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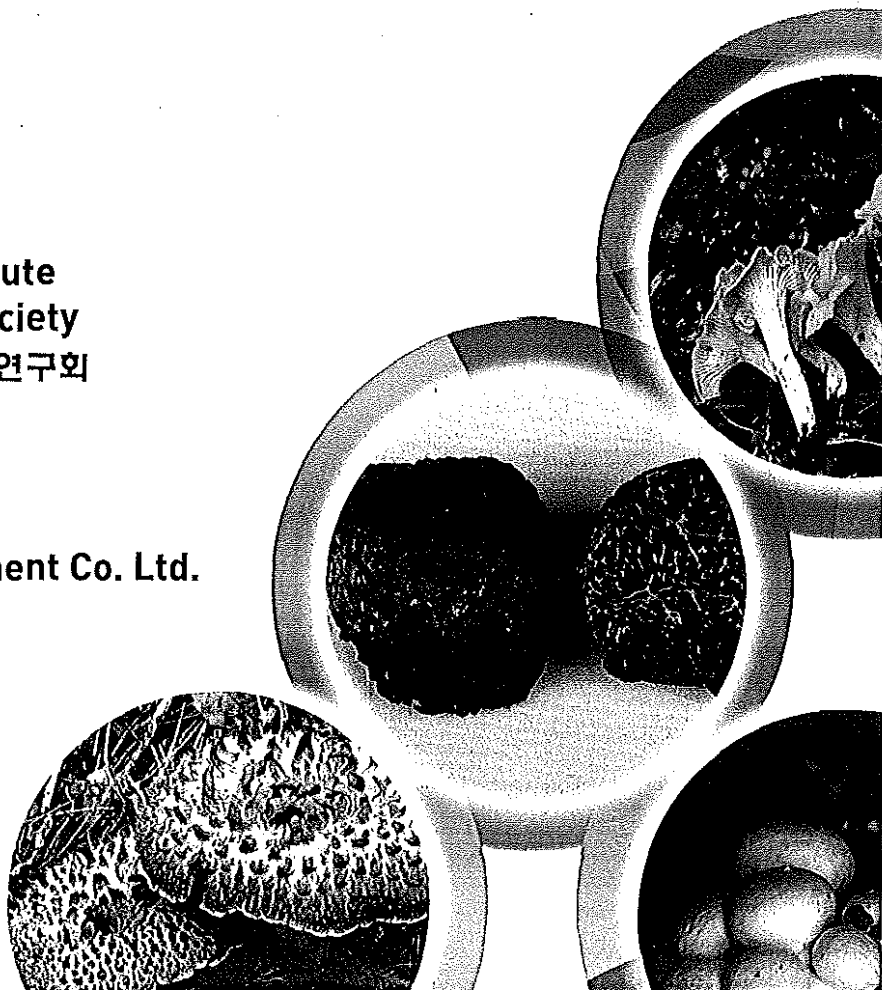
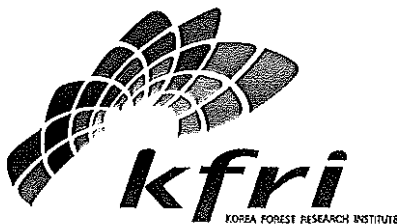
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# Truffle cultivation and commercially harvested native truffles

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## Abstract

Truffles (true and false) are fruiting bodies of ectomycorrhizal fungi and some of them produce appealing aromas, are recreationally and commercially harvested, and even cultivated. Until recently, commercial truffles have all been Mediterranean in distribution but some of these species are now cultivated around the world and other native species are being collected and marketed. While cultivation of black truffles can be complicated by horticultural challenges, production of other species appears to be less problematic. The potential for the discovery and commercialization of novel native truffles is good, but only if trained dogs are used for exploration and harvesting can this potential be sustainably and ethically realized.

