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Full Paper

Fire and the production of *Astraeus odoratus* (Basidiomycetes) sporocarps in deciduous dipterocarp-oak forests of northern Thailand

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Abstract: The genus *Astraeus* (Diplocystidiaceae) forms ectomycorrhizal associations with many tree species and is a common gasteromycete in tropical and temperate ecosystems worldwide. In Thailand, *Astraeus* is most prevalent in deciduous dipterocarp-oak forest (DOF) in the north and north-east and its ecology is uniquely associated with fire. Rural villagers often burn the seasonally dry DOF ground vegetation causing significant environmental disturbance to promote the growth of *Astraeus* sporocraps—a local culinary delicacy and important source of household income. The purpose of this work is to investigate whether the practice of burning DOF stimulates the production of A*straeus* sporocarps in DOF. Burned and unburned *Astraeus* habitat was surveyed over two years at two sites in Chiang Mai province and one site in Mae Hong Son province. Changes in soil fungi after a fire as well as vascular vegetation growing with *Astraeus* were studied. All sporocarps collected were identified as *Astraeus odoratus*. *Astraeus* sporocarps were found in both burned and unburned areas in 2010. In 2011, an unusually wet year, no sporocarps were found in burned or unburned areas. The top 2 cm of soil experienced high temperatures which killed fungi, but lower depths were well insulated from the heat. A wide range of vascular flora grew in *Astraeus* habitat, the most common tree species being *Dipterocarpus tuberculatus* var. *tuberculatus* and *Dipterocarpus obtusifolius* var. *obtusifolius*. This study shows that *Astraeus* can produce sporocarps without fire and future work can focus on more environmentally benign methods of harvesting this popular mushroom.

Keywords: *Astraeus odoratus*, deciduous dipterocarp-oak forest, ectomycorrhizal fungi

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

INTRODUCTION

Deciduous dipterocarp-oak forest (DOF) is the most common forest type in South-east Asia, covering more area than any other forest type and extends from north-eastern India and Myanmar through north and eastern Thailand, southern Laos, Cambodia and southern Vietnam [1]. This forest type is mainly a result of anthropogenic disturbance and is usually associated with a hot-dry season, poor soil, and significant disturbance including logging, grazing and seasonal fires fueled by a layer of dry accumulated plant material [2-6] (Figure 1). Deciduous dipterocarp-oak forest is an important resource for local communities providing timber, grazing, wild plants and edible mushrooms.

In the north and north-eastern Thailand fire in DOF is frequently ignited by mushroom hunters who believe that it promotes the production of *Astraeus odoratus* Phosri, Watling, M.P. Martín, & Whalley sporocarps ("earthstars" or "het tawp"), which are a popular and expensive culinary delicacy [7]. Fire is lit in the dry season (February-April) and the burned soil is scraped and scoured by gatherers looking for the immature, submerged sporocarps produced at the beginning of the following rainy season (end of May-June). The genus *Astraeus* is a cosmopolitan ectomycorrhizal (ECM) fungus found throughout temperate and tropical regions of the world and has been shown to form a relationship with several tree families including Dipterocarpaceae, Fagaceae, Betulaceae and Pinaceae [8-10]. Outside of Asia *Astraeus* is not considered edible and is not associated with fire. Frequent burning by forest gatherers has deleterious ecological consequences, causing an increase in seedling and sapling mortality, loss of biodiversity and primary forest, an increase in the proportion of grassy ground flora and a decrease in soil nutrients [3,11-13]. In addition, smoke haze from fires can be an acute public health hazard, particularly in dry years [5,14]. If *Astraeus* sporocarps can be produced without fire, then a significant motivation for burning DOF can be eliminated which will contribute reforestation and restoration goals across the north and northeast of Thailand.

Despite the importance of *Astraeus* to the local economy and DOF, both as an ectomycorrhizal symbiont and as a major reason for forest fires, the ecology of this mushroom in relation to fire is not well understood. This study examines several aspects of fire-*Astraeus* dynamics in DOF, including the amount of *Astraeus* collected in burned and unburned DOF in 2010 and 2011, a molecular analysis of *Astraeus* collected from 3 previously unsurveyed areas in Mae Hong Son and Chiang Mai provinces, the effects of fire on soil characteristics and fungi in areas where *Astraeus* sporocarps were found, as well as a survey of the vascular vegetation associated with *Astraeus*. The overall objective is to test the widely held hypothesis that fire has a positive effect on *Astraeus* sporocarp production.

Figure 1. Deciduous dipterocarp-oak forest on 14 January, 2010 , before a fire with a thick layer of combustible dry vegetation (A) and on 7 June 2011 after burning and the start of the rainy season with quickly emerging herbs and leafing, coppicing trees (B). Photo by K. Kennedy (Pa Daeng National Park)

METHODS

Collection and Survey

Fresh immature *Astraeus* sporocarps were collected from three research sites: Pa Daeng National Park, Chiang Dao district, Chiang Mai province (CD); Huay Hong Krai, Doi Saket district, Chiang Mai province (DS); and Tham Pla-Namtok Pha Suea National Park, Muang district, Mae Hong Son province (MHS). Site descriptions are shown in (Table 1). Samples were collected with local villagers in May and June in 2010 and 2011 and were brought to the Sustainable Development of Biological Resources Laboratory, Chiang Mai University, where they were cleaned and their morphological characteristics (microscopic and macroscopic) were recorded and studied. The sporocarps were then dried in an oven at 45−50°C overnight and stored at the Chiang Mai University Herbarium, Faculty of Science, Chiang Mai University.

Table 1. Data for the vegetation survey plots at three sites

Plot	Elevation (m)	Easting	Northing	Ground cover (%)	Substrate
CD	625	47494739	2170774	60	Limestone/granite
MHS	500	4751456	2150325	45	Limestone/sandstone
DS	350	47522446	2090735	40	Limestone

Vegetation surveys were conducted in *Astreaus* habitat at CD (2 December 2010), MHS (8 January 2011) and DS (28 June 2011) research sites in order to identify the *Astraeus* host range. Five-meter radius plots were established at six points at each site that had been identified by villagers as areas where *Astraeus* was collected the previous year. For each plot, all woody vegetation taller than 1.5 m was measured for diameter at breast height and total height, identified and recorded. Later the Shannon and Simpson indices of diversity were calculated. Plants and cover abundance of understory vegetation shorter than 1.5 m within the plots were recorded using the Braun-Blanquet scale (x=sparse; 1=small cover; 2=5-25%; 3=25-50%). Fire history was established based on burn evidence and villager input. The vegetation condition and cover, elevation, bedrock and UTM coordinates for each plot were also noted.

