Contents lists available at ScienceDirect



Trends in Food Science & Technology



journal homepage: http://www.journals.elsevier.com/trends-in-food-scienceand-technology

Review

Nutrition, safety, market *status quo* appraisal of emerging functional food corn smut (huitlacoche)



Seema Patel

Bioinformatics and Medical Informatics Research Center, San Diego State University, 92182, 5500 Campanile Dr, San Diego, CA, USA

ARTICLE INFO

Article history: Received 23 September 2015 Received in revised form 14 September 2016 Accepted 16 September 2016 Available online 20 September 2016

Keywords: Corn smut Ustilago maydis Teliospores Functional food Essential amino acids

ABSTRACT

The inequitable availability of food compared to burgeoning population has propelled the search for novel food candidates as well as revival of relegated nutrient sources. In this context, the kingdom fungi hold immense prospects. Fungus constitutes a highly paradoxical domain. Many members of this group are consumed as functional food and appreciated for their medicinal values; whereas some species are recognized as pathogens for animals and plant; incriminated as sources of mutagenic mycotoxins; food spoiling agents; and allergens. The basidiomycota species *Ustilago maydis* is member with both traits. It is dreaded as the etiological agent of corn smut, the gall disease of maize crop. On the other hand, it is being consumed as delicacy (huitlacoche or corn truffle) since ages and recently, its popularity has risen immensely. This dual, conflicting behavior motivated the author to explore its nutritional composition and dietary safety. Functional food prospect of this enigmatic fungus has been estimated from multiple angles, by gleaning credible information from literature. Also, lacunae in this field have been shown and production scale-up strategies have been suggested. With nutritional profusion and scarce toxic contents, it appears to be a safe edible fungus, worthy of cultivation.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

The specter of food insecurity and deficiency of adequate nutrition has led to the search for novel, hitherto obscure food sources (Gany et al., 2013). The fungal kingdom encompasses many potential candidates (Jo Feeney, Miller, & Roupas, 2014). In this regard, huitlacoche or cuitlacoche, a fungal gall on corn cobs (Zea mays L.) deserves prominence (Pataky & Chandler, 2003). The fungus Ustilago maydis (corn smut), a biotrophic fungus, belonging to order Ustilaginales is the causative agent of this gall and resultant corn crop spoilage (María Elena Valverde, Talía Hernández-Pérez, & Octavio Paredes-Lopez, 2012). The ethnic name 'huitlacoche' originating from Aztec Nahuatl language means 'raven's excrement'. It is likely to be derived from the unappealing, dark appearance of the gall. However, edibility of this smut is known since the Aztec times (Juárez-Montiel, Ruiloba de León, Chávez-Camarillo, Hernández-Rodríguez, & Villa-Tanaca, 2011). It is considered a delicacy in Mexican and Latin American cuisine (Valverde, Paredes-López, Pataky, & Guevara-Lara, 1995). It is used in a variety of Mexican foods as soups, sauce, tamales, tacos, tortilla, quesadillas, enchiladas etc. It is so ingrained in Mexican culture that even murals symbolize them (McMeekin, 1999). Even the Native American Hopi, Zuni and Cochiti tribes residing in South Western parts of the USA use this fungus as a part of their diet and medicine (Munkacsi, Stoxen, & May, 2008). Further, recent archaeological evidences retrieved from mineralized tartar of human fossils in Santa Cruz de Tenerife (Italy) imply corn smut consumption at that time (Afonso-Vargas, La Serna-Ramos, & Arnay-de-la-Rosa, 2015).

In this era of cross-cultural dietary habits, this fungal ingredient has risen to unprecedented popularity. Gourmets crave its characteristic fungal umami taste while skeptics criticize its nutritional and safety status. Compared to its functional food potential, the investigations done on it are very limited. Only a few reviews have assessed its nutraceutical attributes and associated anti-nutrients. The myco-chemical profile of the smut and yield enhancement by fermentation technology has been reviewed (Valverde et al., 1995). Its functional food prospect has been reviewed (Juárez-Montiel, Ruiloba de León, Chávez-Camarillo, Hernández-Rodríguez, & Villa-Tanaca, 2011). However, since those publications, significant development in knowledge and change in perspective on food consumption has occurred. This review combs through the existing literature and gleans information to present an updated and unbiased account on relevance of corn smut as a functional food. Also,

E-mail address: seemabiotech83@gmail.com.

critical hypotheses have been formulated that might fuel further research on it and prove catalyst in its wider popularity. For holistic purpose, the characteristics of the fungus, biology of plant pathogenesis, and bioactive profile of the smut, yield augmentation techniques, risk assessment, current scenario and future perspectives have been discussed. The topic was capped off with visionary opinions.

2. The fungus

Ustilago is a basidiomycetes fungus genus in the order Ustilaginales and family Ustilaginaceae. The genus name is derived from the Latin term ustilare meaning 'to burn' indicating the black infection it causes (McTaggart, Shivas, Geering, Vánky, & Scharaschkin, 2012). This genus encompasses more than two hundred species of parasitic smuts on monocots, including economically-important crops as barley, oat, wheat, sorghum, maize and sugarcane (Bortfeld, Auffarth, Kahmann, & Basse, 2004; Zhang, Guan, Tao, Ojaghian, & Hyde, 2013). Among all the species in this genus, Ustilago maydis, the causative agent of corn smut is the most-studied. It is conventionally used as a robust fungal pathogenic model to shed light on genetic, physiological, ecological, and phyto-pathological traits (Valverde et al., 1995). Investigation on this fungus has contributed immensely to DNA recombination, signaling and plant-pathogen cross-talk. This is a heterothallic, dimorphic fungus with two distinct phases of life (Bolker, 2001). It alternates between a saprobic budding haploid and an obligate pathogenic filamentous dikaryon (Islamovic et al., 2015). It infects primordia of all aerial parts of maize, causing gall formation (Schilling, Matei, Redkar, Walbot, & Doehlemann, 2014). The morphological distinction between healthy and infected corn cob has been shown in Fig. 1(A) and (B). Inside the tumors, the fungus sporulates, generating blue-black sexual teliospores. These globose, echinulate, thick-walled, melanin-rich resting spores, characteristic of rusts and smuts develop the basidium (Peraza-Reyes & Berteaux-Lecellier, 2013; Smut Fungi of Thailand). In fact, the common name 'smut' is derived from the sooty appearance of the teliospores. These spores are the dispersal agents of the fungus (Donaldson & Saville, 2013). The teliospores germinate to produce sporidia of different mating type that grow saprophytically and multiply mitotically by budding (Wollenberg & Schirawski, 2014). The hyphae and teliospores of *U. maydis* have been shown in Fig. 1(C) and (D). The pathogenic hyphae secrete a large repertoire of effector compounds (more than 500) when coming in contact with the host epidermal cells which suppress host plant immunity (Bielska et al., 2014; Djamei & Kahmann, 2012). The secreted effectors include chorismate mutase (metabolite of the shikimate pathway), sesquiterpenes, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one, Cmu1 (Seedling efficient effector 1), Sho1 (synthetic high osmolarity sensitive), Msb2 (multicopy suppressor of a budding defect), Pep1 (Protein essential during penetration-1), Tin2 (anthocyanin biosynthesis protein), defensins etc. (Djamei & Kahmann, 2012; Hemetsberger, Herrberger, Zechmann, Hillmer, & Doehlemann, 2012: Lanver, Mendoza-Mendoza, Brachmann, & Kahmann, 2010: Redkar, Villajuana-Bonegui, & Doehlemann, 2015; Tanaka et al., 2014). The fungal-upregulated genes include pit1, pit2, cmu1, sho1, msb2, pep1, tin2, Tam, Iad etc. (Cisse et al., 2013; Djamei & Kahmann, 2012; Hemetsberger et al., 2012; Lanver et al., 2014). Subsequent penetration in host tissue and circumvention of host defense involves a multitude of transcriptional regulators (Zahiri, Heimel, Wahl, Rath, & Kämper, 2010). Also, the capacity of the pathogen to modulate the metabolome of infected plant part has been unveiled. Repression of defense signaling pathways, including MAPK-triggered phosphorylation have been detected (Djamei & Kahmann, 2012). The resultant host tissue necrosis is cancelled if the host plant exerts immunity, as revealed from studies in related fungus Ustilago hordei (Ali et al., 2014). The conventional strategies to eradicate the fungal infection such as crop rotation, sanitation, seed treatments, application of foliar fungicides, modification of fertility, and biological controls have not proved completely effective in eradicating this pathogen. Host plant resistance towards *U. maydis* has been recognized as the only safeguard against the pathogenesis. Consequently this fungus is a major impediment in productivity of corn, a major cereal crop worldwide. Annual yield loss due to corn smut accounts to billions of dollars (Chavan & Smith. 2014).

3. Mycochemistry of huitlacoche, food applications and biological roles

It is antithetical that the corn smut which causes colossal economic loss is considered a delicacy. Huitlacoche is considered a gourmet food article in Latin America and parts of the world with people from those region and that ethnicity (Muñoz et al., 2005). Evidences suggest its dietary importance since pre-Hispanic era (María Elena Valverde, Hernández-Pérez, & Paredes-López, 2015). The mushroom-like soft, velvety texture and flavor ranging from sweet, savory, earthy, muddy, and smoky to woody makes huitlacoche prized in culinary circuit.