## Introduction

Around the world, truffles are harvested primarily because of their enticing aromas. They are generally considered as a delicacy and a luxury. All truffles (true and false) are the fruiting bodies of ectomycorrhizal fungi and therefore are associated with living host plants, usually trees or shrubs. In Europe, most commercial truffles are members of the genus *Tuber* but in dry ecosystems of Africa other genera dominate, e.g. *Terfezia* and *Tirmania*.

Because of their ectomycorrhizal nature, some truffles can be cultivated in orchards with their plant hosts. Both wild-harvested and cultivated truffles are highly sought-after and some species command extraordinary prices; Hall et al. (2007) quote retail prices in 2005 for Italian white truffle (*Tuber magnatum*) of up to €6,000 per kilogram and for Périgord black truffle (*Tuber melanosporum*) of €3,000. Market prices taken from Bonito et al. (2013) indicate that prices per kilogram in 2009 in the USA ranged from \$110 USD for *Tuber indicum* to \$5060 for *Tuber magnatum* (Table 1). Charity auctions in Alba, northern Italy, often catch media interest as prices paid for Italian white truffles can be astronomical. In 2010, for instance, a giant (900 gm) white truffle was sold to Jeannie Cho Lee, a South Korean wine critic living in Hong Kong, for \$144,000.

These high prices make the prospect of cultivating truffles very attractive and have led to a great deal of research and development in the truffle industry globally. Unfortunately, the hope of big financial returns has also fostered an air of secrecy and even deception in parts of the truffle industry. Despite some highly rewarding success stories in truffle cultivation, many truffle orchards fail to produce commercial amounts of truffles for a variety of reasons, some of which will be mentioned below.

**Table 1.** Economically important truffle species determined by market prices (USD).  
Adapted from Table S2 in Bonito et al. 2013 and from Morte et al. 2012.

Species	Market price per kg	Source
<i>Tuber indicum</i>	\$110	Asia
<i>Tuber canaliculatum</i>	\$220	North America
<i>Tuber gibbosum</i>	\$220	North America
<i>Tuber lyonii</i>	\$220	North America
<i>Tuber oregonense</i>	\$220	North America
<i>Tuber borchii</i>	\$440	Europe
<i>Tuber brumale</i>	\$660	Europe
<i>Tuber macrosporum</i>	\$660	Europe
<i>Tuber melanosporum</i>	\$1760	Europe
<i>Tuber magnatum</i>	\$5060	Europe
Desert truffles*	\$26 - \$330	Europe, Africa

\*from Morte et al. 2012.

## Truffles and false truffles

True truffles are ascomycetes, primarily in the genus *Tuber*, and false truffles are basidiomycetes; the majority of commercial truffles are members of the genus *Tuber*. Bonito et al (2010a) predicted that global *Tuber* species richness would be a minimum of 180–230 species based on their meta-analysis of *Tuber* ITS rDNA sequences. Because of small size, disagreeable odor, or rarity, not all species of *Tuber* are considered desirable for personal or commercial harvest. Among the approximately 350 hypogeous fungi in the Pacific Northwest region of USA including true truffles and false truffles (Trappe et al. 2009), only a small handful of species are considered edible and choice. In their comprehensive treatment of truffles and truffle cultivation, Hall et al. (2007) outline the 30 or so truffle and false truffle species of commercial importance globally.

The commercially important Mediterranean true truffles include some species that are now cultivated well outside of their native ranges: Périgord black truffle (*Tuber melanosporum*), summer truffle (*Tuber aestivum*), and bianchetto (*Tuber borchii*). In China, a number of truffle species are harvested; among them *Tuber indicum* is the most important. Growing interest in native truffles in North America has provided a market for Oregon white truffles (primarily *Tuber gibbosum* and *Tuber oregonense*) and the pecan truffle (*Tuber lyonii*).