Identification of *Astraeus*

Astraeus speciation in Thailand is still unclear and morphologically similar species have been recently separated into at least three species: *A. odoratus*, *A. asiaticus* and *A. hygrometricus*. This study was the first survey of *Astraeus* sporocarps from these study sites. *Astraeus* sporocarps were collected and identified based on morphological characteristics and molecular analysis using DNA extracted following the method of Phosri et al. [9, 10]. Polymerase chain reaction (PCR) amplification was conducted using internal transcribed spacer regions of nuclear rDNA and ITS4 and ITS5 primers. The thermal conditions were 95°C for 2 minutes, 30 cycles at 95°C for 30 seconds, 50°C for 30 seconds and 72°C for 1 minute, followed by cycling at 72°C for 10 minutes. Amplicons were then examined under UV light on 1% agarose gels stained with ethidium bromide. The specimens were cleaned using the NucleoSpin^{R} Extract II Purification Kit (Macherey-Nag, Dueren, Germany) according to the manufacturer's protocol. Purified products were sequenced and determined in a genetic analyser (1st Base, Selangor, Malaysia). Sequences were used to query GenBank via BLAST (http://blast.ddbj.nig.ac.jp/top-e.html) and a phylogenetic tree was constructed using the PUAP beta 10 software version 4.0 [15].

***Astraeus* Yield at Chiang Dao and Doi Saket**

A two-year survey of *Astraeus* yields from burned and unburned DOF was conducted in May-June 2010 and May-June 2011. One large plot approximately 0.5 km^2 was established at the CD and DS research sites in DOF identified as *Astraeus* habitat by local collectors. At the end of the dry season (February-May) the burned and unburned areas within both plots were mapped by walking the boundaries of burned areas with a handheld GPS unit and the paths were uploaded to a digital elevation model using ARCGIS (ESRI, California, USA). During the period of *Astraeus* sporocarp production, three surveys were conducted by villagers and park employees on 30 May, 3 June and 9 June 2010. Leaf litter in unburned plots was removed using a rake in order to expose the soil surface and facilitate observation and collection of submerged *Astraeus* sporocarps (Figure 2). The wet and dry weights of all *Astreaus* sporocarps collected for the day were calculated for both the burned and unburned plots as well as the sizes of 50 specimens. Information on rainfall and air temperatures for 2010 and 2011 at the two sites were obtained from the Thai Meteorological Department, Chiang Mai (Figure 3).

Figure 2. Method of *Astraeus odoratus* harvesting using a metal claw, with subterranean (A, B, C) and a mature, dehisced specimen (D) from Pa Daeng National Park, 30 May, 2010. Photo by K. Kennedy

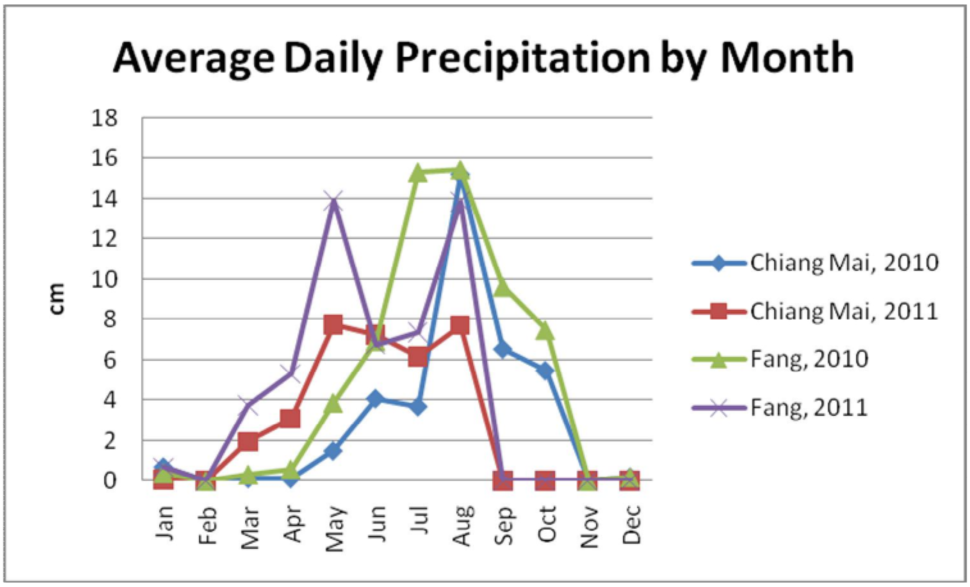

Figure 3. Average daily precipitation measured for Chiang Mai city and Fang district reflects the rainfall for the Pa Daeng and Doi Saket sites respectively

Fire and Soil Characteristics of *Astraeus* Habitat in Chiang Dao

An analysis of soil temperature during a fire event was undertaken on 15 March 2010 at the CD site in order to assess whether fire damages existing fungal hyphae in the soil. Pyrometers were constructed using Tempilaq ™ heat sensitive labels that were compressed between small sheets of aluminum and fastened with paper clips. The pyrometers covered a temperature range of 40-249°C and five sensors were placed buried 6 cm below the soil surface in a line. The sensors

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

were buried, the soil compacted and 6 cm of leaf litter was placed on top and burned. This method was repeated with sensors buried at the depths of 4, 2, 1, and 0 cm below the ground surface

In a separate study, the effect of heat from a fire on soil microbes was examined. A spread plate technique was used to enumerate soil microbes on potato dextrose agar (PDA). Soil samples were taken from the CD site approximately 12 hours after a fire that occurred on 27 April 2010. Soil was collected from six random sampling sites within both burned and unburned areas. Ash was removed and soil was collected from the top 2 cm of soil. The six samples were then combined and mixed into a composite sample. One gram of the composite soil was added to 10 ml of sterile water and vigorously shaken in order to make the initial solution. Serial ten-fold dilutions up to 10^{-6} were then prepared. PDA was autoclaved at 121°C and 15 psi for 15 minutes. A trace amount of 0.01% chloramphenical was added to the PDA media in order to suppress bacterial growth. Approximately 25 ml of the medium was added to each sterile Petri dish and allowed to cool to room temperature. A 1-ml pipette was then used to transfer 0.1 ml of each soil dilution onto a Petri dish and was spread over the surface with a sterile glass spreader. Each dilution was spread in triplicate for both burned and unburned soil samples. All the plates were incubated at 25°C for 48 hours and the number of colony forming units per milliliter was determined. Plates with no soil solutions were used as a control.

Locations of *Astraeus* collection points and the number of sporocarps within a 3-meter radius of the collection point was recorded with a GPS to see if there was a correlation between fire and location of *Astraeus* sporocarps**.** These locations were uploaded to a digital elevation model of each research site obtained from the Geographic Information System Centre, Geography Department, Faculty of Humanities, Chiang Mai University and analysed using ArcMap software (ESRI, Redlands, California, USA). Spatial autocorrelation was calculated using the Moran's I index.

RESULTS

Collection and Survey Results

Astraeus was found in a wide range of DOF conditions, from relatively intact forest with many trees to sparse, open canopies, with thick ground cover and eroded rocky soil at the base of 20-m tall trees. In all, 169 plant species were recorded in the 18 plots (Table 2). *Dipterocarpus tuberculatus* Roxb. var. *tuberculatus* (56 trees) followed by *Dipterocarpus obtusifolius* Teijsm. *ex* Miq. var. *obtusifolius* (34 trees) were the most common trees and at least one of these two species was present in every plot. *Shorea obtusa* Wall. *ex* Bl. (21 trees), *Gluta usitata* (Wall.) Hou, (17 trees), and *Tristaniopsis burmanica* (Griff.) Wils.var. *rufescens* (Hance) Parn. & Lug. (16 trees) were also prevalent (Table 3). The most diverse site was DS with average Shannon and Simpson indices of 1.62 and 0.22 respectively, indicating a high species richness and diversity. The CD site had the lowest diversity with a Simpson index value of 0.94 and the MHS site had the lowest richness with a Shannon index value of 1.50.

