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Black List of Unreported Pathogenic Bambusicolous Fungi Limiting the Production of Edible Bamboo

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Abstract

Edible bamboo species are now domesticated and commercialized because of their nutraceutical values. The production of edible bamboo species are restrained by diseases caused by pathogenic bambusicolous fungi valued at 40% losses of the total $818.6 million generated annually in bamboo trade in North East India. Based on a systematic survey performed for 2 years in succession, only one Basidiomycota, a *Perenniporia* sp. was identified and validated by pathogenicity test. Ascomycota was the dominant and diverse group of pathogenic bambusicolous fungi. Some rDNA locus sequences failed to match sequences in the up-to-date databases and indicated novel species or genera. Divergence study based on rDNA locus showed that pathogenic bambusicolous fungi were located in the class of Ascomycetes, Sordariomycetes, Eurotiomycetes, Dothideomycetes and Basidiomycetes. The data demonstrated for the first time that *Fusarium*, *Cochliobolus*, *Daldinia*, *Leptosphaeria*, *Phoma*, *Neodeightonia*, *Lasiodiplodia*, *Aspergillus*, *Trichoderma*, *Peyronellaea*, *Perenniporia*, *Nigrospora* and *Hyporales* are potent pathogenic bambusicolous fungi genera restraining the production of edible bamboo *Dendrocalamus hamiltonii*.

Keywords: Fungal diversity; Phylogeny analysis; Pathogenicity test; *Trichoderma asperellum*; *Dendrocalamus hamiltonii;* rDNA

Introduction

Woody bamboo species are highly diverse and abundantly represented in Asian countries such as China, Japan and India etc. Raw bamboo products generate annual revenue of $818.60 million in North East India alone [1]. Bamboo is used in paper making, landscaping, soil conservation, handicrafts, construction, as well as food [2,3]. Nonetheless, it is predicted that half of the world woody bamboo species are in risk of extinction [4,5]. Because of the multipurpose usage and the risk of extinction, techniques for *in vitro* propagation and cultivation of endangered edible bamboo shoots had been developed [6,7].

Remarkably, bush fire, shifting cultivation, flowering boom followed by erratic death [3,8,9], pest and diseases are important factors accelerating the extinction of bamboo species. Although edible bamboo cultivation is plagued by these factors, low level production is exacerbated by harmful bambusicolous fungi. Bambusicolous means organismal life on bamboo [10]. Even though some bambusicolous fungi records are indexed (http://nt.ars-grin.gov/fungaldatabases), the list is not comprehensive for the following reasons: 1) The bamboo species hosting bambusicolous fungi are often not reported, 2) most bamboo species are in the wild and not domesticated for phytopathological scrutiny, and 3) the complex lifestyle of bamboo species which encompasses fast growth, giant height, often growing in difficult terrain limits surveillance and impedes insights on bamboo pathology.

Fungal diseases weaken the rate of growth and the quality of edible bamboo shoots. This is because bamboo shoots development depends on the health status of mother clump-rhizome and leaf canopy. To achieve the optimal production of edible bamboo, pathogenic fungi limiting cultivation must be identified. *Dendrocalamus hamiltonii* Nees et Arn. ex Munro is a sympodial commercial species, with erect and curve culms, and highly valued for its nutraceutical values [3,11]. It is richly distributed in North Eastern Himalayan region, India [12]. Young succulent bamboo shoots of *D. hamiltonii* are consumed fresh or fermented as vegetable; and preferred over other species because its fermented products retained good taste and low water content [13]. At present, there is no report on the diversity of pathogenic bambusicolous fungi of any edible bamboo species. To address this issue, landraces of edible bamboo species of *D. hamiltonii* were surveyed for a period of 2 years in succession for fungal diseases and pathogenicity test was used to validate the disease causing potential of the fungi. Herein, new pathogenic bambusicolous fungi and their phylogenetic link are established.