The few yet important component analysis studies have illuminated on the proximate composition and nutritional relevance of huitlacoche. The predominant myco-chemicals in the smut and their molecular structures have been presented in Fig. 2 (Bolton, Wang, Thiessen, & Bryant, 2008). Huitlacoche has substantial

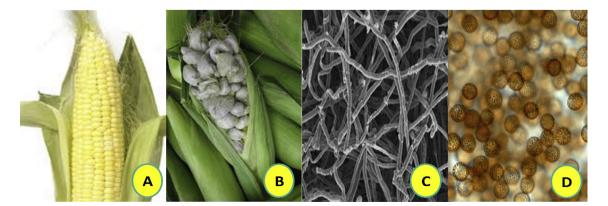


Fig. 1. (A) Healthy corn (B) U. maydis infected corn (C) The hyphae of U. maydis (D) The teliospores of U. maydis (with visible echinulations) (Source: Smut fungi of Thailand).

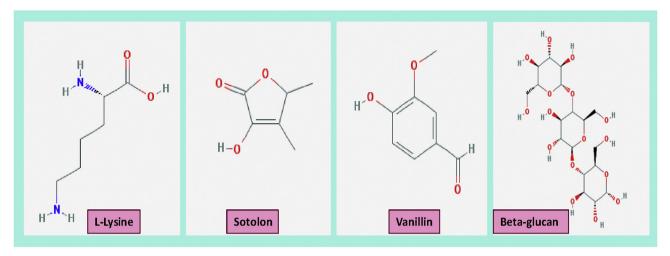


Fig. 2. Molecular structures of dominant bioactive ingredients in corn smut (Source: Pubchem).

amount of crude protein (9.8-11.3% depending on the corn cultivars). Also, the total dietary fiber, β -glucans, and total free sugars were reported to be higher in it than edible mushrooms (Juárez-Montiel et al., 2015; Valdez-Morales et al., 2010). Beta-glucan is a fungal cell wall polysaccharide that plays part in plant pathogenesis (Ruiz-Herrera, Ortiz-Castellanos, Martínez, León-Ramírez, & Sentandreu, 2008). Its synthesis in filamentous fungi occurs at the hyphal tip and at branching points, catalyzed by β -1,3-glucan synthase enzyme (Fesel & Zuccaro, 2016). The characteristics like molecular weight, water solubility, viscosity, and stability of the smut β -glucans are sparsely determined. Though investigation on β -glucans from this smut has been wanting, diversified health importance of β -glucan from fungal and plant origin has been widely reviewed. The β -glucans such as pleuran from Pleurotus, lentinan from Lentinus, grifolan from Grifola frondosa, schizophyllan from Schizophyllum commune, and crestin from Trametes versicolor have been well-investigated (Rop, Mlcek, & Jurikova, 2009). Immunomodulation, anti-diabetic, anticancer and antiobesity roles of this mycelial cell wall component has been validated in myriad in vitro, in vivo and clinical trials (Chen & Raymond, 2008; El Khoury, Cuda, Luhovyy, & Anderson, 2012; Rop et al., 2009).

The proximate protein and fatty acid content of corn smut was measured. Protein content ranged from 10 to 14.5% and fat content from 2.7 to 6.5%. High contents of oleic and linoleic acids was reported (Vanegas, Valverde, Paredes-Lopez, & Pataky, 1995). The direct correlation between higher dietary linoleic acid intake and lower coronary heart disease risk is well-substantiated (Farvid et al., 2014). Quantitative studies have revealed that these corn galls contain much higher amount of lysine, compared to healthy corn. Characterization of corn smut amino acid revealed the predominance of lysine (3.21 mg/g dry weight), followed by glycine, valine, leucine, and glutamic acid. Tryptophan is particularly important as it acts as precursor for indole pigments and indole acetic acid (IAA) formation (Bölker, Basse, & Schirawski, 2008; Jasso-Robles et al., 2016). IAA amplifies auxin levels in the host plant tissues (Maor, Haskin, Levi-Kedmi, & Sharon, 2004; Reineke et al., 2008). U. maydis also produces hormone cytokinins, abscisic acid (ABA), and other growth regulators as polyamines putrescine, spermidine, spermine and thermospermine (Jasso-Robles et al., 2016). Apart from the presence of 14 out of the 20 common amino acids, non-protein amino acids like y-aminobutyric acid (GABA), ornithine, and tricholomic acid were also found. The concentrations of all amino acids ranged between 0.08 and 3.21 mg/g (Lizárraga-Guerra & López, 1996). The fungal α -aminoadipate pathway is implicated for lysine biosynthesis (Fazius, Shelest, Gebhardt, & Brock, 2012; Xu, Andi, Qian, West, & Cook, 2006). Though literature on up-regulation of this pathway does not exist, it could be responsible for lysine accumulation in the galls. Lysine is an essential amino acid and is critical for survival, as its deficiency exacerbates metabolism, leading to mental and physical disabilities (Papes, Surpili, Langone, Trigo, & Arruda, 2001). Genetic engineering approaches to fortify plants with essential amino acids is being considered (Galili & Amir, 2013). In this scenario, tapping the lysine content of huitlacoche appears pragmatic.

Carotenoids are required in human diet for their antioxidant role. Various carotenoids such as β-carotene, lycopene, zeaxanthin, and lutein have been evidenced to avert cancer and ocular disease risks (Johnson, 2002). These terpenoid pigments are produced in fungi to mediate many physiological functions, especially for protection against oxidative stress and visible light or UV irradiation (Avalos & Carmen Limón, 2014). Carotenoid biosynthesis in U. maydis was unraveled to provide the chromophore retinal for photoactive protein opsin (Estrada et al., 2009). Information on carotenoid pigment biosynthesis in this smut is scanty, but parallels can be drawn with other plant pathogen like Taphrina deformans (causing leaf curl diseases). The genes required for the pigment synthesis occur in a cluster, some key members of which code for geranylgeranyl pyrophosphate synthase, lycopene cyclase/phytoene synthase and phytoene dehydrogenase (Cisse et al., 2013). Some fungi such as Cordyceps militaris have been identified as potent source of carotenoids and commercial-scale extraction from them is being considered (Yang, Sun, Lian, Wang, & Dong, 2014). In this context, corn smut carotenoid content is worthy of investigation.

Flavor is an important part of food as it is a decisive factor for consumer acceptance (Loliger, 2000). Umami is a distinct taste associated with several foods, including mushrooms. This taste has strong correlation with food organoleptic properties (Yamaguchi & Ninomiya, 2000). Aroma extract dilution analysis and gas chromatography (GC)-olfactometry head-space analysis of huitlacoche was performed to profile the odorants. The flavor compounds in it were identified as sotolon, hexanal, octanal, decanal, (*E*,*E*)-deca-2,4-dienal, (*E*)-undec-2-enal, and vanillin (Lizárraga-Guerra, Guth, & López, 1997). Sotolon (3-hydroxy-4, 5-dimethyl-2(5H)-furanone) is a chiral furanone common to wide variety of foods like

maple syrup, sake, white wine, and fenugreek. It is known to provide meaty, spicy and nutty aroma to foods (Colin Slaughter, 1999). Sotolon has also been characterized in edible mushroom Lactarius rufus (milkcaps) (Ma, Ruan, & Liu, 2008) as well as Pleurotus sp. (Lizárraga-Guerra et al., 1997). Vanillin is the major component in vanilla, the popular food and pharmaceutical flavor (Sinha, Sharma, & Sharma, 2008). Vanillin synthesis from bioengineered fungi and veasts is being considered (Gallage & Møller, 2015). As for vanillin secretion from U. maydis, it has been discovered to be an intermediate in the lignin biodegradation pathway. Like other wood rot fungi (like Phanerochaete chrysosporium), U. maydis elaborates laccase and tyrosinase enzyme for lignocellulosic biomass degradation (Bianco & Perrotta, 2015; Couturier et al., 2012). As part of lignin catabolism, an array of compounds are produced (such as 4hydroxybenzyl alcohol, phenol, 3-hydroxyanthranilate, 4hydroxybenzoid acid, aniline, acetovanillone, methyl vanillate, syringaldehyde, acetosyringone, and *p*-coumaric acid), along with vanillin (Bianco & Perrotta, 2015; Couturier et al., 2012). It has been found that vanillin production in smut is accompanied by upregulation of citric acid and down-regulation of glyoxylate cycles (Rosa Martha Desentis-Mendoza et al., 2006).

Carbohydrate profiling of the smut revealed the presence of glucose (143.2 mg/g), fructose (71.10 mg/g), glycerol (8.5 mg/g), sorbitol (4.45 mg/g), and mannitol (3.17 mg/g) (Lizarraga-Guerra & Lopez, 1998). Glucose is the major cellular carbohydrate in edible mushroom *Volvariella volvacea* (Diamantopoulou et al., 2012), and medicinal mushroom *Ganoderma lucidum* (Wachtel-Galor, Yuen, Buswell, & Benzie, 2011).