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 2. Species and abundance of ground flora growing with *Astraeus* sporocarps by site and plot: CD in blue, MHS in red and DS in brown. For habit: a= annual; d= deciduous; e= evergreen; v= vine; h= herbaceous; wc= woody climber; t= tree; tl= treelet; sc= scandent. For abundance: x=sparse; 1=small cover; 2=5-25%; 3=25-50%

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Abrus precatorius L.	Leguminosae, Papilionoideae	a, v			x		x													
Abrus pulchellus Wall. *ex* Thw. ssp. *pulchellus*	Leguminosae, Papilionoideae	a, v																x	x	x
Acacia megaladena Desv. var. *megaladena*	Leguminosae, Mimosoideae	d, wc										x								
Adiantum zollingeri Mett. *ex* Kuhn	Parkeriaceae	d, h			x			x												
Albizia chinensis (Osb.) Merr	Leguminosae, Mimosoideae	d, t																x		
Albizia odoratissima (L. f.) Bth.	Leguminosae, Mimosoideae	d, t									x									
Alpinia galanga (L.) Willd. var. *galanga*	Zingiberaceae	e, h														x	x			
Alysicarpus bupleurifolius (L.) DC.	Leguminosae, Papilionoideae	a, h								x										
Amalocalyx microlobus Pierre *ex* Spire	Apocynaceae	d, v													x					
Amorphophallus sp.	Araceae	d, h													x		x			x
Amphioneuron marginatum (Roxb.) Midd.	Apocynaceae	d, wc									x						x			
Anneslea fragrans Wall.	Theaceae	d, t				x									x		x			x
Antidesma acidum Retz.	Euphorbiaceae	d, tl									x	x	X							
Antidesma ghaesembilla Gaertn.	Euphorbiaceae	d, tl		x											x					
Antidesma soothepensis Craib	Euphorbiaceae	d, tl									x									
Apluda mutica L.	Gramineae	d, h	3	3	2		2	2			1	2								
Aporosa octandra (B.-H. *ex* D. Don) Vick. var.*octandra*	Euphorbiaceae	d, tl																x		
Aporosa villosa (Lindl.) Baill.	Euphorbiaceae,	d, tl		x		x	x				x				x	x	x	x	x	
Ardisia crenata Sims var. *crenata*	Myrsinaceae	d, wc													x	x				
Aristolochia pierrei Lec.	Aristolochiaceae	d, v	x																	
Barleria cristata L.	Acanthaceae	d, h			x															
Blumea lacera (Burm. f.) DC.	Compositae	a, h		x	1				x	x	x			x						
Blumeopsis flava (DC.) Gagnep.	Compositae	a, h	x	x	x															
Bombax anceps Pierre var. *anceps*	Bombacaceae	d, t																		
Breynia glauca Craib	Euphorbiaceae	d, tl													x	x		x	x	x

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Buchanania lanzan Spreng.	Anacardiaceae	d, t		x		x			x	x		x	X							
Buchnera cruciata B.-H. *ex* D. Don var. *cruciata*	Scrophulariaceae	a, h				x														
Cajanus volubilis (Blanco) Blanco	Leguminosae, Papilionoideae	a, v									x	x								
Canarium subulatum Guill.	Burseraceae	d, t										x					x	x		
Capillipedium parviflorum (R. Br.) Stapf	Gramineae	d, h			x		x													
Carex continua Cl.	Cyperaceae	d, h		2																
Cassia fistula L.	Leguminsae, Caesalpiniodeae	d, t									x									
Cassytha filiformis L.	Lauraceae	e, v																x		
Catunaregam spathulifolia Tirv.	Rubiaceae	d, l		x				x	x											
Chionanthus ramiflorus Roxb.	Oleaceae	e, t															x			
Chloranthus nervosus Coll. & Hemsl.	Chloranthaceae	d, h										x								
Chukrasia tabularis A. Juss.	Meliaceae	d, t									x	x								
Cissus hastata Miq.	Vitaceae	d, wc													x	x	x			x
Clerodendrum serratum (L.) Moon var. *wallichii* Cl.	Verbenaceae	d, tl										x								
Colona floribunda (Wall. *ex* Kurz) Craib	Tiliaceae	d, t									x	x								
Commelina diffusa Burm. f.	Commelinaceae	d, h							x											
Costus speciosus (Koeh.) J.E. Sm. var. *speciosus*	Zingiberaceae	d, h		x																
Craibiodendron stellatum (Pierre) W.W. Sm.	Ericaceae	e, tl				x							X					x	x	
Cratoxylum formosum (Jack) Dyer *ssp. pruniflorum* (Kurz) Gog.	Guttiferae	d, t	1		x		x													
Crotalaria alata D. Don	Leguminosae, Papilionoideae	a, h							x	x	x									
Crotalaria albida Hey. *ex* Roth	Leguminosae, Papilionoideae	a, h	x	x	x		x	x					X	x						
Crotalaria bracteata Roxb. *ex* DC.	Leguminosae, Papilionoideae	a, h									x									
Crotalaria kurzii Baker *ex* Kurz	Leguminosae, Papilionoideae	a, h							x	x	x			x						
Crotalaria neriifolia Wall. *ex* Bth.	Leguminosae, Papilionoideae	d, h			x															

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Croton oblongifolius Roxb.	Euphorbiaceae	d, t													x					
Curcuma plicata Wall. ex Bak. complex	Zingeberaceae	d, h							x	x			X		x	x				
Dalbergia rimosa Roxb.	Leguminosae, Papilionoideae	d, wc																		
Dalbergia cana Grah. *ex* Bth. var. *cana*	Leguminosae, Papilionoideae	d, t									x									
Dalbergia cultrata Grah. *ex* Bth.	Leguminosae, Papilionoideae	d, t	x	x	x	x	x	x							x	x	1	x		x
Dalbergia oliverii Gamb. *ex* Prain	Leguminosae, Papilionoideae	d, t							x								x			
Dalbergia velutinum DC. var. *velutinum*	Leguminosae, Papilionoideae	d, s										x								x
Desmodium heterocarpon (L.) DC. ssp. *heterocarpon* var. *birmanicum* (Watt. ex Prain) Oha.)	Leguminosae, Papilionoideae	d, h	x																	
Desmodium longipes Craib	Leguminosae, Papilionoideae	d, tl			x													x		
Desmodium motorium (Houtt.) Merr.	Leguminosae, Papilionoideae	a, h					x		x	x	x	x						x		
Desmodium oblongum Wall. *ex* Bth.	Leguminosae, Papilionoideae	d, l																		
Desmodium velutinum (Willd.) DC. var. *velutinum*	Leguminosae, Papilionoideae	d, s									2							x		
Dioscorea bulbifera L.	Dioscoreaceae	d, v													x	x	x	x	x	x
Dioscorea glabra Roxb.	Dioscoreaceae	d, v			x															
Dioscorea pentaphylla L.	Dioscoreaceae	d, v		x																
Diospyros ehretioides Wall. *ex* G. Don	Ebenaceae	d, t					x							x						
Dipterocarpus obtusifolius Teijsm. *ex* Miq. var *obtusifolius*	Dipterocarpaceae	d, t	1	1	1	x	1	1						1		x		x	x	x
Dipterocarpus tuberculatus Roxb. var. *tuberculatus*	Dipterocarpaceae	d, t	x						1	1	x	x	1		x		x			
Dumasia leiocarpa Bth.	Leguminosae, Papilionoideae	a, v									x									
Dunbaria bella Prain	Leguminosae, Papilionoideae	d, v			x												x	x		
Embelia tsjeriamcottam (Roem. & Schult.) A. DC. var. *tsjeriamcottam*	Myrsinaceae	d, wc	x																	
Eugenia cumini (L.) Druce var. *cumini*	Myrtaceae	d, t	1				x			x										x
Eulalia leschenaultiana (Decne.) Ohwi	Gramineae	d, h								x	x		X	x						
Eulalia siamensis Bor	Gramineae	d, h	3	3	2	3	2	3												