In dry ecosystems of the Carpathian Basin, Middle East, Mediterranean Basin, and North Africa, other hypogeous ascomycetes are harvested including *Mattirolomyces terfezioides*, *Terfezia arenaria*, *Kalaharituber pfeilii*, *Tirmania nivea*, *Delastria rosea*, and *Picoa lefebvrei* (Hall et al. 2007). Desert truffles tend not to have the pungent aromas of *Tuber* species so rather than being harvested with the help of trained dogs, the characteristic cracks that form in the soil directly above them are recognized by experienced harvesters. Considered a treat by some, desert truffles have also traditionally supplied much needed nutrition to people living in harsh, arid environments.

Among the false truffles, *Rhizopogon luteolus*, *R. piceus* and *R. roseolus* ( $\equiv$  *R. rubescens*) are considered edible (Boa 2004), and in New Zealand *R. roseolus* is being cultivated (Visnovsky et al. 2010).

## Commercially harvested wild truffles

Europe is home to a number of commercially import truffle species (Hall et al. 2007). In the black truffle group are *Tuber melanosporum*, *Tuber aestivum*, *Tuber brumale*, *T. mesentericum*, and *T. macrosporum*. The white truffles include *Tuber magnatum*, *T. borchii*, and *T. dryophilum*. To the real truffle connoisseur who knows where and when to look, many more species are available and Alessandra Zambonelli (personal communication, 2011) can enjoy truffles every weekend of the year that are wild-harvested within reasonable driving distance of her home.

Commercial Asian truffles of the black truffle group are still somewhat in taxonomic flux (Zhang et al. 2005, Wang et al. 2006, Bonito et al. 2010a) but *Tuber indicum* is thought to be the most important species (Hall et al. 2007). Shin et al. (1995) reported finding *Tuber aestivum* in Gyerong-san National Park, South Korea, under *Quercus*, but re-examination of this collection using molecular techniques is warranted given the current state of taxonomic flux. There has been a recent proliferation of new *Tuber* species descriptions from China (Fan and Cao 2012, Fan et al. 2011a, Fan et al. 2011b, Fan et al. 2012, Zhang et al. 2012), so it seems reasonable to anticipate that the hypogeous fungi of Asia are much more diverse than it may currently appear (Wang 2012). How many of them will appeal to the palate remains to be seen.

White truffles, black truffles (*Leucangium carthusianum*), and brown truffles (*Kalapuya brunnea*) are commercially harvested from the wild on the west coast of North America. Although all of these commercial truffles fruit in young Douglas-fir (*Pseudotsuga menziesii*) stands, the Oregon white truffles in particular fruit abundantly in over-grown Douglas-fir Christmas tree farms that were planted in agricultural fields adjacent to native Douglas-fir forests (Pilz et al. 2009). Although nursery inoculations of Douglas-fir with *Tuber oregonense*, *T. gibbosum*, and *L. carthusianum* have resulted in well-colonized seedlings (Lefevre 2012), attempts to establish orchards have been limited by the cost of nursery production. According to Lefevre (2012), three eastern North American species have commercial potential: *Tuber lyonii*, *Tuber canaliculatum*, and *Imaia gigantea*. *Tuber lyonii*, the pecan truffle, is harvested from native forests but also from orchards of *Carya illinoensis* where it seems to thrive under the conditions of irrigation, fertilization and chemical weed control practiced in pecan production. *Tuber canaliculatum* and *Imaia gigantea* are known to have good culinary attributes but are relatively seldom encountered in the wild and not yet cultivated.



Desert truffles have a long history of use in many arid and semi-arid parts of the Mediterranean basin and Africa (Morte et al. 2012). In contrast to the other truffles which primarily associate with trees and some shrubs, desert truffles form mycorrhizas with members of the Cistaceae including both perennial and annual *Helianthemum* species.