Several pharmacologically-active compounds with anticancer prospects were isolated from the smut. Among them, 4 phenylethyl cinnamides showed cytotoxicity against human leukemic K562/ A02 cell line. These components were N-trans-p-coumaroyltyr-*N-cis-p*-coumaroyltyramine, N-trans-feruloyl-3amine. methoxytyramine and N-cis-feruloyl-3-methoxytyramine. These compounds at 5 µM dose, counteracted multidrug-resistance as determined by 3-(4,5-dimethylthiazol-2-yl)-2,5diphenyltetrazolium bromide (MTT) assay (Wang, Wang, Li, Di, & Lou, 2014). These amine derivatives have been previously studied to possess pharmaceutical properties. N-trans-p-coumaroyltyramine isolated from gooseberry has been verified to inhibit acetyl cholinesterase, cell proliferation and platelet aggregation, and confer antioxidant activity. It is known to bind to the plasma protein human serum albumin (HSA) causing conformational changes of the protein domain, thus affecting its flexibility and leading to high ligand promiscuity (Deeb, Rosales-Hernández, Gómez-Castro, Garduño-Juárez, & Correa-Basurto, 2010; Neelam, Gokara, Sudhamalla, Amooru, & Subramanyam, 2010). It is critical as HSA acts as transporter for many metabolites and drugs, thus a major player in pharmacodynamics and pharmacokinetics (Zhivkova, 2015). Ntrans-p-coumaroyltyramine, N-cis-p-coumaroyltyramine and Ntrans-feruloyltyramine have been validated to possess inhibitory activity against α -glucosidase (Liu, Luo, & Kong, 2011). Alphaglucosidase inhibitors are considered potent therapeutics against type 2 diabetes, as they improve blood glucose homeostasis (Kalra et al., 2013). N-trans-p-coumaroyltyramine and N-trans-feruloyltyramine sourced from Polygonum hyrcanicum (knotweed) has been verified to exert anti-trypanosomal activity (Moradi-Afrapoli et al., 2012). Above findings pave the way for in-depth characterization of corn smut metabolites and their biological pertinence. Also, the antimutagenic activity has been attributed to a suite of secondary metabolite production by the host plant as a defense strategy. The synthesis of sesquiterpenes, phenolic compounds and indoles by vulnerable corn plant to fight fungal invasion have come forth (Valdez-Morales et al., 2010). The major components of the smut and their amounts have been listed in Table 1 (Valverde et al., 2015). The comprehensive account of the bioactive myco-chemicals in *U. maydis* has been reviewed (Bölker et al., 2008).

4. World market and yield enhancement

Corn smut has long been considered a type of blight: however it's potential as an appetizer, food garnish and flavoring condiment has started to be appreciated. High-end restaurants are serving it as a culinary delight (Valverde et al., 2015). Its popularity is catching up in countries like China, Japan, France, Spain and Germany (Valverde et al., 2012). Huitlacoche is sold fresh, frozen or canned in markets of Mexico and other parts of the globe with Mexican communities. An ethnobotanical study conducted in Mexico reflected that in terms of frequency of recognition and edible uses, U. maydis ranks fourth just below Amanita caesarea and Amanita rubescens (Quiñónez-Martínez et al., 2014). Survey indicates that consumers in the United States and Canada are also seeking it. As the sole reliance for this fungal edible is on natural U. maydis infection of corn, the supply is insufficient to keep up with the rising popularity. The skewed supply-demand scenario is leading to exorbitant cost of this fungus (as high as 80z at \$10.00). Trade giants like Amazon and credible food manufacturers like Goya are selling canned huitlacoche. The gourmet truffle Tuber magnatum is also expensive for its meager production compared to requirement (lotti et al., 2014). It necessitates commercial farming of this corn truffle. Consequently, huitlacoche yield enhancement by fermentation is being considered. Fermentation strategy, both solid state (Ren, He, Cheng, & Chang, 2014) and submerged (Vamanu, 2012) has significantly improved mushroom biomass and bioactive production such as exopolysaccharides and intracellular polysaccharides. Even, volatile organic compounds (VOCs) production from truffles has been adjusted with fermentation techniques (Li et al., 2014).

5. Shelf life and safety concern

For edibility, the corn smut needs to be harvested when the gall is young and intact. The stage of development is crucial for optimum taste. Further, the galls are perishable and shelf life is limited. In this regard, the relevance of refrigeration and modified air packaging (MAP) to improve postharvest quality has been investigated. MAP was not that effective in freshness retention but refrigeration enhanced the shelf life up to 30 days (Monroy-Gutiérrez, Valle-Guadarrama, Espinosa-Solares, Martínez-Damián, & Pérez-López, 2013).

Bibliometric search did not result in any significant toxicity incidences causal of huitlacoche consumption. Only sparse precautionary information was obtained. The sensitization of asthmatics and rhinitis patients to some Ustilago species has been documented (Weber & Levetin, 2013). Also, occupational hypersensitivity pneumonitis on exposure to U. esculenta has been reported (Weber & Levetin, 2013). U. maydis alkaloids and the Fusarium mycotoxin fumonisin B1 exerted hepato-, renal-neurotoxicity in rats. The adverse effect was explained to be due to the synergistic interaction of alkaloids with the mycotoxin (Pepeljnjak, Petrik, & Klarić, 2005). Further, disruption of sphingolipid metabolism and resultant disintegration of membrane by the mycotoxin was advocated (Müller, Dekant, & Mally, 2012; Pepeljnjak et al., 2005). Codevelopment of U. maydis with toxic fungi Fusarium needs to be checked as the latter elaborates fumonisin (Chatterjee, Kuang, Splivallo, Chatterjee, & Karlovsky, 2016). Literature on U. maydis alkaloid ustilagine is scanty, but it is similar to the much-studied ergot alkaloid (from Claviceps species). Ergot has dual and antagonizing role of health promotion as well as exacerbation. For its affinity to receptors for biogenic amine neurotransmitters

Table	1
Major	components of corn smut.

Components		Amount	Reference
Protein	Total protein	9.7–16.4%	Valverde et al. 2015
	Lysine	6.3–7.3 g/100 g protein	
	Serine, glycine, aspartic and glutamic acid	44.3–48.9% of total amino acids	
Carbohydrate	Glucose and fructose	81% of total carbohydrates	Valverde et al. 2015
	Glucose	143.2 mg/g	Lizarraga-Guerra & Lopez, 1998
	Fructose	71.10 mg/g	
	Glycerol	8.5 mg/g	
	Sorbitol	4.45 mg/g	
	Mannitol	3.17 mg/g	
	β-glucans	20-120 mg/g	Valverde et al. 2015
Fat	Total fat	2.7-6.5%	Vanegas et al. 1995
	Oleic acid and linoleic acid	54.5–77.5% of total fat	Valverde et al. 2015
Phenolic compounds	Total phenols	636.8-667.4	Valverde et al. 2015
	Gallic acid	2.4-2.6	
	Ferulic acid	514.1-544.2	
	Caffeic acid	26.3-27.4	
	p-Coumaric acid	10.2-10.6	
	o-Coumaric acid	4.4-4.8	
	Rutin	6.2-6.4	
	Catechin	11.0-11.7	
	Quercetin	42.4-45.2	

(serotonin, dopamine, and adrenaline), ergot fungi has neural manipulation properties (Schardl, Panaccione, & Tudzynski, 2006). Also, a peptide ergot alkaloid ergopeptine (such as bromocriptine and ergovaline) acts as vasoconstrictor (Klotz et al., 2007; Schardl et al., 2006).

Corn smut as an edible item is rather new to the USA and European Union (EU), so there are no approvals from Food and Drug Administration (FDA) or European Food Safety Authority (EFSA) yet. The major consumer base encompass Mexico, Latin America and parts of the world with Mexican populace (including San Diego, and Seattle in the USA; Canada; France; Germany etc.) (Jo Feeney et al., 2014). As the consumers comprise a small fraction of global population and the availability of corn smut is confined to limited regions, it has not been evaluated enough for its generally recognized as safe (GRAS)) status. As it comes to public knowledge, interest may spike and food safety authorities will assess its edibility or pharmaceutical prospect.

6. Critical thoughts

Going by the literature and consumer awareness, huitlacoche is obviously an underutilized food. Here, some critical thoughts with potential to fuel nutritional research on this smut have been proposed. Existing literature search did not reveal any toxicity incidences. So, it is probably safe for consumption. Just because Ustilago is a plant pathogen, it does not undermine its candidacy as a functional food source. In fact, many edible and prized mushrooms such as *Laetiporus sulphureus*, *Grifola frondosa*, *Pleurotus ostreatus*, *Inonotus obliquus* and *Armillaria mellea* are plant saprophytes or parasites.

A distinct trait of *U. maydis* infection is the formation of tumors and the induction of anthocyanin pigment production in the host plant tissue (Tanaka et al., 2014). The infected part accumulates anthocyanins as a response to oxidative stress on the host plant, that is assumed to be the reason most galls appear red or blue (Belhadj et al., 2008; He & Giusti, 2010). Anthocyanins are flavonoids encompassing aglycones along with their glycosylated and acylated derivatives (Welch, Wu, & Simon, 2008). These pigments are abundant in fruits and vegetables: in the form of cyanidin, delphinidin, pelargonidin, petunidin, peonidin, malvidin etc. (de Pascual-Teresa, Moreno, & García-Viguera, 2010). Dietary intake of anthocyanins is validated to confer antiinflammatory, anti-carcinogenic, anti-diabetic, anti-obesity and cardioprotective properties (He & Giusti, 2010). From the above reports, it can be suggested that the bluish corn smut galls are abundant in anthocyanins and thus, ideal for consumption. However, sophisticated phytochemical analysis can better illuminate this aspect.

Truffles are prized and expensive foods, for their unique aroma compounds which food connoisseurs depict as seductive and unique (Pacioni, Cerretani, Procida, & Cichelli, 2014; Splivallo, Ottonello, Mello, & Karlovsky, 2011). Headspace solid-phase extraction followed by GC-MS analysis has enabled identification of the contributing aroma compounds. A sulfur compound 3methyl-4,5-dihydrothiophene was detected to be the most dominant fragrance component in *Tuber borchii* (Splivallo & Ebeler, 2015). A recent finding conveys that the captivating aroma of truffles can be due to surface bacterial community. *Tuber borchii* surface colonizing bacteria, mainly α - and β -proteobacteria were implicated to transform non-volatile precursors of truffles into volatile compounds (Splivallo et al., 2014). These exciting assays can be replicated for evaluation of the corn smut VOCs that might augment its food value.