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Eupatorium odoratum L.	Compositae	a, h	x												x		x			
Eurycoma longifolia Jack	Simoroubaceae	d, l				x												x	x	x
Flacourtia indica L.	Flacourtiaceae	d, t															x			
Flemingia sootepensis Craib	Leguminosae, Papilionoideae	d, h		x	x				x	x			X	x						
Gardenia obtusifolia Roxb. *ex* Kurz	Rubaceae	d, l								x			X	x						
Gardenia sootepensis Hutch.	Rubiaceae	d, t		x	x				x											
Geniosporum coloratum (D. Don) O. K.	Labiatae	d, h									x						x		x	
Globba nuda K. Lar.	Zingiberaceae	d, h																x	x	x
Globba reflexa Craib	Zingiberaceae	d, h															x			
Glochidion eriocarpum Champ.	Euphorbiaceae	d, t(l)									x									
Gluta usitata (Wall.) Hou	Anacardiaceae	d, t													x	x	1		x	x
Grewia abutilifolia Vent. *ex* Juss.	Tiliaceae	d, s										x			x		x			
Grewia eriocarpa Juss.	Tiliaceae	d, t										x								
Hedyotus auricularia L.	Rubiaceae	a, h						x												
Hedyotus capitellata Wall. *ex* G. Don	Rubiaceae	a, h															x			
Hedyotus tenelliflora Bl. var. *kerrii* (Craib) Fuku.	Rubiaceae	a, h	x	x	x	x		x	x	x	x	x	X	x						
Helicteres elongata Wall. *ex* Boj.	Sterculiaceae	d, ls									x	x								
Hyparrhenia rufa (Nees) Stapf var. *siamensis* Clayton	Gramineae	d, h		2																
Hypoxis aurea Lour.	Amaryllidaceae	d, h	x													x				
Inula cappa (Ham. *ex* D. Don) DC.	Compositae	a, h	2	x	x	1	1	x					X	x				x	x	
Inula indica L.	Compositae	a, h		1	x		x	x	x	x	x		X	x						
Irvingia malayana Oliv. *ex* Benn.	Irvingiaceae	e, t																x		
Kaempferia rotunda L.	Zingiberaceae	d, h																x		x
Kaempferia siamensis Siri.	Zingiberaceae	d, h													x	x	x			
Leea indica (Burm. f.) Merr.	Leeaceae	d, hs	x	x	x	1					x	x			1	x	x			
Lithocarpus polystachyus (Wall. *ex* A. DC.) Rehd.	Fagaceae	e, t																		x
Lophopetalum walichii Kurz	Celastraceae	d, t					x			x					x	x			x	

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Lygodium polystachyum Wall. *ex* Moore	Schizaeaceae	d, v															x	x		
Lygodium flexuosum (L.) Sw.	Schizaeaceae	d, v	x		x	x	1	x	x	x	x	x	X	x	x				x	
Memecylon scutellatum (Lour.) Hk. & Arn.	Melastomataceae	e, tl																	x	
Meyna pubescens (Kurz) Roby	Rubiaceae	d, l										x								
Millettia extensa (Bth.) Bth. *ex* Baker	Leguminosae, Papilionoideae	d, wc	x	2		x		x	x	x	x	1	X	x						
Mnesithea striata (Nees *ex.* Steud.) Kon. & Sos.	Gramineae	d, h								x	x	x	X	x						
Mucna bracteata A. DC. *ex* Kurz	Leguminosae, Papilionoideae	a, v									x									
Murdannia edulis (Stokes) Fad.	Commelinaceae	d, h								x										
Mussaenda parva Wall. *ex* G. Don	Rubiaceae	d, wc																x		x
Nervilia aragoana Gaud.	Orchidaceae	d, h													x					
Ochna Integerrima (Lour.) Merr.	Ochnaceae	d, tl						x									x	x		x
Oroxylum indicum (L.) Bth. *ex* Kurz	Bignoniaceae	d, tl									x									
Paederia pallida Craib	Rubiaceae	a, v							x		x	x					x			
Panicum notatum Retz.	Gramineae	a, h									x	x								
Parinari anamensis Hance	Rosaceae	d, t																		
Pavetta fruticosa Craib	Rubiaceae	d, s		x	x		x	x												
Pavonia repanda (Roxb. *ex* J. E. Sm.) Spr.	Malvaceae	d, l,sh	x								x	x								
Pennisetum polystachyon (L.) Schult.	Gramineae	d, h			x															
Pheonix loureiroi Kunth var. *loureiroi*	Palmae	e, tl													2	1	2			
Phoebe lanceolata (Nees) Nees	Lauraceae	e, t														x	x	x		
Phyllanthus emblica L.	Euphorbiaceae	d, t		x																
Polytoca digita (L. f.) Druce	Gramineae	d, h		x	x	x		1	1	1			x		x	2	2	1	x	
Premna herbacea Roxb.	Verbenaceae	d, h							x											
Psuedopogonatherum irritans (R. Br.) A. Camus	Gramineae	d, h					x	x												
Pterocarpus macrocarpus Kurz	Leguminosae, Papilionoideae	d, t	x	x	x											x		x	x	
Pueraria stricta Kurz	Leguminosae, Papilionoideae	d, sc						x												
Quercus brandisiana Kurz	Fagaceae	d, t																x		
Quercus kerrii Craib	Fagaceae	d, t	1	1	x	x		1							x	x		x	x	1