Materials and Methods

Study area, sampling and morphological identification of fungal pathogens

Landraces of edible bamboo species (*Dendrocalamus hamiltonii* GenBank® accession JX564903) were systematically surveyed in bamboo farms for 2 years in succession for the occurrence of fungal diseases during the month of July–August of 2011 to 2013. The farms are located in Imphal – East District, Manipur, India (Figure 1). The average age of bamboo clumps were 5-7 years old. The area often received an average rainfall of 1320 ± 3 mm and temperature of 29 ± 3°C during the months of July to August. Diseased plant tissue fragments (< 1 cm^2) from leaves, nodes and internodes were surface

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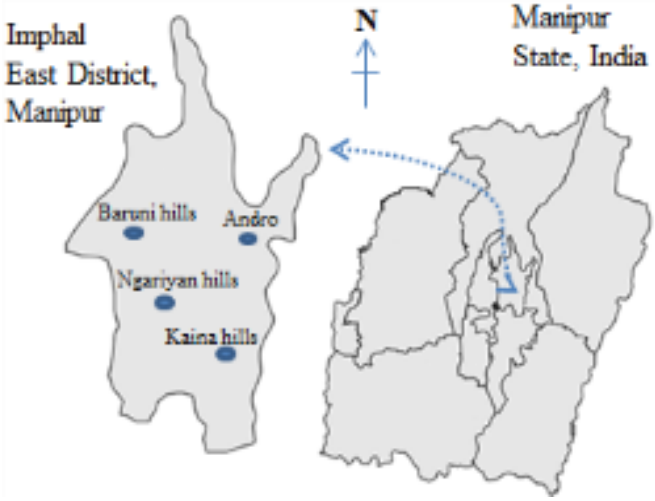


Figure 1: Locations of landraces population of *Dendrocalamus hamiltoniiin* Manipur, India where pathogenic bambusicolous fungi was explored.

sterilised in 0.1% sodium hypochlorite (5 min), 70% ethanol (2 min), and followed by washing in sterile water with three changes. The leaf pieces were plated on potato dextrose agar (PDA) medium (HiMedia®) fortified with 250 mg/L chloramphenicol and incubated at 25°C in the dark. Developed colonies were further purified on V8 agar medium for distinct morphological identification based on standard monographs taxonomic keys with the help of a microscope (Olympus BX61®, Japan).

DNA phylogeny

Sporulating fungi and non-sporulating fungi (that could not be identified morphologically) were characterised at the rDNA locus. Total genomic DNA was isolated from mycelium using UltraClean™ Microbial DNA isolation kits (MO Bio-Laboratories, Carlsbad, CA, USA) as described by the manufacturer. The integrity and quality of DNA was checked by agarose gel electrophoresis and absorbance measurements using a biospectophotometer (Shimadzu® BioSpec, Japan), respectively. rDNA locus comprising of partial sequence of 5.8S rRNA, complete internal transcribed region two (ITS2) and partial 28S rRNA region was amplified using the primer set (5′-tcctccgcttattgatatgc-3′, 5′-gcatcgatgaagaacgcagc-3′) [14] and the PCR conditions were as follows. PCR was performed in a 25 µl volume containing 2.5 µl of 10× DreamTaq buffer green, 1 µl of 2 mM dNTPs, 1 µl of 10 µM of forward and reverse primers each, 0.25 µl of DreamTaq® polymerase (ThermoScientific, UK) 1 µl of 10 ng DNA template and 18.5 µl nuclease free water. DNA template was denatured at 95°C for 3 min, followed by 35 cycles of 95°C for 30s, 55°C for 30s, 72°C for 48s and a final extension at 72°C for 5 min in a thermcycler (Bio-rad, C1000®). All products were profiled by electrophoresis on a 1% agarose gel and stained with ethidium bromide. The PCR products were purified and sequenced. Sequences were assigned to molecular species based on 98–100% sequence similarity threshold in the DNA database of Japan (DDBJ®) in accordance with standard monograph taxonomic keys. Multiple sequence alignment was performed in Muscle program [15] at default settings. Best substitution model parameters for phylogenetic inference were determined based on Akaike Information Criterion, corrected (AICc) and Bayesian Information Criterion (BIC). The maximum likelihood (ML) method was used for phylogenetic inference. All analysis was performed in MEGA 6.06 (updated v. 6140226) software [16]. The ML tree was statistically tested by 1000 bootstrap iterations.