Several fungi are known to elaborate lethal toxins as aflatoxin, fumonisin, citrinin, ochratoxin, patulin and ergot (De Saeger, Audenaert, & Croubels, 2016). Ingestion or exposure to these mycotoxins has adverse health effects. Though no reports of Ustilago mycotoxin exist, it is recommended to confirm its absence by sensitive analyses. Application of sophisticated mass spectrometry (MS) and nuclear magnetic resonance (NMR) techniques are ideal for unbiased targeted as well as untargeted secondary metabolite detection and quantification (Gomez-Casati, Zanor, & Busi, 2013).

The corn smut causes great economic loss to the farmers. But, it is paradoxical that the technically-spoiled crop, values higher than the healthy corn (Wang et al., 2014). So, controlled inoculation of corn crop with the fungus can be tried, for mass production of the smut. Investigating the effect of different *U. maydis* strains on various corn cultivars and subsequent analyses of the chemical makeup of the smut appears interesting. Depending on the result, the best nutritional smut can be selected and further optimized. An artificial inoculation experiment revealed that yield of the smut

was best when corn ears were inoculated 4–8 day after the midsilk growth stage (Pataky & Chandler, 2003). Corn farmers in Brazil, in regions where this infection is endemic are attempting for innovative smut cultivation strategies (Moura, Pedrosa, & Guimarães, 2001). Milpa, a traditional agrosystem prevalent in Mexico centers on co-cultivation of subsistence crops as beans, squash, chile and maize. Huitlacoche production is a part of this cropping system (Huber-Sannwald et al., 2012).

Finally, the averseness towards corn smut as a food article seems to arise from the fact that microfungi are rarely considered edible. Most of the palatable fungi are macrofungi. A plethora of macrofungi is widely consumed as food sources for their flavors, gustatory appeal and nutrients. Agaricus bisporus, Boletus edulis, Volvariella volvacea, Lentinus edodes, Pleurotus spp., Grifola frondosa, and Flammulina velutipes are the valued edible mushrooms (Guo et al., 2012; Suárez Arango & Nieto, 2013; Valverde et al., 2015). Pharmacological aspects such as anticancer, cholesterol lowering, antidiabetic, antiviral, antibacterial and immunomodulation of mushrooms have been an intense area of research since decades, continuing till now (Lindequist, Niedermeyer, & Jülich, 2005; Wu et al., 2014). It explains the rejection of huitlacoche, a microfungus, and a plant tumor on top of it, as a regular food article. However, inclusion of microfungi in food processing is not an unfamiliar concept. Since the dawn of food preservation, microfungi have been harnessed for fermentation. A gamut of culinary delights is prepared by fungal fermentation. Fungal-fermented foods are especially predominant in Asian countries. Food-grade molds such as Aspergillus, Rhizopus, Penicillium, Actinomucor, Saccharomyces, Kluvveromvces, Zvgosaccharomvces, Monascus etc. are used as starters to ferment cereals, pulses, vegetables, meat and fish. Cheese, tempeh, red yeast rice, miso, meju, soy sauce, doenjang, kombucha, sake and palm wine are some of the most popular fungal-fermented foods (Aidoo, Nout, & Sarkar, 2006; Feng, Passoth, Eklund-Jonsson, Alminger, & Schnürer, 2007; Hofrichter, 2011; Kim, Kim, Kwon, Lee, & Hong, 2013). Application of Baker's yeast (Saccharomyces cerevisiae) in dough to produce leavened bread is a global practice (Yeh, Charles, Ho, & Huang, 2009). Apart from the usage as fermentation starters, several molds have nutritional properties. Whole yeast cells as well as phosphorylated protein concentrate have properties like soy protein. Their amino acid contents and digestibility was high, indicating inclusion plausibility in foods as protein source (Yamada & Sgarbieri, 2005). Probiotic importance and gastroenteritis-alleviation property of Saccharomyces cerevisiae var. boulardii is well-established (Hatoum, Labrie, & Fliss, 2012; McFarland, 2010). Kluvveromyces marxianus grown on bovine lactoferrin released peptides with antihypertensive potential, validated from its angiotensin-converting enzyme (ACE)-inhibitory effects (García-Tejedor et al., 2014). Blue mold Penicillium roqueforti is used to ripen cheese, since ages (Nielsen, Dalsgaard, Smedsgaard, & Larsen, 2005). Red yeast rice, the Monascus purpureus-fermented product has been a key ingredient of Chinese traditional medicine and continues to be a popular food garnish (Ma et al., 2000). Several empirical studies have verified its role in cholesterol reduction and blood circulation improvement. In fact, the active ingredient has been characterized as monacolin K, a polyketide (Wang & Lin, 2007). As the standard-of-care (SOC) lovastatin shows adverse effects like myopathy and liver malfunction, consumption of red yeast rice is escalating in popularity (Klimek, Wang, & Ogunkanmi, 2009). Recently, a strain of U. maydis has proven effective in inhibiting wine quality degrading-mold Brettanomyces bruxellensis (Santos, Navascués, Bravo, & Marquina, 2011).

Microbial pathogens are causing immense morbidity and mortality, rendering conventional therapy with antibiotics defunct. In this regard, vaccines are being searched for prophylaxis. *U. maydis* has been genetically engineered to assess expression and immunogenicity of the B subunit of the cholera toxin (secreted by *Vibrio cholerae*) (Juárez-Montiel et al., 2015). Mice immunized with the toxin elicited significant humoral responses, raising the hope that the smut-derived toxin can be used as an oral vaccine (Juárez-Montiel et al., 2015). The above facts support the food prospects of huitlacoche.

Also, aesthetics play big role in consumer desirability. Statistical analysis of head magnetic resonance imaging (MRI) data discloses

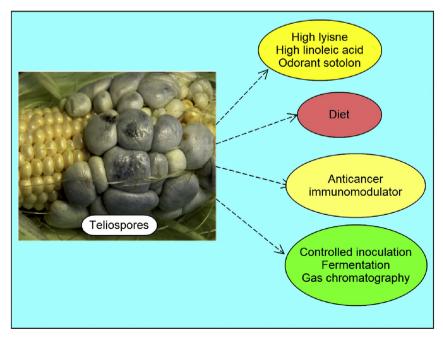


Fig. 3. Huilacoche key components, health impact and scale-up strategies.

that appearance matters in food choices (Van der Laan, De Ridder, Viergever, & Smeets, 2012). Apparently, the unsightly and tumorous smut repels consumers. Though, it encases spores just like truffles do. In the latter however, the spores are hidden beneath a globular chitin and β -1,3-glucan shell (De Bellis et al., 1998). Also, food neophobia, the propensity to decline novel or unknown foods might be the reason in refusal to taste it (Demattè, Endrizzi, & Gasperi, 2014). Further, the name 'huitlacoche' itself meaning 'crow faeces' is not appetizing. The new marketed name 'Mexican truffle' seems a better option to boost sensorial appeal, though the smut (Class Ustilaginomycetes) and true truffle (Class ascomycetes) are phylogenetically distant (Patel, 2012). Also, another name of corn smut 'Aztec caviar' has nothing to do with caviar, the fish eggs. As food insecurity is surfacing, prospecting of nutrient deficiencymitigating, health-promoting food has become the need of the hour (Patel, 2015). The corn smut, rich in essential amino acids and linoleic acids can be an important source of nutrition to vegetarians, like most edible fungi (Ghorai et al., 2009). Huitlacoche is likely to serve as a functional food, given due research attention (Juárez-Montiel et al., 2011). Latin Americans have been consuming it since ages, without any significant health issues (Valverde et al., 1995). So, it is expected to be edible for others as well. However, tolerance to a food item is determined by immune status and genomic makeup of each individuals (Hunter, 2008), so safety needs to be evaluated. Fig. 3 sums up the key nutrients, odorant, food, biological impact and scale-up strategies of corn smut.

7. Conclusion

Clearly, huitlachoche is an underexploited, nourishing food candidate. The nutritional and safety assessment conducted on this smut is surprisingly meager compared to other edible basidiomycetes and ascomycetes. It summons for deeper investigation from multiple perspectives. Among the key aspects, the detailed component profiling using cutting-edge technology, assessing the feasibility of commercial cultivation and nullifying toxicity risks are the top priorities. This review presenting the current level of understanding on corn smut as a functional food article is expected to fast-track further inquisition into it.

Conflicts of interest

The author declares there is no conflict of interest in submission of this manuscript to this journal.