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Sacciolepis indica (L.) A. Chase	Gramineae	a, h				x														
Sauroporus quadrangularis (Willd.) M.-A.	Euphorbiaceae	d, h									x									
Scleria levis Retz.	Cyperaceae	d, h							x	x			x	x						
Scleria lithosperma (L.) Sw.	Cyperaceae	e, h																	x	x
Scleria terrestris (L.) Fass.	Cyperaceae	d, h		2	x	1	2													
Selaginella ostenfeldii Hier.	Selaginellaceae	d, h							x	x			x	x						
Shorea obtusa Wall. *ex* Bl.	Dipterocarpaceae	d, t	2	1	1			1	x	x		x	x	x	x		x		x	
Shorea siamensis Miq. var. *siamensis*	Dipterocarpaceae	d, t	x	x	1		1	1										x		
Smilax lanceifolia Roxb. var. *lanceifolia*	Smilacaceae	e, v															x			
Smilax ovalifolia Roxb.	Smilacaceae	d, v								x		x				x				
Smilax verticalis Roxb.	Smilacaceae	d, v		x																
Sonerila erecta Jack	Melastomataceae	a, h				x														
Sorghum verticilliflorum (Steud.) Stapf	Gramineae	d, h										x								
Spatholobus parviflorus (Roxb.) O.K.	Leguminosae, Papilionoideae	d, wc	x	2				x							x	x		x		
Sterculia balanghas L.	Sterculiaceae	d, t	x																	
Streptocaulon juventas (Lour.) Merr.	Asclepiadaceae	e, v			x	2														
Strobilanthes apricus (Hance) T. And. var. *pedunculatus* (Craib)Ben.	Acanthaceae	d, s							x		x		x	x						
Strobilanthes glaucescens Nees	Acanthaceae	d, h										x								
Strychnos nux-vomica L.	Loganiaceae	d, t													x	x	x			
Symplicos racemosa Roxb.	Symplocaceae	d, tl	x				x													
Tectona grandis L. f.	Verbinaceae	d, t										x								
Terminalia alata Hey. *ex* Roth	Combretaceae	d, t							x					x						
Terminalia chebula Retz. var. *chebula*	Combretaceae	d, t																		
Terminalia mucronata Craib & Hutch.	Combretaceae	d, t	x	x																

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 2. (continued)

SPECIES			CD						MHS						DS					
Botanical Name	**Family**	**Habit**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Thespesia lampas (Cav.) Dalz. & Gibs. var. *lampas*	Malvaceae	d, l										x								
Thunbergia alata Boj. *ex* Sims	Acanthaceae	e, v	x																	
Thysanolaena latifolia (Roxb. *ex* Horn.) Honda	Gramineae	e, h																x		
Tristaniopsis burmanica (Griff.) Wils. & Wat. var. *rufescens* (Hance) Parn. & Lug.	Myrtaceae	e, tl	1		x		2						x					x	1	
Vaccinium sprengelii (D. Don) Sleum.	Ericaceae	e, tl	x				x													
Vernonia parishii Hk. f.	Compostae	d, lh	1	x														x	x	
Vernonia squarrosa (D. Don) Less. var. *orientalis* Kit.	Compostae	d, h							x	x		x	x							
Vigna dalzelliana (O.K.) Verd. var. *dalzelliana*	Leguminosae, Papilionoideae	a, v									x	x								
Vitex peduncularis Wall. *ex* Schauer	Verbenaceae	d, t	x	x											x					
Walsura trichostemon Miq.	Meliaceae	e, t					x													
Wendlandia tinctoria (Roxb.) DC.	Rubiaceae	e, tl	x		x	x		x	x	x			x		1	x	x			
Xylia xylocarpa (Roxb.) Taub. var. *kerrii* (Craib & Hutch.) Niels.	Leguminosae, Mimosoideae	d, t										x								
Zingiber bradleyanum Craib	Zingiberaceae	d, h	x																	
Ziziphus rugosa Lmk. var. *rugosa*	Rhamnaceae	d, t													x	x				

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 3. Most common tree species based on number of trees in 5-m radius plots

		Site			
Species	Family	Chiang Dao	Mae Hong Son	Doi Saket	Total
Dipterocarpus tuberculatus var. *tuber.*	Dipterocarpaceae	0	40	16	56
Dipterocarpus obtusifolius var. *obtus.*	Dipterocarpaceae	13	0	21	34
Shorea obtuse	Dipterocarpaceae	5	10	6	21
Gluta usitata	Anacardiaceae	0	0	17	17
Tristaniopsis burmanica	Myrtaceae	7	0	9	16
Dalbergia cultrate	Leguminosae, Papilionoideae	0	0	13	13
Aporusa villosa	Euphorbiaceae	3	0	6	9
Quercus kerrii	Fagaceae	7	0	2	9
Pterocarpus macrocarpus	Leguminosae, Papilionoideae	7	0	0	7
Buchanania lanzan	Anacariaceae	4	2	0	6
Simpson Index		0.94	0.35	0.22	
Shannon Index		1.55	1.50	1.62	
Total species per site		49	64	98	

The ground flora was also significantly represented by saplings (mostly coppices) of *D. tuberculatus* var. *tuberculatus, D. obtusifolius* var. *obtusifolius, Shorea siamensis* Miq. var. *siamensis, S. obtusa,* and *Quercus kerrii* Craib, which were all present as coppices and seedlings comprising 1-5% of the total cover of more than one plot. *Dalbergia cultrata* Grah. *ex* Bth., *Lygodium flexuosum* (L.) Sw. and *Polytoca digita* (L f.) Druce, a deciduous tree, deciduous vine and deciduous grass respectively were present as ground cover in 12 of the 18 plots though in low abundances. The most commonly represented plants in the plots were deciduous herbs, with 39% of all plot records, followed by deciduous trees with 25%. Most species had low abundances (≤1% cover area). Many grasses were consistently present in high densities, including *Eulalia siamensis* Bor and *Apluda mutica* L., which had densities of 25-50% in several plots. The percentage of ground cover in the plots varied greatly with a range of 10-95% and an average of 51%.

Astraeus Identification Results

The morphological characteristics of sporocarps collected were consistent at all three collection sites. The sub-globose fruiting bodies were approximately 2.0 x 2.0 x 1.5 cm. The outer peridium was light brown in color changing to darker brown after maturing. The endoperidium was dark brown with no peristome. The gleba of immature sporocarps was white or cream changing to dark brown-black in mature specimens. Basidiospores were globose and 7-15 µm in diameter (Table 4).

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

Table 4. Morphology of *Astraeus odoratus* sporocarps

Basidiomes	Sub-globose, approximately 2.0 x 2.0 x 1.5 cm. Strongly hydroscopic and emits a musty soil odor.
Outer peridium	Light brown surface, smooth and rubbery when submerged, hardening and splitting radially after emergence
Endoperidium	Dark brown to black with no peristome
Gleba	White or cream when immature, changing to dark brown-black
Basidiospores	globose, 7.5-15 μm
Habitat	Deciduous dipterocarp-oak forest on sandy, rocky and clay soils from May to July
Distribution	North and north-eastern Thailand

For molecular identification, the internal transcribed spacer 1, 5.8S ribosomal DNA gene and internal transcribed spacer 2 sequences of samples from the CD (CMU-HP9), DS (CMU-HP11), and MHS (CMU-HP8) sites were deposited in GenBank as JQ292818, JQ292819 and JQ292817 respectively. The aligned dataset of these 17 sequences consisted of 820 characters, of which 413 characters were constant, 180 variable characters were parsimoniously uninformative, and 227 characters were parsimoniously informative. Heuristic searches resulted in nine equally parsimonious trees with a length of 635 steps (CI=0.863, RI=0.881, RC=0.7603 and HI=0.137), one of which is shown in Figure 4. Phylogenetic analyses by Phosri et al. [9, 10] indicated that *Astraeus* species were divided into 4 clades including *A. ordoratus* (clade A), *Astraeus pteridis* (Shear) Zeller (clade B), *Astraeus hygrometricus* Pers. Morgan (clade C) and *Astraeus asiaticus* Phosri, Watling, M.P.Martín, & Whalley (clade D). All *Astraeus* samples collected in this study (Kennedy 1, 2 and 3, from the CD, DS and MHS sites respectively) belonged to *A. odoratus* in clade A, which is a sister group of *A. pteridis* with 82% bootstrap support.

