NS Culture Collection	(a) maintained in potato- dextrose agar / inoculating in cellulose-azure agar containing yeast extract and peptone at 25 °C (b) Monitoring release of azure dye	(Bucher et al. 2004)
<i>Calathella mangrovei</i> , <i>Cirrenalia tropicalis</i>	Culture collection isolates from <i>Avicennia</i> , <i>Aegiceras</i> and <i>Kandelia mangroves</i> from Thailand, Hong Kong and Vietnam	(a) maintained in corn meal or potato-dextrose agars / inoculating in agar containing CMC or in broth containing filter paper, yeast extract and tryptone at 25°C (b) Congo red stain, clear zone around colony and mycelial growth on agar containing filter paper as carbon source	(Luo et al. 2005)
<i>Aspergillus sp.</i> , <i>Chaetomium sp.</i>	Leaves and wood litter of <i>Sonneratia alba</i> , <i>Avicennia</i> <i>marina</i> , <i>A. officianlis</i> , <i>A. alba</i> and <i>Rhizophora mucronata</i> mangroves from Goa, India	(a) maintained in malt extract agar / plate assays after incubation in medium with yeast extract and CMC having pH of 5,7 and 12 at 50 °C (b) Congo red stain, clear zone around colony	(Ravindran et al. 2010)
<i>Trichosporon sp.</i> , <i>Aspergillus sp.</i> , <i>Fusarium sp.</i>	Leaves of <i>Rhizophora</i> <i>mucronata</i> and <i>Avicennia</i> <i>marina</i> mangroves from the southeast coast of India	(a) maintained in various agar media / plating in yeast extract, peptone and CMC (b) Congo red stain, clear zone around colonies	(Kathiresan et al. 2011)
Species of the genera <i>Aspergillus</i> , <i>Fusarium</i> , <i>Curvularia</i> , <i>Halocyphina</i> , <i>Helicascus</i> , <i>Lignicola</i> , <i>Trichoderma</i> , <i>Penicillium</i> , <i>Rhizopus</i> , <i>Neurospora</i> , <i>Alternaria</i>	Driftwood from Muthupet mangrove forest in Tamil Nadu, India	(a) maintained in potato- dextrose agar / Incubation with yeast, peptone and glucose at 28 ± 2 °C (b) Congo red stain, yellow areas around colonies	(Immaculate jeyasanta and Panneerselv am 2011)
<i>Coniochaeta sp.</i>	Soil below rotten wood of non-specified mangrove from Singapore	(a) maintained and cultured in corn stover and Mandel's mineral salt medium at 30 °C (b) SDS-PAGE with CMC, Congo red stain	(Ravindran et al. 2012)
<i>Williopsis saturnus</i> , <i>Aspergillus terreus</i>	NS	(a) maintained in Czapek Dox agar / Inoculation under submerged fermentation conditions using sugarcane bagasse residue or in liquid medium containing yeast extract and minerals at 30 °C (b) Filter paper test (Xiao et al. 2004)	(Kamat et al. 2012)
<i>Pestalotiopsis sp.</i> NC16	Trunks and roots of <i>Rhizophora stylosa</i> mangrove from Saint Vincent Bay, Southern Province of New Caledonia	(a) maintained on Bacto agar containing malt and yeast extracts / Inoculating in medium containing malt extract, yeast extract and mangrove wood as substrate having a pH of 6.3 at 26 °C (b) Transcriptome sequencing and assembly, and LC-MS/MS	(Arfi et al. 2013)

Off the Red Sea Coast, Egypt, El-Morsy (2000) used roots of *Avicennia marina* mangrove to isolate cellulose degrading fungi on agar and recovered *Aspergillus Niger*, *Cladosporium cladosporoides*, *Cladosporium sphaerospermum*, *Penicillium chrysogenum*, *Scopulariopsis brevicaulis*, *Stachybotrys chartarum*, *Verticillium cocolosporum*, and *Chaetomium hamadae*. Mtui and Masalu (2008) isolated *Laetiporus sulphureus* from mangrove forests in Dar es Salaam, Tanzania and hypothesize that it may be the primary degrader of cellulose and hemicellulose of mangrove trees in Tanzania.