References

- Afonso-Vargas, J., La Serna-Ramos, I., & Arnay-de-la-Rosa, M. (2015). Fungal spores located in 18th century human dental calculi in the church "La Concepción" (Tenerife, Canary Islands). *Journal of Archaeological Science: Reports, 2*, 106–113. http://dx.doi.org/10.1016/j.jasrep.2015.01.003.
- Aidoo, K. E., Nout, M. J. R., & Sarkar, P. K. (2006). Occurrence and function of yeasts in Asian indigenous fermented foods. FEMS Yeast Research, 6(1), 30–39. http:// dx.doi.org/10.1111/j.1567-1364.2005.00015.x.
- Ali, S., Laurie, J. D., Linning, R., Cervantes-Chávez, J. A., Gaudet, D., & Bakkeren, G. (2014). An immunity-triggering effector from the Barley smut fungus Ustilago hordei resides in an Ustilaginaceae-specific cluster bearing signs of transposable element-assisted evolution. *PLoS Pathogens*, 10(7), e1004223. http:// dx.doi.org/10.1371/journal.ppat.1004223.
- Avalos, J., & Carmen Limón, M. (2014). Biological roles of fungal carotenoids. Current Genetics. http://dx.doi.org/10.1007/s00294-014-0454-x.
- Belhadj, A., Telef, N., Saigne, C., Cluzet, S., Barrieu, F., Hamdi, S., et al. (2008). Effect of methyl jasmonate in combination with carbohydrates on gene expression of PR proteins, stilbene and anthocyanin accumulation in grapevine cell cultures. *Plant Physiology and Biochemistry: PPB/Société Française de Physiologie Végétale*, 46(4), 493–499. http://dx.doi.org/10.1016/j.plaphy.2007.12.001.
- Bianco, L., & Perrotta, G. (2015). Methodologies and perspectives of proteomics applied to filamentous fungi: From sample preparation to secretome analysis. *International Journal of Molecular Sciences*, 16(3), 5803–5829. http://dx.doi.org/ 10.3390/ijms16035803.

- Bielska, E., Higuchi, Y., Schuster, M., Steinberg, N., Kilaru, S., Talbot, N. J., et al. (2014). Long-distance endosome trafficking drives fungal effector production during plant infection. *Nature Communications*, 5, 5097. http://dx.doi.org/10.1038/ ncomms6097.
- Bölker, M., Basse, C. W., & Schirawski, J. (2008). Ustilago maydis secondary metabolism—From genomics to biochemistry. *Fungal Genetics and Biology*, 45, S88–S93. http://dx.doi.org/10.1016/j.fgb.2008.05.007.
- Bolker, M. (2001). Ustilago maydis A valuable model system for the study of fungal dimorphism and virulence. *Microbiology*, 147(6), 1395–1401. Retrieved from http://mic.sgmjournals.org/content/147/6/1395.full.
- Bolton, E. E., Wang, Y., Thiessen, P. A., & Bryant, S. H. (2008). Chapter 12 PubChem: Integrated platform of small molecules and biological activities. In *Annual reports in computational chemistry* (Vol. 4, pp. 217–241). http://dx.doi.org/10.1016/ S1574-1400(08)00012-1.
- Bortfeld, M., Auffarth, K., Kahmann, R., & Basse, C. W. (2004). The Ustilago maydis a2 mating-type locus genes lga2 and rga2 compromise pathogenicity in the absence of the mitochondrial p32 family protein Mrb1. *The Plant Cell*, *16*(8), 2233–2248. http://dx.doi.org/10.1105/tpc.104.022657.
- Chatterjee, S., Kuang, Y., Splivallo, R., Chatterjee, P., & Karlovsky, P. (2016). Interactions among filamentous fungi Aspergillus Niger, Fusarium verticillioides and Clonostachys rosea: Fungal biomass, diversity of secreted metabolites and fumonisin production. *BMC Microbiology*, *16*(83). http://dx.doi.org/10.1186/ s12866-016-0698-3.
- Chavan, S., & Smith, S. M. (2014). A rapid and efficient method for assessing pathogenicity of ustilago maydis on maize and teosinte lines. *Journal of Visualized Experiments: JoVE*, 83, e50712. http://dx.doi.org/10.3791/50712.
- Chen, J., & Raymond, K. (2008). Beta-glucans in the treatment of diabetes and associated cardiovascular risks. Vascular Health and Risk Management, 4(6), 1265–1272. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/19337540.
- Cisse, O. H., Almeida, J. M. G. C. F., Fonseca, A., Kumar, A. A., Salojarvi, J., Overmyer, K., et al. (2013). Genome sequencing of the plant pathogen Taphrina deformans, the causal agent of peach leaf curl. *mBio*, 4(3). http://dx.doi.org/10.1128/ mBio.00055-13. e00055-13.
- Colin Slaughter, J. (1999). The naturally occurring furanones: Formation and function from pheromone to food. *Biological Reviews of the Cambridge Philosophical Society*, 74(3), 259–276. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/ 10466251.
- Couturier, M., Navarro, D., Olivé, C., Chevret, D., Haon, M., Favel, A., et al. (2012). Post-genomic analyses of fungal lignocellulosic biomass degradation reveal the unexpected potential of the plant pathogen Ustilago maydis. *BMC Genomics*, 13(1), 57. http://dx.doi.org/10.1186/1471-2164-13-57.
- De Bellis, R., Agostini, D., Piccoli, G., Vallorani, L., Potenza, L., Polidori, E., et al. (1998). The tbf-1 gene from the white truffle Tuber borchii codes for a structural cell wall protein specifically expressed in fruitbody. *Fungal Genetics and Biology: FG & B*, 25(2), 87–99. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/ 9974220.
- de Pascual-Teresa, S., Moreno, D. A., & García-Viguera, C. (2010). Flavanols and anthocyanins in cardiovascular health: A review of current evidence. *International Journal of Molecular Sciences*, 11(4), 1679–1703. http://dx.doi.org/10.3390/ ijms11041679.
- De Saeger, S., Audenaert, K., & Croubels, S. (2016). Report from the 5th international symposium on mycotoxins and toxigenic Moulds: Challenges and perspectives (MYTOX) held in ghent, Belgium, may 2016. *Toxins*, 8(5). http://dx.doi.org/ 10.3390/toxins8050146.
- Deeb, O., Rosales-Hernández, M. C., Gómez-Castro, C., Garduño-Juárez, R., & Correa-Basurto, J. (2010). Exploration of human serum albumin binding sites by docking and molecular dynamics flexible ligand-protein interactions. *Biopolymers*, 93(2), 161–170. http://dx.doi.org/10.1002/bip.21314.
- Demattè, M. L., Endrizzi, I., & Gasperi, F. (2014). Food neophobia and its relation with olfaction. Frontiers in Psychology, 5(127). http://dx.doi.org/10.3389/ fpsyg.2014.00127.
- Desentis-Mendoza, R. M., Hernández-Sánchez, H., Moreno, A., Emilio Rojas del, C., Chel-Guerrero, L., Tamariz, J., & Jaramillo-Flores, M. E. (2006). Enzymatic polymerization of phenolic compounds using laccase and tyrosinase from Ustilago maydis.
- Diamantopoulou, P., Papanikolaou, S., Katsarou, E., Komaitis, M., Aggelis, G., & Philippoussis, A. (2012). Mushroom polysaccharides and lipids synthesized in liquid agitated and static cultures. Part II: Study of Volvariella volvacea. *Applied Biochemistry and Biotechnology*, 167(7), 1890–1906. http://dx.doi.org/10.1007/ s12010-012-9714-8.
- Djamei, A., & Kahmann, R. (2012). Ustilago maydis: Dissecting the molecular interface between pathogen and plant. *PLoS Pathogens*, 8(11), e1002955. http:// dx.doi.org/10.1371/journal.ppat.1002955.
- Donaldson, M. E., & Saville, B. J. (2013). Ustilago maydis natural antisense transcript expression alters mRNA stability and pathogenesis. *Molecular Microbiology*, 89(1), 29–51. http://dx.doi.org/10.1111/mmi.12254.
- El Khoury, D., Cuda, C., Luhovyy, B. L., & Anderson, G. H. (2012). Beta glucan: Health benefits in obesity and metabolic syndrome. *Journal of Nutrition and Metabolism*, 2012, 851362. http://dx.doi.org/10.1155/2012/851362.
- Estrada, A. F., Brefort, T., Mengel, C., Díaz-Sánchez, V., Alder, A., Al-Babili, S., et al. (2009). Ustilago maydis accumulates beta-carotene at levels determined by a retinal-forming carotenoid oxygenase. *Fungal Genetics and Biology: FG & B*, 46(10), 803–813. http://dx.doi.org/10.1016/j.fgb.2009.06.011.
- Farvid, M. S., Ding, M., Pan, A., Sun, Q., Chiuve, S. E., Steffen, L. M., et al. (2014). Dietary linoleic acid and risk of coronary heart disease: A systematic review and

meta-analysis of prospective cohort studies. *Circulation*, 130(18), 1568–1578. http://dx.doi.org/10.1161/CIRCULATIONAHA.114.010236.