## Cultivated truffles

*Tuber melanosporum* is now cultivated in all of the continents with arable land including throughout Europe (Hall et al. 2007); Africa (Morocco, Abdelaziz Laqbaqbi, personal communication, 2011); Asia (China, Wang and Hall 2004); Australia (Australia and New Zealand, Hall et al. 2007); North America (USA, Lefevre 2012); and South America (Chile, Cordero et al. 2011). *Tuber aestivum* and *Tuber borchii* are also now widely cultivated and 'superb' bianchetto truffles are being harvested in a trial plantation in New Zealand (Alexis Guerin-Laguet, Plant and Food Research, personal communication, July 2013). These two species have broad host ranges, wide ecological tolerance, and established markets (Benucci et al. 2012). However, despite repeated attempts, the most highly priced truffle, *Tuber magnatum* or the Italian white truffle, has not yet been produced in cultivation. Cultivation of these Mediterranean *Tuber* species usually involves establishment of orchards of truffle-inoculated oak (*Quercus*) or hazelnut (*Corylus*) trees.

Since 1999, *Terfezia clavayi* has been cultivated in Spain, Israel, Abu Dhabi and Argentina on a variety of *Helianthemum* species (Morte et al. 2012) and recently the cultivation of *Terfezia boudieri* on *Helianthemum sessiliflorum* in Tunisia has been reported (Slama et al. 2010).

*Rhizopogon roseolus* (synonym *Rhizopogon rubescens* Tul.) or shoro has been cultivated on *Pinus radiata* in New Zealand for the Japanese shoro market (Wang et al. 2012). Visnovsky et al. (2010) reported that the shoro crop from New Zealand was "deemed unsuitable due to consumer sensitivity in Japan to the origin of the products and doubts surrounding the authenticity of the fruiting bodies as Japanese shoro". They determined that shoro produced in New Zealand was more closely related to collections from North America than it is to shoro from Japan, a finding that is consistent with the originally incidental and later intentional introduction of *Rhizopogon roseolus* to New Zealand for the cultivation of *Pinus radiata*. Now however, Japanese isolates of this fungus are being

cultivated in New Zealand and they may prove to be more acceptable to the Japanese market (Alexis Guerin-Laguette, Plant and Food Research, personal communication, July 2013).

## **Recent achievements in truffle cultivation in North America**

Périgord black truffles have been harvested from truffle orchards in California, North Carolina, and Tennessee (USA) for a number of years although the amount of commercial product is still quite limited. A truffière in the Willamette Valley recently provided Oregon's first Périgord black truffles

(<http://www.truffletree.com/first-cultivated-french-black-truffle-found-in-oregons-willamette-valley/>).

Three Périgord black truffles were harvested by trained dog from a truffle orchard in the Lower Fraser Valley in Abbotsford, British Columbia, Canada in March 2013 (<http://www.bctruffles.ca/Home/NewsDetail/26>). These truffles represent the first independently-confirmed production in a truffle orchard in Canada.

In February of 2012, North America's first bianchetto truffles were harvested in Idaho, USA (<http://www.truffletree.com/new-idaho-tuber/>).

## **Challenges**

The major challenge is that despite a global effort to establish truffle orchards over the past few decades, truffle production continues to decline and Hall et al. (2007) provided an array of reasons why many truffle orchards fail to produce. The original motivation for establishing a truffle orchard for many is not actually to produce truffles, though that would be a pleasant bonus, but to take advantage of tax breaks and grants or to skirt around regulations intended to protect agricultural land from development. Many truffières are established under sub-optimal conditions of climate, soil, or plant/fungus quality and many are not properly managed after establishment.

Cultivating exotic species in novel environments creates the risk that exotic species may invade native ecosystems and cause problems. There are many examples of this happening



when plants (e.g. trees and shrubs, Richardson and Rejmánek 2011) and animals (Jeschke and Strayer 2005) are purposefully introduced; problems created by non-native fungi are often the result of accidental rather than intentional introductions, e.g. *Ophiostoma novo-ulmai* (Dutch elm disease, Temple et al. 2006) and *Amanita phalloides* (death cap mushroom, Pringle et al. 2009) in North America. Truffles such as *Rhizopogon* species were inadvertently introduced into New Zealand on the roots of *Pinus radiata* seedlings (Visnovsky et al. 2010) decades before they were intentionally cultivated there.