Pathogenicity test

To validate Koch's postulates for the pathogenic bambusicolous fungi, pathogenicity test was performed as follows. Bamboo seeds of *D. hamiltonii* (GenBank® accession JX564903) were propagated in MS culture medium following previously established protocol [17] in a 20 cm long x 15 cm^3 diameter test tube. Following rooting, plants were progressively transferred to sterile soil (consisting of rice-straw vermin-compose-sand mixture (3:1)) in a 10 cm diameter pots under greenhouse conditions. Following the development of internodal culms with 15-20 true leaves, plants were sprayed with a suspension of 10^6 conidia/ml of each fungal pathogen under aseptic conditions. Each inoculated plant was enclosed with a plastic bag to create a near 100% humidity. Plants were observed every 12 h for the development of symptoms and pathogenicity test was performed three times. Only fungal pathogens which produced similar symptoms to those observed in the field are reported.

Results and Discussion

In Manipur, India, landraces of *D. hamiltonii* are densely populated in Imphal East District (Figure 1). This region often witness sporadic rainfall, foggy weather, and strong wind movement during July–August each year. *D. hamiltonii* is rich in nutraceutical values and highly demanded by consumers [3,11]. Because of the nutritional attributes and important population size of *D. hamiltonii* in Manipur, the study was focused on the fungal pathogens of this edible bamboo species.

A total of 32 bambusicolous pathogenic fungi identified and validated by Koch's postulates was deposited in DDBJ accessions (Table 1) and were used for phylogenetic reconstruction. Of the 32 fungal pathogens, 31 were Ascomycota distributed within the class of Dothideomycetes, Eurotiomycetes, Sordariomyctes and one was unclassified. Nonetheless, it has been shown that most fungi in these subclasses are pathogens [18,19]. Only one of the fungal pathogen (i.e. *Perenniporia* sp.) was Basidiomycetes (Table 1). Additionally, the pathogenic bambusicolous fungi belonged to the genera of *Fusarium*, *Cochliobolus*, *Daldinia*, *Leptosphaeria*, *Phoma*, *Neodeightonia*, *Lasiodiplodia*, *Aspergillus*, *Trichoderma*, *Peyronellaea*, *Perenniporia*, *Nigrospora* and *Hyporales*. It is estimated that there are over 630 Ascomycetes, 150 Basidiomycetes and 330 mitosporic taxa (100 coelomycetes and 230 hyphomycetes) infecting bamboo [10,20]. The finding in this study is in accordance with other data [10,20], that predominant bambusicolous fungi of bamboo are Ascomycetes (Table 1). Although *Hypocreaceae* is understood to be the common bambusicolous fungi [10], only one - *Hypocreales* sp. strain B101 was identified as a pathogenic bambusicolous via Koch's postulates (Table 1).

The combined sequences had an estimated transition/transversion bias ratio of 1.26. The Kimura 2-parameter [21] substitution model (+G, 5 categories, parameter = 3.50) produced the following nucleotide frequencies: A = 25.00%, T/U = 25.00%, C = 25.00%, G = 25.00% and sequence alignment is shown (Figure 2). The rate variations model that allowed for some sites to be evolutionarily invariable [+ I] was 4.71%. In the dataset, a total of 425 patterns were found out of 496 sites. Only 129 sites were without polymorphism (26.01%). From the sequence set, AICc = 2092.67, BIC = 2493.58 and the best substitution model used was T92 + G + I. Initial ribotype tree for the heuristic search was obtained by applying the Neighbor-Joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach.