Various marine ascomycetes and their anamorphs (some of which are commonly found in mangroves) were tested for their wood decay ability by Bucher et al. (2004). Fungi were grown in different cultures and inoculated for 24 weeks with woods blocks. Enzyme assays revealed that 89% of cultured fungi expressed cellulolytic activity using cellulose-azure agar. *Marinosphaera mangrovei* was found to produce cellulases *in vitro*. Pointing et al. (1998) used Congo red staining of CMC agar plate cultures in order to test cellulase production by 15 marine fungal isolates (10 Ascomycota, 1 Basidiomycota and 4 Mitosporic). They found that all isolates produced endoglucanase and cellobiohydrolase with no clear effect of salinity.

Studies that focused on optimizing cellulases production from mangrove fungal isolates used different substrates and physiochemical conditions. For example, Gilna and Khaleel (2011) worked on optimizing cellulases production from *Aspergillus fumigatus* isolated from mangrove soil in India. They found that maximum cellulase production is at pH 6.5, temperature 32°C, yeast extract as Nitrogen source, and sawdust as a substrate. The study by Kathiresan and Manivannan (2006) showed similar results for the fungus *Penicillium fellutanum* obtained from coastal soil of the mangrove *Rhizophora annamalayana* in India. Also from India, Devanathan et al. (2007) and Sasi et al. (2012) isolated *Aspergillus niger* (from mangrove soil), and *A. flavus* (from mangrove water samples), respectively, to test against maximum cellulases production under different physio-chemical conditions. Both studies showed that the optimum temperature for cellulase production is 30°C and at pH 8. As for substrates that showed highest cellulase activity, *A. niger* used wheat bran substrate and peptone as Nitrogen source, whereas *A. flavus* used rice bran and ammonium sulphate (Devanathan et al. 2007; Sasi et al. 2012). Pointing et al. (1999), on the other hand, looked into effect of salinity and culture motility on the production of endoglucanase, cellobiohydrolase and β -glucosidase in five mangrove fungi (*Hypoxylon oceanicum*, *Julella avicenniae*, *Lignicola laevis*, *Savoryella lignicola* and *Trematosphaeria mangrovei*). They found that only stationary cultures showed cellulases production (highest by *H. oceanicum*), whereas salinity alterations generally reduced enzyme production (*J. avicenniae* was unaffected).

Conclusions and Future Prospects

Cellulosic biomass is the most abundant and ubiquitous polysaccharide on earth. The ability of cellulases to saccharify lignocellulosic material makes them a valuable commodity in industry, agriculture and biofuels. Current processes of raw biomass degradation and fermentation to produce biofuels (bio-refinery process) are far from being economically feasible. They are essentially dependent on the cellulases used and their efficiency. Highly specific and stable biomass degrading enzymes to be integrated in the world fuel market is a need that is growing rapidly. Additionally, with the focus on sustainability – there is a movement towards the use of halophytes for biofuel production (Abideen et al.

2011; Intriago 2012; Kamei et al. 2012). These plants can be watered using sea water instead of fresh water. However, the biomass of these plants tends to be saline which could impact efficient enzymatic processes (Malik et al. 1980; Pointing et al. 1999). Therefore there is a need to identify and isolate fungi from saline environments because the enzymes they produce are active at the salinity range required for halophyte biomass degradation.

Mangrove forests are an untapped resource for halo efficient enzymes and there is opportunity for identifying novel fungal species that carry novel genes with biotechnological potential (Thatoi et al. 2013). Many findings listed in this work support this notion by providing evidence of various efficient fungal cellulases obtained from different mangrove reservoirs. Nonetheless, this topic has yet to be given more attention from scholars worldwide. Most researchers have worked on screening isolated fungi from different mangrove reservoirs for cellulases activity using traditional methods. However, as far as we know, very little effort has been invested in investigating mangrove fungal cellulases from a genomic, transcriptomic or proteomic perspective. We invite scientists in this field to shift their focus towards highly saline environments, such as the mangroves, and screen for halotolerant cellulolytic fungi using both, culture dependent approach and molecular level analyses based on genomics and metatranscriptomics. Major enzyme producing companies are in favor of reducing enzyme production costs; however, research is still far from near to understanding gene regulation and function of cellulases. The knowledge of genomic and proteomic contents of cellulolytic fungi of mangrove environments represents a potential path in improving the industry of biofuels. Such approach could lead to identifying novel genes of reliable fungal biomass deconstructing enzymes with unique properties which could be better substitutes of current commercial enzymes. Alternatively, such knowledge could be employed in mutagenesis research for engineering optimum cellulolytic fungi and artificial cellulase systems. Such kind of knowledge is critical in the overall goal of reducing the cost of the bio-refinery process.

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