- Fazius, F., Shelest, E., Gebhardt, P., & Brock, M. (2012). The fungal α-aminoadipate pathway for lysine biosynthesis requires two enzymes of the aconitase family for the isomerization of homocitrate to homoisocitrate. *Molecular Microbiology*, 86(6), 1508–1530. http://dx.doi.org/10.1111/mmi.12076.
- Feng, X. M., Passoth, V., Eklund-Jonsson, C., Alminger, M. L., & Schnürer, J. (2007). Rhizopus oligosporus and yeast co-cultivation during barley tempeh fermentation-nutritional impact and real-time PCR quantification of fungal growth dynamics. Food Microbiology, 24(4), 393–402. http://dx.doi.org/10.1016/ j.fm.2006.06.007.
- Fesel, P. H., & Zuccaro, A. (2016). β-glucan: Crucial component of the fungal cell wall and elusive MAMP in plants. *Fungal Genetics and Biology*, 90, 53–60. http:// dx.doi.org/10.1016/j.fgb.2015.12.004.
- Galili, G., & Amir, R. (2013). Fortifying plants with the essential amino acids lysine and methionine to improve nutritional quality. *Plant Biotechnology Journal*, 11(2), 211–222. http://dx.doi.org/10.1111/pbi.12025.
- Gallage, N. J., & Møller, B. L. (2015). Vanillin-bioconversion and bioengineering of the most popular plant flavor and its de novo biosynthesis in the vanilla orchid. *Molecular Plant*, 8(1), 40–57. http://dx.doi.org/10.1016/j.molp.2014.11.008.
- Gany, F., Bari, S., Crist, M., Moran, A., Rastogi, N., & Leng, J. (2013). Food insecurity: Limitations of emergency food resources for our patients. *Journal of Urban Health: Bulletin of the New York Academy of Medicine*, 90(3), 552–558. http:// dx.doi.org/10.1007/s11524-012-9750-2.
- García-Tejedor, A., Sánchez-Rivera, L., Castelló-Ruiz, M., Recio, I., Salom, J. B., & Manzanares, P. (2014). Novel antihypertensive lactoferrin-derived peptides produced by Kluyveromyces marxianus: Gastrointestinal stability profile and in vivo angiotensin I-converting enzyme (ACE) inhibition. *Journal of Agricultural and Food Chemistry*, 62(7), 1609–1616. http://dx.doi.org/10.1021/jf4053868.
- Chorai, S., Banik, S. P., Verma, D., Chowdhury, S., Mukherjee, S., & Khowala, S. (2009). Fungal biotechnology in food and feed processing. *Food Research International*, 42(5–6), 577–587. http://dx.doi.org/10.1016/j.foodres.2009.02.019.
- Gomez-Casati, D. F., Zanor, M. I., & Busi, M. V. (2013). Metabolomics in plants and humans: Applications in the prevention and diagnosis of diseases. *BioMed Research International*, 2013, 792527. http://dx.doi.org/10.1155/2013/792527.
- Guo, Y.-J., Deng, G.-F., Xu, X.-R., Wu, S., Li, S., Xia, E.-Q., et al. (2012). Antioxidant capacities, phenolic compounds and polysaccharide contents of 49 edible macro-fungi. *Food & Function*, 3(11), 1195–1205. http://dx.doi.org/10.1039/ c2fo30110e.
- Hatoum, R., Labrie, S., & Fliss, I. (2012). Antimicrobial and probiotic properties of yeasts: From fundamental to novel applications. *Frontiers in Microbiology*, 3(421). http://dx.doi.org/10.3389/fmicb.2012.00421.
- He, J., & Giusti, M. M. (2010). Anthocyanins: Natural colorants with healthpromoting properties. Annual Review of Food Science and Technology, 1, 163–187. http://dx.doi.org/10.1146/annurev.food.080708.100754.
- Hemetsberger, C., Herrberger, C., Zechmann, B., Hillmer, M., & Doehlemann, G. (2012). The Ustilago maydis effector Pep1 suppresses plant immunity by inhibition of host peroxidase activity. *PLoS Pathogens*, 8(5), e1002684. http:// dx.doi.org/10.1371/journal.ppat.1002684.
- Hofrichter, M. (Ed.). (2011). Industrial applications. Berlin, Heidelberg: Springer Berlin Heidelberg. http://dx.doi.org/10.1007/978-3-642-11458-8.
- Huber-Sannwald, E., Palacios, M. R., Moreno, J. T. A., Braasch, M., Peña, R. M. M., de A. Verduzco, J. G., et al. (2012). Navigating challenges and opportunities of land degradation and sustainable livelihood development in dryland socialecological systems: A case study from Mexico. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 367*(1606), 3158–3177. http://dx.doi.org/10.1098/rstb.2011.0349.
- Hunter, P. (2008). We are what we eat. The link between diet, evolution and nongenetic inheritance. *EMBO Reports*, 9(5), 413–415. http://dx.doi.org/10.1038/ embor.2008.61.
- Iotti, M., Leonardi, M., Lancellotti, E., Salerni, E., Oddis, M., Leonardi, P., et al. (2014). Spatio-temporal dynamic of tuber magnatum mycelium in natural truffle grounds. *PloS One*, 9(12), e115921. http://dx.doi.org/10.1371/ journal.pone.0115921.
- Islamovic, É., García-Pedrajas, M. D., Chacko, N., Andrews, D. L., Covert, S. F., & Gold, S. E. (2015). Transcriptome analysis of a ustilago maydis ust1 deletion mutant uncovers involvement of laccase and polyketide synthase genes in spore development. *Molecular Plant-Microbe Interactions: MPMI*, 28(1), 42–54. http://dx.doi.org/10.1094/MPMI-05-14-0133-R.
- Jasso-Robles, F. I., Jiménez-Bremont, J. F., Becerra-Flora, A., Juárez-Montiel, M., Gonzalez, M. E., Pieckenstain, F. L., et al. (2016). Inhibition of polyamine oxidase activity affects tumor development during the maize-Ustilago maydis interaction. *Plant Physiology and Biochemistry*, 102, 115–124. http://dx.doi.org/10.1016/ j.plaphy.2016.02.019.
- Jo Feeney, M., Miller, A. M., & Roupas, P. (2014). Mushrooms-biologically distinct and nutritionally Unique: Exploring a "Third Food Kingdom." Nutrition Today, 49(6), 301–307. http://dx.doi.org/10.1097/NT.00000000000063.
- Johnson, E. J. (2002). The role of carotenoids in human health. Nutrition in Clinical Care: An Official Publication of Tufts University, 5(2), 56–65. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12134711.
- Juárez-Montiel, M., Ruiloba de León, S., Chávez-Camarillo, G., Hernández-Rodríguez, C., & Villa-Tanaca, L (2011). Huitlacoche (corn smut), caused by the phytopathogenic fungus Ustilago maydis, as a functional food. *Revista Iber*oamericana de Micología, 28(2), 69–73. http://dx.doi.org/10.1016/ j.riam.2011.01.001.