With the intentional introduction of high value truffle species into novel ecosystems comes the possibility, perhaps even likelihood, of unintended introduction of other truffle species. Within the black truffle group, *Tuber melanosporum* has the greatest commercial value which makes it the species most often introduced, however, other lower value but morphologically similar black truffle species such as *Tuber brumale* and *Tuber indicum* have been reported from Périgord black truffle orchards in Australia, Italy, New Zealand, and United States of America (USA) (respectively, Linde and Selmes 2012, Murat et al. 2008, Ho et al. 2008, Bonito et al 2010b), presumably as a result of mistaken inclusion of these species in the sporocarp-based inoculant used in commercial nurseries to produce truffle-colonized seedlings for out-planting in truffle orchards. In fact, Bonito et al (2010a) have provided evidence suggesting the presumably accidental introduction of many other truffles species (*T. foetidum*, *T. menseri*, *T. rapaeodorum*, *T. levissimum*, *T. maculatum*, *T. rufum*, *T. seperans*, *T. californicum*, as well as a number of un-named *Tuber* species) among Europe, North America, New Zealand, and Argentina.

While import regulations may be intended to assure the quality and identity of truffle products, in reality it would be impossible to stop the movement of undesirable or prohibited truffle species. Collections of Périgord black truffles being imported into the USA, for instance, have been found to contain other black truffle species (Jim Trappe and Charles Lefevre, personal communications 2012). Border agents cannot be expected to be able to identify truffle species when truffle exporters, who should be able to do so, clearly make mistakes. Murat et al. (2008) reported that a specific regulation established in 1985 and modified in 1991 prohibits the importation of *Tuber indicum* into Italy; sadly, that regulation failed to keep it out of a *Tuber melanosporum* orchard. Similarly, New Zealand's biosecurity standard for importation of fresh or frozen truffles (New Zealand Ministry of Agriculture and Forestry 1993, amended 2011) permits the importation of four species only (*Tuber aestivum*, *T. borchii*, *T. magnatum*, and *T. melanosporum*). When *Tuber brumale* was detected in a quarantine facility in New Zealand in 2006, an eradication

program was launched; when *T. brumale* was subsequently found on the roots of trees planted much earlier, the program was terminated (Ho et al. 2008).

Seedlings in commercial nurseries are inoculated with slurries (Hall and Zambonelli 2012). These slurries are often made from truffles with imperfections that make them more affordable than marketplace specimens and from pieces of truffles. It is both difficult and time consuming to distinguish among similar truffle species by examining whole truffles or pieces of truffle that are imported as inoculum. Truffle experts now rely on DNA sequencing to confirm the identity of truffles. Truffle exporters with the very best of intentions cannot DNA sequence every piece of truffle that is exported; truffle exporters who are seduced by the possibility of making even more profit by substituting low value for high value truffle species might slip a few *Tuber brumale* or *Tuber indicum* into a shipment purported to be pure *Tuber melanosporum*. Reputable commercial growers of inoculated seedlings are obliged to DNA check each and every truffle or piece of truffle used as inoculant and to record to which inoculant lot each seedling belongs so that any contamination can be traced from source to shipment to orchard. If even a tiny shard of low value truffle makes it through the checking process, the mature spores in it could contaminate an entire lot of host tree seedlings.

Other quality control criteria include the extent of colonization by the desired truffle species, the absence or minimization of colonization by undesired ECM fungi, size and vigour of the seedling (Bonet et al. 2009, Fischer and Colinas 1996), and in North America the resistance of the *Corylus avellana* variety to a fungal blight *Anisogramma anomala*. In Europe, growers are discouraged from planting *Corylus avellana* not because of this blight fungus but because hazelnut is more likely to host *Tuber brumale* than are oaks.