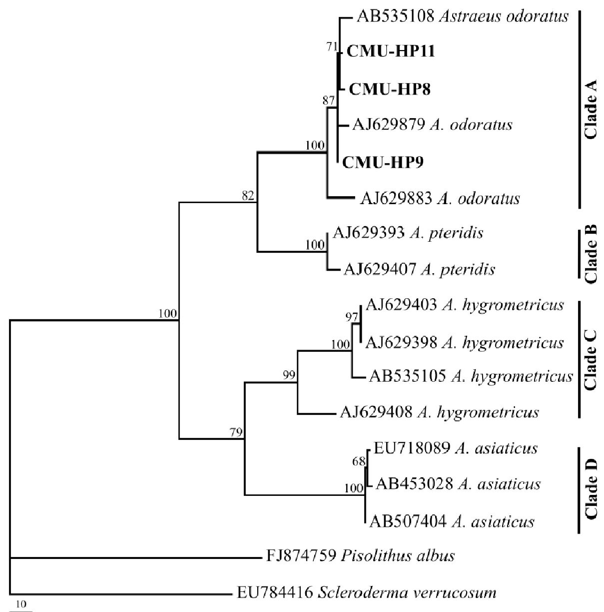

Figure 4. One of the six parsimonious trees inferred from a heuristic search of the internal transcribed spacer 1, 5.8S ribosomal RNA gene and internal transcribed spacer 2 sequence alignments of 17 isolates

Maejo Int. J. Sci. Technol. **2012**, *6*(3), 483-504

***Astraeus* Yield at Chiang Dao and Doi Saket**

Many immature *Astraeus* sporocarps were found at the CD and DS sites in 2010 and none were found at either site in 2011. The weather, particularly in March-May, was significantly different during these two years. Year 2010 was an unusually dry year with a long fire season and a late rainy season starting mid-May. In contrast, 2011 exhibited an early and prolonged rainy season starting at the beginning of March and there were no fires.

In 2010 sporocarps were found in abundance in burned areas (2,233 g and 1,015 g total cumulative wet weight for CD and DS respectively, or 9.75 x 10^{-3} g/m^2) and with a much lower frequency in unburned areas (22 g and 14 g wet weight for Pa Daeng and Doi Saket, respectively, or 3.99 x 10^{-3} g/m^2). In 2010, 97% of the plots were burned (Figure 5). *Astreaus* sporocarps were first observed at the CD site at the end of May and could be found in abundance for 10 days, after which the plots had been completely scoured and dug up by mushroom hunters. During this period, three surveys were conducted with the help of the national park employees. The highest yield was obtained in burned areas on the first survey day and decreased thereafter (1028 g, 682 g and 523 g wet weight for 30 May, 3 June and 9 June 2010 respectively). Only one cluster of *Astraeus* sporocarps with a total wet weight of 22 g was found in the unburned area (30 May) (Figure 6).

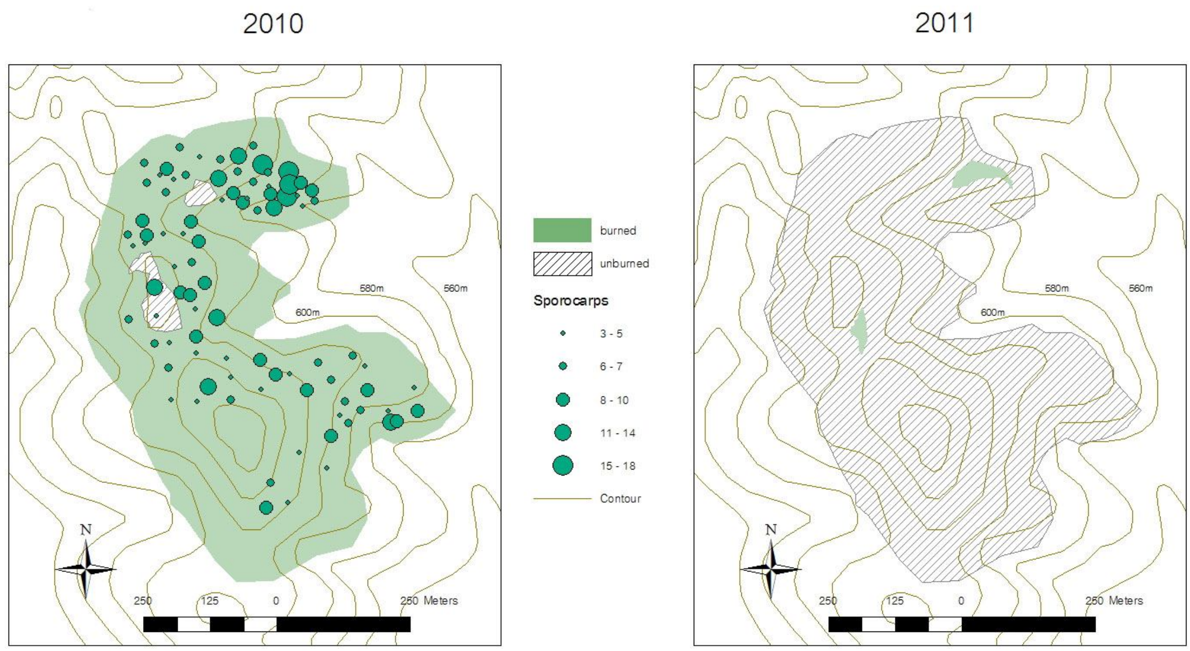

Figure 5. The extent of burning and *Astraeus odoratus* sporocarps collected in Pa Daeng National Park, Chiang Dao district, Chiang Mai province in May and June 2010 and 2011

The DS site collection profile was similar to that at CD. Most (94%) of the plot was burned in 2010. The rainy season in the more southern Doi Saket site started several weeks later and *Astreaus* sporocarps first appeared at the end of June. Two surveys were conducted with the help of locals on 20 June (1.7x10^{-3} and 4.1x10^{-5} g/m^2) and 25 June 2010 (1.2x10^{-3} and 0 g/m^2) in burned and unburned areas respectively.