Pathogens	DDBJ Accession	Strain	Tissue	Phylum	Class/Subclass	Collection date	Period of occurrence
Fusarium incarnatum	AB918015	B120	Leaf	Ascomycota	Sordariomycetes	10-06-2012	May-June
Fusarium chlamydosporum	AB918016	B121	Internode	Ascomycota		18-07-2012	June-July
Fusarium camptoceras	AB918017	B122	Node	Ascomycota		07-07-2013	June-July
Fusarium proliferatum	AB918018	B124	Internode	Ascomycota		12-07-2013	June-July
Nigrospora oryzae	AB918019	B125	Leaf	Ascomycota		19-08-2013	July-September
Fusarium chlamydosporum	AB918020	B126	Leaf	Ascomycota		21-08-2012	July-August
Nigrospora sphaerica	AB918021	B127	Leaf	Ascomycota		15-03-2014	March-April
Fusarium oxysporum	AB918022	B129	Leaf	Ascomycota		03-05-2012	May-June
Chaetomium bostrychodes	AB918027	L3	Internode	Ascomycota		06-06-2012	June-July
Trichoderma reesei	AB918031	L9	Leaf	Ascomycota		15-07-2013	July-August
Fusarium proliferatum	AB918023	B130	Leaf	Ascomycota		04-07-2014	July-August
Trichoderma asperellum	AB918007	L7	Leaf	Ascomycota		10-11-2012	October-November
Fusarium incarnatum	AB918010	B110	Leaf	Ascomycota		10-07-2012	July-August
Hypocreales sp	AB918034	B101	Leaf	Ascomycota		09-07-2012	June-July
Daldinia eschscholzii	AB918033	S1	Internode	Ascomycota		10-09-2013	August-September
Phoma plurivora	AB918009	B104	Leaf	Ascomycota	Dothideomycetes	10-07-2013	June-July
Phoma herbarum	AB918006	L29	Leaf	Ascomycota		04-10-2013	October-November
Cochliobolus lunatus	AB918004	L26	Leaf	Ascomycota		09-06-2014	June-July
Lasiodiplodia theobromae	AB918000	L1	Node	Ascomycota		15-07-2012	June-July
Cochliobolus miyabeanus	AB918003	L17	Leaf	Ascomycota		13-08-2013	July-September
Peyronellaea glomerata	AB918011	B116	Leaf	Ascomycota		05-08-2012	August-November
Alternaria sp	AB918012	B117	Leaf	Ascomycota		07-10-2013	September-December
Leptosphaeria sacchari	AB918024	L10	Leaf	Ascomycota		09-08-2013	July-September
Lasiodiplodia theobromae	AB918025	L14	Leaf	Ascomycota		05-07-2012	July -August
Phoma herbarum	AB918026	L16	Internode	Ascomycota		06-08-2013	July -August
Lasiodiplodia theobromae	AB918028	L18	Leaf	Ascomycota		07-07-2014	June-August
Cochliobolus miyabeanus	AB918032	LUN1	Leaf	Ascomycota		13-06-2012	July-October
Neodeightonia subglobosa	AB918035	S3	Leaf	Ascomycota		19-11-2013	October-November
Aspergillus fumigatus	AB918018	B118	Leaf	Ascomycota	Eurotiomycetes	03-08-2013	June-August
Aspergillus flavus	AB918002	L12	Leaf	Ascomycota		08-05-2012	
Aspergillus niger	AB918001	L11	leaf	Ascomycota		7-05-2013	
Ascomycetes sp	AB918014	B119	Leaf	Ascomycota	Unclassified	14-06-2013	June-August
Perenniporia sp.	AB918008	B100	Leaf	Basidiomycota	Basidiomycetes	02-06-2013	June-July

Table 1: Hit list of unreported pathogenic bambusicolous fungi limiting edible bamboo production.