On the surface, it seems that another approach to quality control would be to set criteria for commercial nurseries. Italy, France and Spain all have protocols for certification of truffle-inoculated nursery trees and the Australian Truffle Growers Association is considering a similar approach (Carter 2011). All of these approaches raise the bar by demanding conscious commitment to high quality but not all ECM tips or all seedlings from a nursery can be examined before shipment so the possibility of contamination, even if very low, will always exist.

Truffles are traditionally harvested using a trained dog or a pig because these animals have keen noses and will mark only mature truffles with good commercial value. In China, much of the truffle harvest is raked and this may have lead to a decline in

volume harvested over the years. According to Murat et al. (2008), before 1993 over 20 tons of *Tuber indicum* were harvested in Huidong County alone while in 2003 less than 5 tons were harvested from the same area. In the Pacific Northwest, USA, truffles were for awhile harvested almost exclusively by people with rakes which led to the collection of many immature truffles with poor aroma that sold for rather low prices (Lefevre 2010); education and proper training have contributed to the increase in the number of Oregon white, black and brown truffles that are now dog-harvested.

## Opportunities

While cultivation of *Tuber melanosporum* seems fraught with difficulties related to contamination of truffières by morphologically-similar but lower-value species, cultivation of *Tuber aestivum* and *Tuber borchii* appears to be more promising. Although the potential returns are lower when compared to successful cultivation of *Tuber melanosporum*, many growers may prefer the lower risk associated with summer truffle and bianchetto.

The imposition of proper harvesting techniques using trained dogs in North America (Lefevre 2012) and China (Wang 2012) will without a doubt improve the quality and thereby the value of their native truffles.

Because they will help ensure that mature truffles are found and available to truffle taxonomists, trained truffle dogs will also be very useful in expanding what we know of the truffle mycota of the parts of the world where little is currently known. The systematic application of DNA techniques to truffle taxonomy in combination with more traditional morphological approaches will guarantee that the new species being found can be integrated into our global knowledge of these fungi.

Additionally, phylogenetic analysis could be used to assess the potential edibility and commercial potential of new species being found. Wang (2012) points out that two Chinese truffle species could have commercial potential because they are closely related to *Tuber borchii*.

The native Oregon truffle industry developed in part because the truffles of Oregon have been extensively collected and studied by Dr. Jim Trappe, his students, and by members of the North American Truffling Society (NATS). By organizing regular truffle forays, producing guidelines to protect the truffle environment and minimize harvest of immature truffles, promoting truffle dog training, and closely collaborating with truffle

taxonomists, NATS has fulfilled its mission “to enhance the scientific knowledge of North American truffles and truffle-like fungi”. Application of this model elsewhere would do a lot to improve our knowledge of truffles. Whether we have enough truffle taxonomists or jobs for students of truffle taxonomy to support local truffling groups is a question that remains to be addressed.