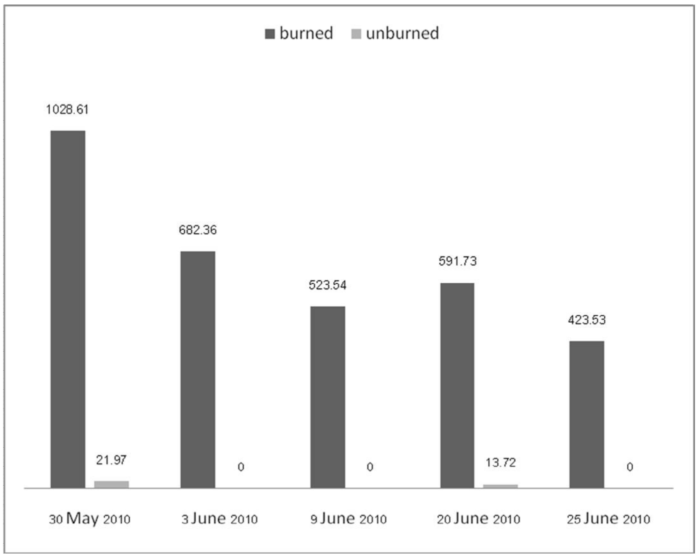

Figure 6. Yields of *Astraeus* in burned and unburned areas in grams for 2010

The sporocarp size from 50 random specimens taken from burned areas each day averaged 6.3 cm^3 and 6.16 cm^3 for CD and DS respectively. Average sizes for sporocarps collected in unburned areas were smaller, 1.89 cm^3 and 0.245 cm^3 for CD and DS respectively. Sporocarps from burned areas were heavier. The average fresh weight of individual sporocarps from CD were 2.5 and 1.3 g for burned and unburned areas respectively. The average fresh weight of individual sporocarps from DS was 3.6 g and 1.4 g for burned and unburned areas respectively.

Fire and Soil Characteristics of *Astraeus* Habitat at Chiang Dao

Soil temperature experiment showed that the surface of the soil profile became extremely hot during a fire (greater than 249°C, which was the maximum limit of the pyrometer). Below 2 cm there was very little change in the soil temperature from fire. The average temperatures were >249, 122.4, 66.3, 41.6 and <40°C at the depths of 0, 1, 2, 4 and 6 cm respectively (Figure 7). Soil temperature without fire never exceeded 40°C during the experiment. Soils were compact eroded limestone with some granite.

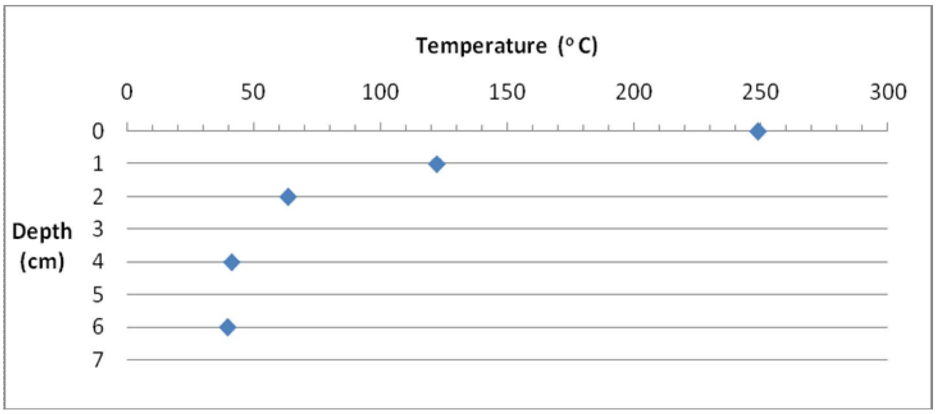

Figure 7. Soil temperatures at different depths during a fire

The soil fire-microbe analysis showed that fire has a negative effect on fungi, which is significant as during a dry year areas are sometimes burned many times. An average of 883 cfu's were found in unburned soil and 162 in burned soil. The control plates containing no soil solutions were blank indicating no contamination. Dilution levels of $1x10^{-3}$ and $1x10^{-4}$ elicited distinct and countable fungal colonies for the unburned soil, while less diluted levels ($1x10^{-2}$ and $1x10^{-3}$) were satisfactory to count the colony forming units in burned soil samples. This indicates that fire has a direct and immediate negative effect on fungi growing at the top layer of soil.

Astraeus sporocarps were always found in clusters of 3 or more. In addition, spatial autocorrelation analysis of *Astraeus* sporocarp collection points and the amount collected showed that there is a clustering pattern. The Moran I Index, which measures dispersion, was 0.14 with a z score of 2.11 indicating that there is less than 5% likelihood that the distribution of sporocarps bunches are themselves clustered.

DISCUSSION

The genus *Astraeus* is associated with a wide range of tree species around the world and particularly dipterocarps in Thailand. However, knowledge of its hosts is far from complete. In vitro experiments have shown that *Astraeus* can form associations with *Dipterocarpus alatus* Roxb. *ex* G. Don, *Eucalyptus camaldulensis* Dehnh. (Myrtaceae) and *Pinus densiflora* Sieb. and Zucc. (Pinaceae) [16, 17]. Our plots were dominated by *Dipterocarpus tuberculatus* var. *tuber*culatus, *Dipterocarpus obtusifolius* var. *obtusifolius* and *Shorea obtusa* as well as *Quercus kerrii* Craib, *Gluta. usitata* (Wall.) Hou and *Dalbergia cultrata* Grah. *ex* Bth. Our study also included many grasses and other herbs, treelets and vines consistently growing in areas that produce *Astraeus* sporocarps. Most of the focus has been on tree species as *Astraeus* hosts. However, it is possible that non-arboreal species are also *Astraeus* hosts and, having faster growth rates, are better candidates for inoculation trials and can potentially lead to commercial *Astraeus* production.

The genus *Astraeus* in Asia has been taxonomically studied in the last decade. *Astraeus* in Thailand was thought to be only *A. hygrometricus*. Phosri et al. [9, 10] showed that *A. odoratus* is a separate species and is commonly found throughout the north and north-east. Morphologically the two species are very similar but *A. hygrometricus* sporocarps tend to have a whiter colour and more basidial rays once they open (5-12 compared to 3-9 rays for *A. hygrometricus* and *A. odoratus* respectively). At a microscopic scale, the basidiospores of *A. odoratus* are slightly smaller (8.75-15.2 µm versus 7.5-12 µm for *A. hygrometricus* and *A. odoratus* respectively) and have longer and narrower spines. *Astraeus asiaticus* is present in Thailand but was not encountered in this study.

This survey of *A. odoratus* sporocarp yields over two years with very different rainfall and consequent fire regimes allows for interesting insights into the ecology of this species. It was found that fire is not an absolute requirement for *A. odoratus* sporocarp production, although this fungus is likely adapted to produce sporocarps in dry soil conditions which can result from a fire. Sporocarps were found in unburned patches of DOF in 2010, but in 2011 they were nonexistent in the small patches of burned forest. This suggests that other factors are influencing sporocarp production along with fire. Rainfall for 2010 and 2011 were very different. Between January and May 2010, 76.3 cm of rain had fallen, while at that same time in 2011, 396.5 cm had fallen. This rainfall variation had a significant effect on the fire regime since in 2010 fires were pervasive and many areas were burned twice in the same year. In contrast, fires in 2011 were almost absent as the leaf litter never reached a critically low moisture level that would allow it to sustain a fire. The amount, average fresh weight, and dimensions of sporocarps from the burned area were significantly larger than those from the unburned area in 2010. The burned area surveyed for 2010 was much larger than the unburned area so it is difficult to make direct comparisons between the two conditions.