The ML tree indicated that all *Fusarium* taxa formed a main node (at bootstrap value = 67%) and strongly supported by internal branches with bootstrap values > 98% (Figure 3). *Fusarium chlamydosporum* (2 isolates), *Fusarium proliferatum* (2 isolates), *Fusarium incarnatum* (2 isolates) were the most common *Fusarium* species (Figures 3 and 4). As shown (Figure 3), bambusicolous fungi population on edible bamboo *D. hamiltonii* is highly diversified. Generally, predominant group of fungi life in bamboo *D. hamiltonii* is the Ascomycota, estimated to fit in about 228 genera and 70 families [10]. In decreasing frequency of occurrences, *Hypocreaceae*, *Xylariaceae*, *Lasiosphaeriaceae*, *Clavicipitaceae, Phyllachoraceae, Lophiostomataceae, Diatrypaceae, hyaloscyhaceae, Paradiopsidaceae, Valsaceae* and *Pseudoperisporaceae* are reported families that successfully thrived on bamboo species [10].

Some fungi species were encountered only once or twice (Table 1), suggesting that the fungal community could change over time or natural fluctuation in the populations. Regardless of the 99% bootstrap values at the node associating Ascomycetes strain b119 and *Peyronellaea glomerata* strain b116 (Figure 3), we did not find similarity at the morphological level using standard monographs. Furthermore, Ascomycetes strain b119 did not match sequences in the databases at 100% threshold value. This may be an indication of the weakness in public DNA repositories to delineate all fungi. Within the surveillance period, dominant fungal genera were *Peyronellaea glomerata, Alternaria* sp., *Fusarium oxysporum, Aspergillus niger, Aspergillus fumigatus, Aspergillus flavus,* and *Cochliobolus lunatus* (Figures 3 and 4). *Fusarium chlamydosporum, Fusarium camptoceras, Fusarium oxysporum, Fusarium proliferatum* and *Fusarium incarnatum* were also identified (Table 1).

Aspergillus species have not been reported among the bambusicolous fungi in previous studies [10,22,23]. In this present study, *Aspergillus niger*, *Aspergillus flavus* and *Aspergillus fumigatus* (Figure 2a), *Neodeightonia subglobosa* (Figure 3b), *Trichoderma* species (Figure 3c and 3d), *F. incarnatum* (Figure 3e) were identified. All the *Aspergillus* species sporulated on *D. hamiltonii* during the infestation period of 72 h (Figure 5a-5c). *Trichoderma* species and *Aspergillus* species were recently shown to be pathogens of *Guadua* species, which are abundantly distributed in Ecuador, Chile and Peru (ftp://ftp.fao.org/docrep/fao/010/ah782e/AH782e00.pdf) only. This present study provide the first report of *Trichoderma* species (Figure 3c and 3d) and *Aspergillus* species causing diseases on edible bamboo *D. hamiltonii* (Figure 5a-5c). Although some *Aspergillus* spp. and *Trichoderma* spp. are used as biocontrol agent [24-26], they are important cellulase producers [27,28], which is an important factor for pathogenicity. On this basis, some *Aspergillus* spp. and *Trichoderma* spp. are opportunistic colonizers of economic importance [29-31].