## References

- Benucci, G.M.N., G. Bonito, L.B. Falini, M. Bencivenga, and D. Donnini. 2012. Truffles, timber, food, and fuel: sustainable approaches for multi-cropping truffles and economically important plants. Chapter 15 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. *Soil Biology* 34: 265-280.
- Boa, E. 2004. Wild edible fungi. A global overview of their use and importance to people. Food and Agriculture Organization of the United Nations, Non-Wood Forest Products 17, Rome. 147 pp.
- Bonet, J.A., D. Oliach, C. Fischer, A. Olivera, J. Martinez de Aragon, and C. Colinas. 2009. Cultivation methods of the black truffle, the most profitable non-wood forest product; a state of the art review. In *Modelling, valuing, and managing Mediterranean forest ecosystems for non-timber goods and services*. Edited by M. Palahi, Y. Birot, F. Bravo, and E. Gorriz. *EFI Proceedings No 57*; 57-71.
- Bonito, G.M., A.I.P. Gryganskyi, J.M. Trappe, and R. Vilgalys. 2010a. A global meta-analysis of *Tuber* ITS rDNA sequences: species diversity, host associations and long-distance dispersal. *Molecular Ecology* 19: 4994-5008.
- Bonito, G., J.M. Trappe, S. Donovan, and R. Vilgalys. 2010b. The Asian black truffle *Tuber indicum* can form ectomycorrhizas with North American host plants and complete its life cycle in non-native soils. *Fungal Ecology* 4(1): 83-93.
- Bonito, G., M.E. Smith, M. Nowak, R.A. Healy, G. Guevara, E. Cazares, A. Kinoshita, D.R. Nouhra, L.S. Dominguez, L. Tedersoo, C. Murat, Y. Wang, B. Arroyo Moreno, D.H. Pfister, K. Nara, A. Zambonelli, J.M. Trappe, R. Vilgalys. 2013. Historical biogeography and diversification of truffles in the Tuberaceae and their newly identified southern hemisphere sister lineage. *PLOS One* 8(1): 1-15.
- Carter, C. 2011. Natural and cultivated truffle production. Quality assurance in Italy, France, and Spain. International Specialized Skills Institute, Melbourne, Australia.

- Cordero, C., P. Cáceres, G. González, K. Quiroz, C. Bravo, R. Ramírez, P.D.S. Caligari, B. Carrasco, and R. García-Gonzales. 2011. Molecular tools for rapid and accurate detection of black truffle (*Tuber melanosporum* Vitt.) in inoculated nursery plants and commercial plantations in Chile. *Chilean Journal of Agricultural Research* 71(3): 488-494.
- Fan, L., and J.-Z. Cao. 2012. Two new species of white truffle from China. *Mycotaxon* 121: 297-304.
- Fan, L., J.-Z. Cao, Y.-Y Li, and Y. Li. 2011a. Two new species of *Tuber* from China. *Mycotaxon* 116: 349-354.
- Fan, L., C.-L. Hou, and J.-Z. Cao. 2011b. *Tuber sinoalbidum* and *T. polyspermum* - new species from China. *Mycotaxon* 118: 403-410.
- Fan, L., C.-L. Hou, and Y. Li. 2012. *Tuber microverrucosum* and *T. huizeanum* - two new species from China with reticulate ascospores. *Mycotaxon* 122: 161-169.
- Fischer, C., and C. Colinas. 1996. Methodology for certification of *Quercus ilex* seedlings inoculated with *Tuber melanosporum* for commercial application. In *Proceedings of the 1st International Conference on Mycorrhizae*. Berkeley, CA, USA.
- Hall, I.R., G.T Brown, and A. Zambonelli. 2007. Taming the truffle. The history, lore, and science of the ultimate mushroom. Timber Press, Inc, Portland OR, USA. 304 pp.
- Hall, I.R., and A. Zambonelli. 2012. Laying the foundations. Chapter 1 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. *Soil Biology* 34: 3-16.
- Ho, W.H., S. Anderson, A. Guerin-Laguet, N. Hesom-Williams, Y. Wang, M. Braithwaite, C.F. Hill, and B.J.R. Alexander. 2008. *Tuber brumale*, a new truffle in New Zealand. *Journal of Plant Pathology* 90(2, Supplement): S101.
- Jeschke, J.M., and D.L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* 102(20): 7198-7202.
- Lefevre, C. 2012. Native and cultivated truffles of North America. Chapter 12 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. *Soil Biology* 34: 209-226.
- Linde, C.C., and H. Selmes. 2012. Genetic diversity and mating type distribution of *Tuber melanosporum* and their significance to truffle cultivation in artificially planted