- Juárez-Montiel, M., Romero-Maldonado, A., Monreal-Escalante, E., Becerra-Flora, A., Korban, S. S., Rosales-Mendoza, S., et al. (2015). The corn smut ('Huitlacoche') as a new platform for oral vaccines. *PloS One*, 10(7), e0133535. http://dx.doi.org/ 10.1371/journal.pone.0133535.
- Kalra, S., Sahay, R. K., Schnell, O., Sheu, W. H. H., Grzeszczak, W., Watada, H., et al. (2013). Alpha-glucosidase inhibitor, acarbose, improves glycamic control and reduces body weight in type 2 diabetes: Findings on indian patients from the pooled data analysis. *Indian Journal of Endocrinology and Metabolism*, 17(Suppl. 1), S307–S309. http://dx.doi.org/10.4103/2230-8210.119634.
- Kim, D.-H., Kim, S.-H., Kwon, S.-W., Lee, J.-K., & Hong, S.-B. (2013). Mycoflora of soybeans used for meju fermentation. *Mycobiology*, 41(2), 100–107. http:// dx.doi.org/10.5941/MYCO.2013.41.2.100.
- Klimek, M., Wang, S., & Ogunkanmi, A. (2009). Safety and efficacy of red yeast rice (Monascus purpureus) as an alternative therapy for hyperlipidemia. P & T: A Peer-Reviewed Journal for Formulary Management, 34(6), 313–327. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi? artid=2697909&tool=pmcentrez&rendertype=abstract.
- Klotz, J. L., Bush, L. P., Smith, D. L., Shafer, W. D., Smith, L. L., Arrington, B. C., et al. (2007). Ergovaline-induced vasoconstriction in an isolated bovine lateral saphenous vein bioassay. *Journal of Animal Science*, 85(9), 2330–2336. http:// dx.doi.org/10.2527/jas.2006-803.
- Lanver, D., Mendoza-Mendoza, A., Brachmann, A., & Kahmann, R. (2010). Sho1 and Msb2-related proteins regulate appressorium development in the smut fungus Ustilago maydis. *The Plant Cell*, 22(6), 2085–2101. http://dx.doi.org/10.1105/ tpc.109.073734.
- Lanver, D., Berndt, P., Tollot, M., Naik, V., Vranes, M., Warmann, T., et al. (2014). Plant surface cues prime Ustilago maydis for biotrophic development. *PLoS Pathogens*, *10*(7), e1004272. http://dx.doi.org/10.1371/journal.ppat.1004272.
 Li, D.-C., Liu, R.-S., Li, H.-M., Yuan, Z.-P., Chen, T., & Tang, Y.-J. (2014). Ranking the
- Li, D.-C., Liu, R.-S., Li, H.-M., Yuan, Z.-P., Chen, T., & Tang, Y.-J. (2014). Ranking the significance of fermentation conditions on the volatile organic compounds of Tuber melanosporum fermentation system by combination of head-space solid phase microextraction and chromatographic fingerprint similarity analysis. *Bioprocess and Biosystems Engineering*, 37(3), 543–552. http://dx.doi.org/ 10.1007/s00449-013-1021-4.
- Lindequist, U., Niedermeyer, T. H. J., & Jülich, W.-D. (2005). The pharmacological potential of mushrooms. *Evidence-Based Complementary and Alternative Medicine: eCAM*, 2(3), 285–299. http://dx.doi.org/10.1093/ecam/neh107.
- Liu, X., Luo, J., & Kong, L. (2011). Phenylethyl cinnamides as potential alphaglucosidase inhibitors from the roots of Solanum melongena. *Natural Product Communications*, 6(6), 851–853. Retrieved from http://www.ncbi.nlm.nih.gov/ pubmed/21815424.
- Lizárraga-Guerra, R., & López, M. G. (1996). Content of free amino acids in huitlacoche (ustilago maydis). Journal of Agricultural and Food Chemistry, 44(9), 2556–2559. http://dx.doi.org/10.1021/jf960017u.
- Lizarraga-Guerra, R., & Lopez, M. G. (1998). Monosaccharide and alditol contents of huitlacoche (ustilago maydis). Journal of Food Composition and Analysis, 11(4), 333–339. http://dx.doi.org/10.1006/jfca.1998.0597.
- Lizárraga-Guerra, R., Guth, H., & López, M. G. (1997). Identification of the most potent odorants in huitlacoche (ustilago maydis) and austern pilzen (Pleurotus sp.) by aroma extract dilution analysis and static head-space samples. *Journal of Agricultural and Food Chemistry*, 45(4), 1329–1332. http://dx.doi.org/ 10.1021/jf960650f.
- Loliger, J. (2000). Function and importance of glutamate for savory foods. *The Journal of Nutrition*, 130(4S Suppl), 915S–20S. Retrieved from http://www.ncbi. nlm.nih.gov/pubmed/10736352.
- Ma, J., Li, Y., Ye, Q., Li, J., Hua, Y., Ju, D., et al. (2000). Constituents of red yeast rice, a traditional Chinese food and medicine. *Journal of Agricultural and Food Chemistry*, 48(11), 5220–5225. Retrieved from http://www.ncbi.nlm.nih.gov/ pubmed/11087463.
- Ma, B.-J., Ruan, Y., & Liu, J.-K. (2008). Chemical constituents study on the fruiting bodies of Lactarius rufus. *Zhong Yao Cai = Zhongyaocai = Journal of Chinese Medicinal Materials*, 31(2), 233–234. Retrieved from http://www.ncbi.nlm.nih. gov/pubmed/18619269.
- Maor, R., Haskin, S., Levi-Kedmi, H., & Sharon, A. (2004). In planta production of indole-3-acetic acid by Colletotrichum gloeosporioides f. sp. aeschynomene. *Applied and Environmental Microbiology*, 70(3), 1852–1854. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15006816.
- McFarland, L. V. (2010). Systematic review and meta-analysis of Saccharomyces boulardii in adult patients. World Journal of Gastroenterology: WJG, 16(18), 2202–2222. Retrieved from http://www.pubmedcentral.nih.gov/articlerender. fcgi?artid=2868213&tool=pmcentrez&rendertype=abstract.
- McMeekin, D. (1999). Different perceptions of the corn smut fungus. *Mycologist*, 13(4), 180–183. http://dx.doi.org/10.1016/S0269-915X(99)80109-8.
- McTaggart, A. R., Shivas, R. G., Geering, A. D. W., Vánky, K., & Scharaschkin, T. (2012). A review of the Ustilago-Sporisorium-Macalpinomyces complex. *Persoonia*, 29, 55–62. http://dx.doi.org/10.3767/003158512X660283.
- Monroy-Gutiérrez, T., Valle-Guadarrama, S., Espinosa-Solares, T., Martínez-Damián, M. T., & Pérez-López, A. (2013). Effect of microperforation and temperature on quality of modified atmosphere packaged huitlacoche (Ustilago maydis). CyTA - Journal of Food. Retrieved from http://www.tandfonline.com/ doi/abs/10.1080/19476337.2012.755712#.VPIHtfnF_pU.
- Moradi-Afrapoli, F., Yassa, N., Zimmermann, S., Saeidnia, S., Hadjiakhoondia, A., Ebrahimi, S. N., et al. (2012). Cinnamoylphenethyl amides from Polygonum hyrcanicum possess anti-trypanosomal activity. *Natural Product Communications*, 7(6), 753–755. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/

22816300.

- Moura, R. M., Pedrosa, E. M. R., & Guimarães, L. M. P. (2001). A rare syndrome of corn smut. *Fitopatologia Brasileira*, 26(4). http://dx.doi.org/10.1590/S0100-41582001000400021, 782–782.
- Müller, S., Dekant, W., & Mally, A. (2012). Fumonisin B1 and the kidney: Modes of action for renal tumor formation by fumonisin B1 in rodents. *Food and Chemical Toxicology*, 50(10), 3833–3846. http://dx.doi.org/10.1016/j.fct.2012.06.053.
- Munkacsi, A. B., Stoxen, S., & May, G. (2008). Ustilago maydis populations tracked maize through domestication and cultivation in the Americas. *Proceedings Biological Sciences/The Royal Society*, 275(1638), 1037–1046. http://dx.doi.org/ 10.1098/rspb.2007.1636.
- Muñoz, A. H. S., Kubachka, K., Wrobel, K., Corona, F. G., Yathavakilla, S. K. V., Caruso, J. A., et al. (2005). Metallomics approach to trace element analysis in ustilago maydis using cellular fractionation, atomic absorption spectrometry, and size exclusion chromatography with ICP-MS detection. *Journal of Agricultural and Food Chemistry*, 53(13), 5138–5143. http://dx.doi.org/10.1021/ jf0505933.
- Neelam, S., Gokara, M., Sudhamalla, B., Amooru, D. G., & Subramanyam, R. (2010). Interaction studies of coumaroyltyramine with human serum albumin and its biological importance. *The Journal of Physical Chemistry B*, 114(8), 3005–3012. http://dx.doi.org/10.1021/jp910156k.
- Nielsen, K. F., Dalsgaard, P. W., Smedsgaard, J., & Larsen, T. O. (2005). Andrastins A-D, Penicillium roqueforti Metabolites consistently produced in blue-mold-ripened cheese. Journal of Agricultural and Food Chemistry, 53(8), 2908–2913. http:// dx.doi.org/10.1021/jf047983u.
- Pacioni, G., Cerretani, L., Procida, G., & Cichelli, A. (2014). Composition of commercial truffle flavored oils with GC-MS analysis and discrimination with an electronic nose. *Food Chemistry*, 146, 30–35. http://dx.doi.org/10.1016/ j.foodchem.2013.09.016.
- Papes, F., Surpili, M. J., Langone, F., Trigo, J. R., & Arruda, P. (2001). The essential amino acid lysine acts as precursor of glutamate in the mammalian central nervous system. *FEBS Letters*, 488(1–2), 34–38. Retrieved from http://www. ncbi.nlm.nih.gov/pubmed/11163791.
- Pataky, J. K., & Chandler, M. A. (2003). Production of huitlacoche, Ustilago maydis: timing inoculation and controlling pollination. *Mycologia*, 95(6), 1261–1270. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21149027.
- Patel, S. (2012). Food, health and agricultural importance of truffles: A review of current scientific literature. *Current Trends in Biotechnology and Pharmacy*, 6(1), 15–27. Retrieved from http://www.indianjournals.com/ijor.aspx?target=ijor: ctbp&volume=6&issue=1&article=002.
- Patel, S. (2015). Emerging bioresources with nutraceutical and pharmaceutical prospects. Cham: Springer International Publishing. http://dx.doi.org/10.1007/978-3-319-12847-4.
- Pepeljnjak, S., Petrik, J., & Klarić, M. S. (2005). Toxic effects of Ustilago maydis and fumonisin B1 in rats. Acta Pharmaceutica Zagreb, Croatia, 55(4), 339–348. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16375823.
- Peraza-Reyes, L., & Berteaux-Lecellier, V. (2013). Peroxisomes and sexual development in fungi. Frontiers in Physiology, 4(244). http://dx.doi.org/10.3389/ fphys.2013.00244.
- Quiñónez-Martínez, M., Ruan-Soto, F., Aguilar-Moreno, I. E., Garza-Ocañas, F., Lebgue-Keleng, T., Lavín-Murcio, P. A., et al. (2014). Knowledge and use of edible mushrooms in two municipalities of the Sierra Tarahumara, Chihuahua, Mexico. *Journal of Ethnobiology and Ethnomedicine*, 10(67). http://dx.doi.org/10.1186/ 1746-4269-10-67.
- Redkar, A., Villajuana-Bonequi, M., & Doehlemann, G. (2015). Conservation of the Ustilago maydis effector See1 in related smuts. *Plant Signaling & Behavior*, 10(12), e1086855. http://dx.doi.org/10.1080/15592324.2015.1086855.
- Reineke, G., Heinze, B., Schirawski, J., Buettner, H., Kahmann, R., & Basse, C. W. (2008). Indole-3-acetic acid (IAA) biosynthesis in the smut fungus Ustilago maydis and its relevance for increased IAA levels in infected tissue and host tumour formation. *Molecular Plant Pathology*, 9(3), 339–355. http://dx.doi.org/ 10.1111/j.1364-3703.2008.00470.x.
- Ren, X., He, L., Cheng, J., & Chang, J. (2014). Optimization of the solid-state fermentation and properties of a polysaccharide from Paecilomyces cicadae (Miquel) Samson and its antioxidant activities in vitro. *PloS One*, 9(2), e87578. http://dx.doi.org/10.1371/journal.pone.0087578.
- Rop, O., MIcek, J., & Jurikova, T. (2009). Beta-glucans in higher fungi and their health effects. Nutrition Reviews, 67(11), 624–631. http://dx.doi.org/10.1111/j.1753-4887.2009.00230.x.
- Ruiz-Herrera, J., Ortiz-Castellanos, L., Martínez, A. I., León-Ramírez, C., & Sentandreu, R. (2008). Analysis of the proteins involved in the structure and synthesis of the cell wall of Ustilago maydis. *Fungal Genetics and Biology*, 45, S71–S76. http://dx.doi.org/10.1016/j.fgb.2008.04.010.
- Santos, A., Navascués, E., Bravo, E., & Marquina, D. (2011). Ustilago maydis killer toxin as a new tool for the biocontrol of the wine spoilage yeast Brettanomyces bruxellensis. *International Journal of Food Microbiology*, 145(1), 147–154. http:// dx.doi.org/10.1016/j.ijfoodmicro.2010.12.005.
- Schardl, C. L., Panaccione, D. G., & Tudzynski, P. (2006). Ergot alkaloids-biology and molecular biology. *The Alkaloids: Chemistry and Biology*, 63, 45-86. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/17133714.
- Schilling, L., Matei, A., Redkar, A., Walbot, V., & Doehlemann, G. (2014). Virulence of the maize smut Ustilago maydis is shaped by organ-specific effectors. *Molecular Plant Pathology*, 15(8), 780–789. Retrieved from http://www.ncbi.nlm.nih.gov/ pubmed/25346968.
- Sinha, A. K., Sharma, U. K., & Sharma, N. (2008). A comprehensive review on vanilla

flavor: Extraction, isolation and quantification of vanillin and others constituents. *International Journal of Food Sciences and Nutrition*, 59(4), 299–326. http:// dx.doi.org/10.1080/09687630701539350.