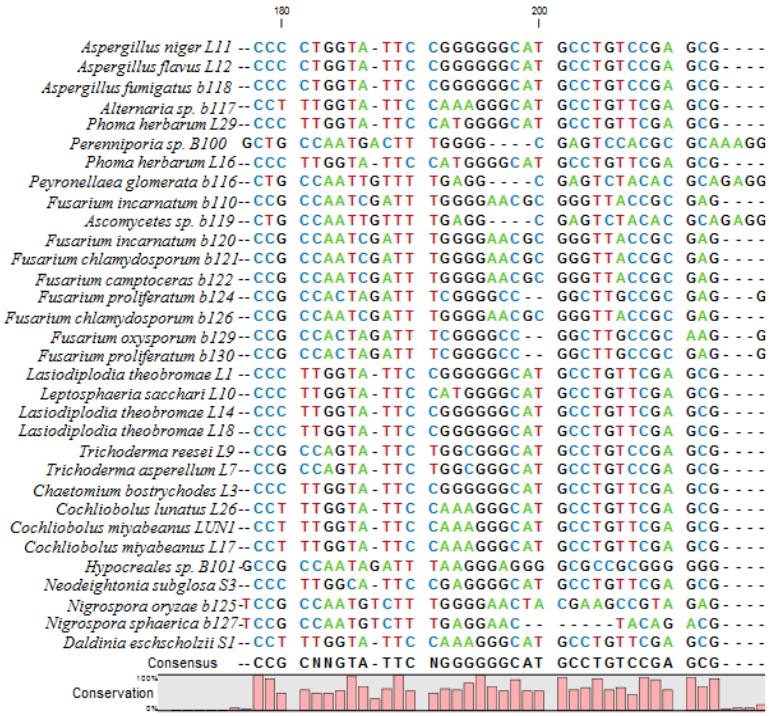


Figure 2: Multiple sequence alignment depicting the variations in bambusicolous fungi the alignment was performed in CLC workbench (Qiagen, Valencia, CA) and variable nucleotides are colored.

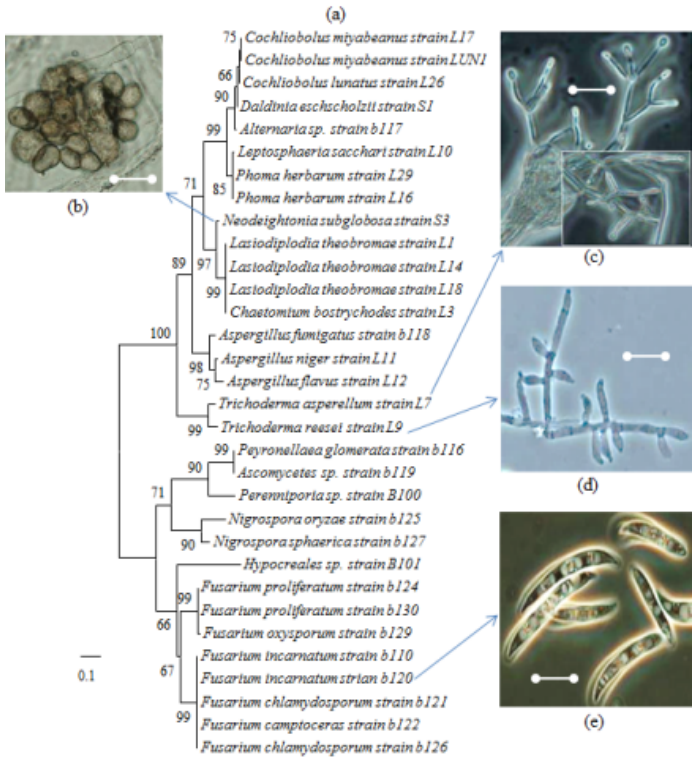


Figure 3: Taxonomical placement of unreported pathogenic bambusicolous fungi of edible bamboo. a: A maximum likelihood tree of highest log likelihood (-1116.47), associated taxa clustered together and supported with 1000 bootstrap reiterations. The ribotype tree is scaled, with branch lengths measured as the number of substitutions per site. b: Brown macroconidia of *Neodeightonia subglobosa*. **c:** Conidiophore of *Trichoderma asperellum* and close-up shows detail of hyphae branching. d: Conidiophore of *Trichoderma reesei*. e: Conidia of *Fusarium incarnatum*. All micrographs were acquired with Olympus DP70 camera (Olympus BX61, USA) at 1000× magnification and scale bars represent 15 µm.