Soil at CD from *A. odoratus* habitat showed a sharp decline in nitrogen after a fire (Figure 8). Trappe and Cormack [18] conducted soil analyses and examined fungal communities in Ponderosa pine forests in Oregon subjected to controlled burns and found that groups of fungal species were present at either above or below a C:N threshold ratio of 26:1. Of 24 species of mushrooms collected only one species was present in soils both above and below the C:N ratio of 26:1; all other species were present in either one or the other, but not both. Autumnal burns significantly reduced the C:N ratio and produced specific fungal species that were also present in unburned areas with a similarly low C:N ratio. In this study, the C:N ratio changed in burned *Astraeus* habitat immediately after a fire as nitrogen was lost. Soil nutrient changes and moisture as catalysts for *Astraeus* sporocarp production are topics that can be explored in future research.

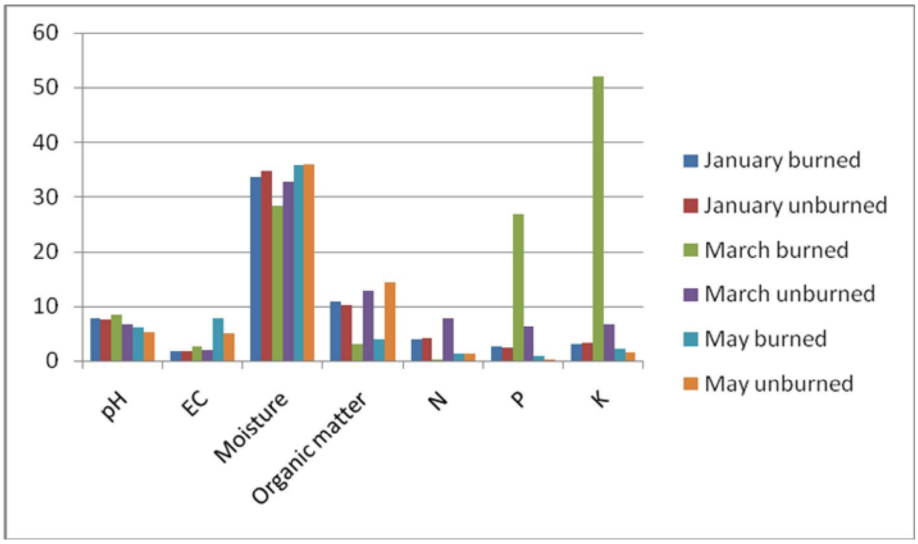

Figure 8. Changes in soil characteristics before and after a fire at CD

This survey of *Astraeus* sporocarp production in burned and unburned areas was complicated by many other people collecting *Astraeus* in the surveyed area. Locals were employed to assist with collection, but many people came from other places and entire tracts of forest were quickly scoured during the short period in which *Astraeus* sporocarps are underground and still edible. The collection method involves digging up areas with a metal claw or crowbar (Figure 2). This can have an adverse effect on the underlying host roots, soil structure and hyphae. Furthermore, only immature sporocarps are collected which do not have a chance to release spores before they are removed from the forest. Only sporocarps that are overlooked or emerge after an area has been harvested have a chance to open and spread their spores. Whether or not harvesting causes recruitment limitation is a topic for further research.

Spatial autocorrelation analysis of *Astraeus* sporocarp clusters collected at CD were not randomly distributed since the method of collection was not entirely random as we were collecting with locals who had specific places that they knew were areas of high yield. At the CD site gatherers tended to stay along the ridge running through the plot and generally avoided the steep slopes of the western and eastern sides, or ascending the steep knoll in the southern end of the plot. Locals generally avoided looking extensively in unburned areas. There was a consensus that *Astraeus* does not need fire to produce sporocarps, although the yield was much greater in burned areas. Whether this is a result of specific conditions created by fire that induce sporocarp formation or whether fire simply makes it easier to find subterranean sporocarps once the leaf litter has been removed can be examined in future research.

A small amount of *Astraeus* was found in unburned patches with particularly gravely soil at the CD site in 2010. At the DS site *Astraeus* was found under a thick leaf litter layer with rich soil. Locals highlighted areas under burned logs as places likely to produce a high yield and this is something that can be further examined. Based on our initial survey the soil and vegetation conditions where *Astraeus* sporocarps were found varies substantially. Helfferich [19] mapped the location of individual *Morcella* sp. basidia after a fire in Alaska using a GPS accurate to 5 cm. They found that the distribution was very clustered though the mechanism that caused sporocarp development in the specific areas was unclear.

Fire, a frequent and characterising component of DOF, has been previously studied. Stott [6] found that a heat sensitive paint with a threshold of 35°C at a depth of 5 cm was not triggered during a fire. Wanthongchai et al. [12] showed that the length of period between fires did not significantly affect soil temperatures in DOF. They measured ambient soil temperature with thermocouples 5 minutes after a fire and found that soil at 1 cm did not exceed 48^0C in either frequently or infrequently burned stands. Our experiment using gradient indicators at a range of depths showed that at depths lower than 2 cm heat from a fire will not always be significant, but at 2 cm and up the soil can reach temperatures that kill mycelia. The soil structure of DOF, which is often very compact, rocky, eroded and has little organic matter, causes minimal heat transfer into the soil profile and allows for the survival of underground parts of many DOF plants and fungi.

Though the effects of fire on soil microbe communities has been extensively examined in other parts of the world, particularly in boreal forests in North America, little research has been conducted on this topic in South-east Asian DOF. Treseder et al. [20] used hyphae length of soil fungi and microbial respiration to estimate abundance in chronosequenced stands of boreal forests in Alaska. They found that a year after a fire there was no significant difference in fungal biomass, although after 6-25 years of a fire there was a significantly lower fungal biomass than the control site which had not been burned in 85 years. Our results showed that the amount of fungi in DOF surface soil decreased immediately after a fire. Widden and Parkinson [21] also showed that the fungi composition in boreal forests changed by fire. They grew soil fungal cultures in Petri dishes with aqueous extracts of burned and unburned leaf litter to show that certain fungi including *Trichoderma polysporum* and *Penicillium janthinellum* were inhibited by the fire. *Cylindrocarpon destructans* was not inhibited and *Gelasinospora* sp. was only found in burned plots. Our research showed that initially after a fire, there was a substantial decrease in the overall level of fungi in surface soil, but further research is needed in order to determine the long-term trends in DOF and the specific changes in fungal composition resulting from fire.

CONCLUSIONS

This study is the first analysis of how fire affects *Astraeus*, an important genus found throughout much of the world. The flora associated with ectomycorrhizal *Astraeus*, its taxonomy in northern Thailand, a comparison of *Astraeus* sporocarp yields in burned and unburned DOF, the soil temperature during a fire and the change in surface soil fungi resulting from fire are quantified.

It was shown that fire is not necessary for the production of *Astraeus* sporocarps but it seems to promote more and larger sporocarps. Heat from fire can have negetative affects on soil fungi and soil quality in the upper soil layer where *Astraeus* hyphae can be found. It is possible that fire indirectly increases harvest yield by eliminating the leaf litter layer and making submerged sporocarps easier to find. The years 2010 and 2011 had drastically different rainfall conditions and *Astraeus* yields, suggesting that other factors such as soil moisture and length of the hot-dry season are also important. A long term survey of the yield and spatial distribution of *Astraeus* clusters in relation to weather conditions and with greater control over the size of burned and unburned areas should be continued at the CD site.

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