- Smut Fungi of Thailand. (n.d.). Retrieved June 24, 2015, from http://collections.daff. qld.gov.au/web/key/thaismutfungi/Media/Html/about.html.
- Splivallo, R., & Ebeler, S. E. (2015). Sulfur volatiles of microbial origin are key contributors to human-sensed truffle aroma. Applied Microbiology and Biotechnology, 99(6), 2583-2592. http://dx.doi.org/10.1007/s00253-014-6360-9.
- Splivallo, R., Ottonello, S., Mello, A., & Karlovsky, P. (2011). Truffle volatiles: From chemical ecology to aroma biosynthesis. *The New Phytologist*, 189(3), 688–699. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21287717.
- Splivallo, R., Deveau, A., Valdez, N., Kirchhoff, N., Frey-Klett, P., & Karlovsky, P. (2014). Bacteria associated with truffle-fruiting bodies contribute to truffle aroma. Environmental Microbiology. http://dx.doi.org/10.1111/1462-2920.12521.
- Suárez Arango, C., & Nieto, I. J. (2013). Biotechnological cultivation of edible macrofungi: An alternative for obtaining nutraceutics. *Revista Iberoamericana de Micología*, 30(1), 1–8. http://dx.doi.org/10.1016/j.riam.2012.03.011.
- Tanaka, S., Brefort, T., Neidig, N., Djamei, A., Kahnt, J., Vermerris, W., et al. (2014). A secreted Ustilago maydis effector promotes virulence by targeting anthocyanin biosynthesis in maize. *eLife*, 3, e01355. http://dx.doi.org/10.7554/ eLife.01355.
- Valdez-Morales, M., Barry, K., Fahey, G. C., Jr., Domínguez, J., de Mejia, E. G., Valverde, M. E., et al. (2010). Effect of maize genotype, developmental stage, and cooking process on the nutraceutical potential of huitlacoche (Ustilago maydis). *Food Chemistry*, 119(2), 689–697. http://dx.doi.org/10.1016/ i.foodchem.2009.07.015.
- Valverde, M. E., Paredes-López, O., Pataky, J. K., & Guevara-Lara, F. (1995). Huitlacoche (Ustilago maydis) as a food source–biology, composition, and production. Critical Reviews in Food Science and Nutrition, 35(3), 191–229. http:// dx.doi.org/10.1080/10408/39509522699.
- Valverde, M. E., Hernández-Pérez, T., & Paredes-Lopez, O. (2012). Hispanic Foods: Chemistry and bioactive compounds. In M. H. Tunick, & E. González de Mejía (Eds.) (Vol. 1109). Washington, DC: American Chemical Society. http:// dx.doi.org/10.1021/bk-2012-1109.
- Valverde, M. E., Hernández-Pérez, T., & Paredes-López, O. (2015). Edible mushrooms: Improving human health and promoting quality life. *International Journal of Microbiology*, 2015. http://dx.doi.org/10.1155/2015/376387, 376387.
- Vamanu, E. (2012). Biological activities of the polysaccharides produced in submerged culture of two edible Pleurotus ostreatus mushrooms. *Journal of Biomedicine & Biotechnology*, 2012. http://dx.doi.org/10.1155/2012/565974, 565974.
- Van der Laan, L. N., De Ridder, D. T. D., Viergever, M. A., & Smeets, P. A. M. (2012). Appearance matters: Neural correlates of food choice and packaging aesthetics. *PloS One*, 7(7), e41738. http://dx.doi.org/10.1371/journal.pone.0041738.
- Vanegas, P. E., Valverde, M. E., Paredes-Lopez, O., & Pataky, J. K. (1995). Production of the edible fungus huitlacoche (Ustilago maydis): Effect of maize genotype on chemical composition. *Journal of Fermentation and Bioengineering*, 80(1), 104–106. http://dx.doi.org/10.1016/0922-338X(95)98187-P.
- Wachtel-Galor, S., Yuen, J., Buswell, J. A., & Benzie, I. F. F. (2011). Ganoderma lucidum (Lingzhi or Reishi). CRC Press. Retrieved from http://www.ncbi.nlm.nih.gov/ books/NBK92757/.
- Wang, T.-H., & Lin, T.-F. (2007). Monascus rice products. Advances in Food and Nutrition Research, 53, 123–159. http://dx.doi.org/10.1016/S1043-4526(07) 53004-4.
- Wang, S.-Q., Wang, X.-N., Li, Y.-Y., Di, X.-X., & Lou, H.-X. (2014). Identification of purine-derived compounds, ustilagomaydisin A–C, from the plant pathogen Ustilago maydis and their modulating effects on multidrug-resistant (MDR) tumors. *Phytochemistry Letters*, 10, 193–197. http://dx.doi.org/10.1016/ j.phytol.2014.09.006.
- Weber, R. W., & Levetin, E. (2013). Allergen of the month-Ustilago maydis. Annals of Allergy, Asthma & Immunology: Official Publication of the American College of Allergy, Asthma, & Immunology, 111(6), A13. http://dx.doi.org/10.1016/ j.anai.2013.10.017.
- Welch, C. R., Wu, Q., & Simon, J. E. (2008). Recent advances in anthocyanin analysis and characterization. *Current Analytical Chemistry*, 4(2), 75–101. http:// dx.doi.org/10.2174/157341108784587795.
- Wollenberg, T., & Schirawski, J. (2014). Comparative genomics of plant fungal pathogens: The ustilago-sporisorium paradigm. *PLoS Pathogens*, 10(7), e1004218. http://dx.doi.org/10.1371/journal.ppat.1004218.
- Wu, H.-T., Lu, F.-H., Su, Y.-C., Ou, H.-Y., Hung, H.-C., Wu, J.-S., et al. (2014). In vivo and in vitro anti-tumor effects of fungal extracts. *Molecules (Basel, Switzerland)*, 19(2), 2546–2556. http://dx.doi.org/10.3390/molecules19022546.
- Xu, H., Andi, B., Qian, J., West, A. H., & Cook, P. F. (2006). The alpha-aminoadipate pathway for lysine biosynthesis in fungi. *Cell Biochemistry and Biophysics*, 46(1), 43–64. http://dx.doi.org/10.1385/CBB:46:1:43.
- Yamada, E. A., & Sgarbieri, V. C. (2005). Yeast (Saccharomyces cerevisiae) protein concentrate: Preparation, chemical composition, and nutritional and functional properties. *Journal of Agricultural and Food Chemistry*, 53(10), 3931–3936. http://dx.doi.org/10.1021/jf0400821.
- Yamaguchi, S., & Ninomiya, K. (2000). Umami and food palatability. *The Journal of Nutrition*, 130(4S Suppl), 921S–6S. Retrieved from http://www.ncbi.nlm.nih. gov/pubmed/10736353.
- Yang, T., Sun, J., Lian, T., Wang, W., & Dong, C.-H. (2014). Process optimization for extraction of carotenoids from medicinal caterpillar fungus, Cordyceps militaris (Ascomycetes). International Journal of Medicinal Mushrooms, 16(2), 125–135.

- Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/24941034. Yeh, L.-T., Charles, A. L., Ho, C.-T., & Huang, T.-C. (2009). A novel bread making process using salt-stressed Baker's yeast. *Journal of Food Science*, 74(9), S399–S402. http://dx.doi.org/10.1111/j.1750-3841.2009.01337.x.
- Zahiri, A., Heimel, K., Wahl, R., Rath, M., & Kämper, J. (2010). The Ustilago maydis forkhead transcription factor Fox1 is involved in the regulation of genes required for the attenuation of plant defenses during pathogenic development. Molecular Plant-Microbe Interactions: MPMI, 23(9), 1118–1129. http://dx.doi.org/

- 10.1094/MPMI-23-9-1118. Zhang, J., Guan, P., Tao, G., Ojaghian, M. R., & Hyde, K. D. (2013). Ultrastructure and phylogeny of Ustilago coicis. *Journal of Zhejiang University Science B*, 14(4), 336–345. http://dx.doi.org/10.1631/jzus.B1200239.
- Zhivkova, Z. D. (2015). Studies on drug-human serum albumin binding: The current state of the matter. Current Pharmaceutical Design, 21(14), 1817–1830. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/25732557.