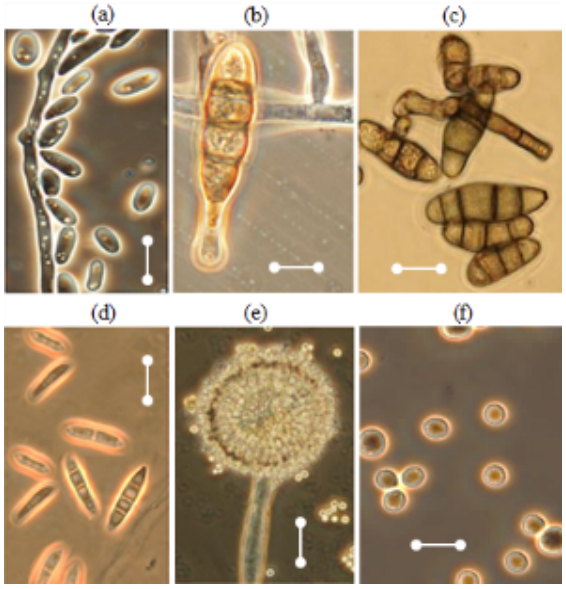


Figure 4: Micrographs of predominant fungi pathogens of edible bamboo *Dendrocalamus hamiltonii* cultured on V8 agar medium. a: *Peyronellaea glomerata* strain b116 showing details of hyphae, conidia and bar=30 µm. b: *Alternaria* sp. strain b117 showing details of hyphae, conidium and bar=10 µm. c: *Cochliobolus lunatus strain* L26 showing details of conidia and bar=20 µm. d: *Fusarium oxysporum* strain b129 and bar=25 µm. e: *Aspergillus flavus* strain L12 and bar=20 µm. f: *Hypocreales sp. strain B101* and scale bar=10 µm. Images were acquired with Olympus DP70 camera (Olympus BX61, USA) at 1000× magnification.

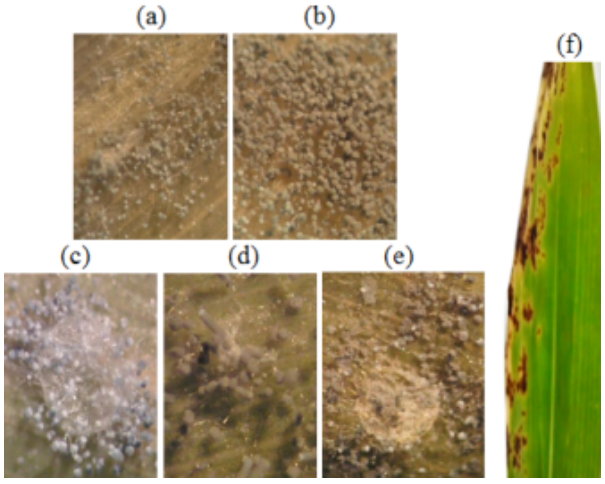
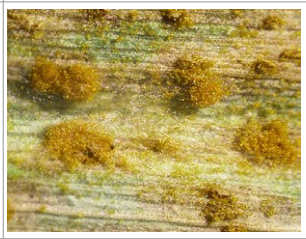


Figure 5: Pathogenicity test performed with plantlets of *D. hamiltonii* in test tube to verify Koch's postulates. a: Sporulating *Aspergillus niger* and colonization leaf tissue (400× magnification). b: Sporulating *Aspergillus fumigatus* and colonization of leaf tissue (400× magnification). c: Sporulating *Aspergillus flavus* and colonization of leaf tissue (400× magnification). d: Leaf rot disease caused by *Fusarium proliferatum*. e: Colonization marked by leaf rot caused by *Fusarium incarnatum* with evidence of fruiting bodies. e: Brown-to-black leaf lesion disease caused by *Cochliobolus lunatus*.