- truffières in Australia. *Applied and Environmental Microbiology* 78(18): 6534-6539.
- Morte, A., A. Andrino, M. Honrubia, and A. Navarro-Rodenas. 2012. *Terfezia* cultivation in arid and semiarid soils. Chapter 14 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. *Soil Biology* 34: 241-263.
- Murat, C., E. Zampieri, A. Vizzini, and P. Bonfante. 2008. Is the Perigord black truffle threatened by an invasive species? We dreaded it and it has happened! *New Phytologist* 178(4) 699-702.
- New Zealand Ministry of Agriculture and Forestry. 1993 (amended 2011). Importation into New Zealand of specified fresh and frozen *Tuber* species (truffles). Biosecurity New Zealand Standard BNZ-IMP-TUBER. <http://www.biosecurity.govt.nz/files/ihs/bnz-imp-tuber.pdf>
- Pilz, D., C. Lefevre, L. Scott, and J. Julian. 2009. Oregon culinary truffles. An emergent industry for forestry, agriculture and culinary tourism. [www.oregontruffles.org](http://www.oregontruffles.org)
- Pringle, A., R.I. Adams, H.B. Cross, and R.D. Bruns. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. *Molecular Ecology* 18(5): 817-833.
- Richardson, D.M, and M. Rejmánek. 2011. Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions* 17: 788-809.
- Shin, K.-S., J.S. Park, and S. Yoshimi. 1995. Note on *Tuber aestivum* subsp. *uncinatum* newly recorded in Korea. *Korean Journal of Mycology* 23: 10-13.
- Slama, A., Z. Fortas, A. Boudabous, and M. Neffati. 2010. Cultivation of an edible desert truffle (*Terfezia boudieri* Chatin). *African Journal of Microbiology Research* 4(22): 2350-2356.
- Temple B., P.A. Pines, and W.E Hintz. 2006. A nine-year genetic survey of the causal agent of Dutch elm disease, *Ophiostoma novo-ulmi* in Winnipeg, Canada. *Mycol. Res.* 110: 594-600.
- Trappe, J. M. R. Molina, D.L. Luoma, E. Cazares, D. Pilz, J.E. Smith, M.A. Castellano, S.L. Miller, and M.J. Trappe. 2009. Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-772. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 194 pp.
- Visnovsky, S.B., A. Guerin-Laguet, Y. Wang, and A.R. Pitman. 2010. Traceability of marketable Japanese shoro in New Zealand: using multiplex PCR to exploit phylogeographic variation among taxa in the *Rhizopogon* subgenus *Roseoli*. *Applied and*



- Environmental Microbiology 76(1): 294-302.
- Wang, Y., Z.M. Tan, D.C. Zhang, C. Murat, S. Jeandroz, F. Le Tacon. 2006. Phylogenetic and populational study of the *Tuber indicum* complex. Mycological Research 110: 1034-1045.
- Wang, Y., N. Cummings, and A. Guerin-Laguet. 2012. Cultivation of basidiomycete edible ectomycorrhizal mushrooms: *Tricholoma*, *Lactarius*, and *Rhizopogon*. Chapter 16 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. Soil Biology 34: 281-304.
- Wang, Y., and I.R. Hall. 2004. Edible ectomycorrhizal mushrooms: challenges and achievements. Can. J. Bot. 82: 1063-1073.
- Wang, X. 2012. Truffle cultivation in china. Chapter 13 in *Edible Ectomycorrhizal Mushrooms*, edited by A. Zambonelli and G.M. Bonito. Soil Biology 34: 227-240.
- Zhang, J.-P., P.-G. Liu, and J. Chen. 2012. *Tuber sinoaestivum* sp. nov., an edible truffle from southwestern China. Mycotaxon 122: 73-82.
- Zhang, L., Z.I. Yang, and D.S. Song. 2005. A phylogenetic study of commercial Chinese truffles and their allies: taxonomic implications. FEMS Microbiology Letters 245: 85-92.