It was observed that all the *Fusarium* species caused rot disease of bamboo shoots, rot of growing culms, and rot of leaf tissues and damping-off of seed plantlets during pathogenicity test (Figure 5d and 5e). Noteworthy, this is the first report of *F. chlamydosporum*, *F. oxysporum*, *F. camptoceras*, *F. oxysporum*, *F. proliferatum* and *F. incarnatum* causing rot disease of bamboo in India. Under field conditions, *Fusarium* infected culms were bend and fallen. Also, *F. moniliforme* var. *intermedium* has been reported to be associated with rot of emerging culms in *B. bambos* [22]. Severe rot and blight diseases of bamboo have been observed in Bangladesh [32,33] and in India [22,34] caused by *Fusarium* species.

Recently in India, it was shown that *Fusarium semitectum* caused both blight and rot disease of *Bambusa tulda* [35]. Also, *F. oxysporum* and *F. chlamydosporum* have been reported in India on *Solanum tuberosum* L and *Capsicum annum* L, respectively [36,37]. *Cochliobolous* species caused foliar and sheath blight diseases, manifested by brownish oval-shaped and water-soaked lesions which became black as the bamboo leaf turned yellowish (Figure 5f). *Cochliobolus* species causes diseases on *Bambusa bambos* and *Dendrocalamus longispathus* [22], with similar characteristic symptoms to those described herein. Symptoms caused by *C. lunatus* in bamboo are similar to leaf spot disease of rice (*Oryza sativa*), wheat (*Triticum aestivum*), cassava (*Manihot esculenta*), sorghum (*Sorghum bicolor*) and potato (*Solanum tuberosum*) [38-42]. It was suggested that *C. lunatus* produced brown-to-black symptoms in many plant hosts because of its melaninated colonizing hyphae [42-44]. Nonetheless, other recurrent leaf spot diseases of bamboo are caused by many species of *Phyllachora* [44]. Interestingly, other studies [35,45,46] have reported new bambusicolous fungi causing a major threat to bamboo production (Table 2). The danger of all the reported bambusicolous pathogenic fungi is that, once bamboo shoots are infected in the field, fungal proliferation continues upto the market level and account to severe economic loses.

Blight and rot diseases of *B. tulda* caused by *Fusarium semitectum* [35].	
Bamboo rust disease of *B. vulgaris* caused by *Uredium* sp [45].	
Kweilingia rust of *B. vulgaris* caused by *Kwelingia divina* (syn. *Dasturella divina*) [45].	
Bamboo witches broom disease of *Phyllostachys bambusoides* caused by *Aciculosporium take* [46].	

*Permission for images was granted by Scot N, Matthew G, Tanaka E and Teron R.

Table 2: Some significant rare bamboo diseases recently communicated.

Conclusion

The study shows that poor pathological management of bambusicolous fungi is valued at 40% losses of the total $818.6 million generated annually in North East India. Until 2010, it was thought fungi belonging to the genera of *Kweilingia*, *Puccinia*, *Uredo*, *Phakospora*, *Stereostratum*, and *Tunicopsora* which caused bamboo rust diseases was the most predominant pathogenic bambusicolous fungi and distributed worldwide. In our study, two principal damages are often caused by these pathogenic bambusicolous fungi, *viz.,* 1) staining of bamboo shoots and 2) structural decay of bamboo shoots which leads to economic loses to all stakeholders in the commercial chain. Our data indicated that *Fusarium*, *Cochliobolus*, *Daldinia*, *Leptosphaeria*, *Phoma*, *Neodeightonia*, *Lasiodiplodia*, *Aspergillus*, *Trichoderma*, *Peyronellaea*, *Perenniporia*, *Nigrospora* and *Hyporales* are new pathogenic bambusicolous fungi genera limiting the production of *D. hamiltonii*. Given most bamboo species are endangered and threatened of extinction [4,5], further studies are required to understand the mechanism of bamboo invasion. The emergence of bambusicolous fungi reported on edible bamboo *D. hamiltonii* in this study illustrated the urgent need for developing a piecemeal control strategy [47].

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