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Ecology and Management of Commercially Harvested Chanterelle Mushrooms

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Cover—Colorful Pacific golden chanterelles (*Cantharellus formosus*) abound each autumn in Douglas-fir and western hemlock forests of the Pacific Northwest. Until recently these avidly collected mushrooms were misidentified as *Cantharellus cibarius*, the golden chanterelle of fame in Europe and elsewhere. Now properly named, it has been honored as the state mushroom of Oregon, and is sold locally, regionally, nationally, and internationally (©2002 Taylor F. Lockwood).

Abstract

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During the last two decades, the chanterelle mushroom harvest from Pacific Northwest forests has become a multimillion dollar industry, yet managers, harvesters, and scientists lack a current synthesis of information about chanterelles. We define chanterelles and then discuss North American species, their place among chanterelle species around the world, international markets for chanterelles, our current understanding of the organism, reasons for declining production in parts of Europe, and efforts to cultivate chanterelles. Shifting focus back to chanterelles of the Pacific Northwest, we describe our species, regional forest management issues, recent studies, and future research and monitoring needed to sustain this prized resource.

Keywords: Chanterelle mushrooms, edible mushrooms, ectomycorrhizae, forest management, nontimber forest products, *Cantharellus*, *Craterellus*, *Gomphus*, *Polyozellus*.

Summary

Chanterelles are globally renowned as one of the best edible forest mushrooms, and their international commercial value likely exceeds a billion dollars annually.
A variety of chanterelle species fruit plentifully in Pacific Northwest forests, and their abundance has spawned a significant commercial harvest industry during the last two decades. Because chanterelles grow symbiotically with the roots of forest trees, managing the fungi for sustainable harvests also means managing forest habitats. This publication summarizes what we currently know about chanterelles. Our intent is to provide forest managers, policymakers, mushroom harvesters, mushroom enthusiasts, and research mycologists with accurate information for an informed debate about chanterelle management. Our commercial harvest in the Pacific Northwest originates within a broad historical, cultural, ecological, and international trade context, and much relevant information about the organism comes from research in Europe. Therefore we also discuss chanterelles throughout North America and worldwide; the international chanterelle market; chanterelle biology, ecology, chemistry, and nutrition; recent chanterelle productivity declines reported from parts of Europe; and current research on chanterelle cultivation. Returning our focus to Pacific Northwest chanterelles, we describe local species, discuss management issues, summarize recent research, and conclude with future research and monitoring designed to ensure a continued abundance of chanterelles in our forests.

Contents

Introduction

Owing to its varied topography and climate, the Pacific slope of western North America is covered with temperate conifer and hardwood forests that are unrivaled in their rich biological diversity. The original human inhabitants no doubt marveled at this region's bountiful heritage of fish, wildlife, and plants that provided them with food and shelter. Native American tribes used native fungi for medicine and food, but as far as we know, mushrooms were minor items in the diets of most Native Americans dwelling in the Pacific Northwest. European settlers, however, brought with them very different cultures and food preferences, including a passion for mushrooms. The diverse flora of the Pacific Northwest supports a correspondingly rich mycota.[1] As all major types of edible mushrooms appreciated in Europe are also found in the Pacific Northwest, often in a profuse variety, settlers and their descendants have harvested edible mushrooms for food and pleasure ever since their arrival. Chanterelles, already much appreciated in parts of Europe, Asia, Africa, and Central America, have become one of the most commonly harvested edible mushrooms in Pacific Northwest forests. Although some chanterelles have been sold locally (plate 1, [on center page]) ever since they were first collected in the region, the nature and scale of mushroom harvesting changed dramatically during the 1980s when they became internationally traded commodities.

Chanterelles are ectomycorrhizal. Mycorrhizal fungi grow in a mutually beneficial, or symbiotic, association with the root tips of green plants. Ectomycorrhizal fungi are a subset of mycorrhizal fungi that form sheaths over the root tips of certain trees and shrubs. (See the section entitled "Morphology and Physiology" for a more thorough explanation). Because chanterelles obtain their carbohydrate nutrition from living trees through this symbiotic association, forests are essential to their survival and productivity. We will discuss efforts to cultivate chanterelles, but currently they are all collected from natural or planted forests. With the onset of widespread commercial harvesting, sustainable chanterelle production has become an important issue for harvesters, consumers, and forest managers alike. Given the interdependence between chanterelles and live trees, everyone interested in sustaining chanterelle production recognizes that appropriate forest management influences their abundance. What constitutes "appropriate" forest management is less clear, however.

The purpose of this publication is to summarize, in a convenient format, what we currently know about chanterelles and management of the forests upon which they depend. Our literature cited section is meant to be inclusive so that it serves as a fairly complete guide to current, global, and historical literature about chanterelles. Our intended audience is broad, including forest managers, mycologists, mushroom enthusiasts, harvesters, ecologists, botanists, administrators, legislators, and the general public. In addition to our primary audience in the Pacific Northwest, we have designed this publication to be of interest to readers around the world. Effective management of chanterelles cannot be adequately addressed without considering the broad historical, cultural, ecological, and commercial context of their harvest. Similarly, much relevant information about the organism comes from research in Europe. After discussing the genera of mushrooms that are considered chanterelles and reviewing North American species, we explore chanterelles around the world and pertinent research conducted

[1] "Flora" can either refer to all plants that grow in a defined region, or to a comprehensive reference (keys and descriptions) to those plants. Flora is often used for fungi, as in "fungal flora," but because fungi constitute a separate kingdom of life (that is actually more closely related to animals than to plants) we use the technically correct term "mycota" in the same manner that "flora" is used.

elsewhere. Thereafter we return our focus to Pacific Northwest chanterelles and regional research. Considering the diversity of interests of our intended audience, we wrote each part of this document so that the reader can skip directly to subject matter of interest without losing continuity.

Chanterelle Names

Although we frequently use scientific names to discuss taxonomic issues and avoid ambiguity, we also use common (English) names for chanterelles to enhance readability. The proper use of both scientific and common names can be tricky, so this section explains some of the issues we faced and the conventions we adopted.

Scientific names—For over two and a half centuries, scientists have referred to the organisms they study by using the binomial system of nomenclature introduced by Linnaeus in his "Species Plantarum" (1753). Despite universal adherence to the rules of standardized nomenclature, names change. In fact, names must change as our understanding of taxonomic distinctions between organisms improves. For instance, *Cantharellus formosus* is the scientific name for the common golden chanterelle of the Pacific Northwest. Yet the name *Cantharellus cibarius* (the accepted scientific name for the golden chanterelle of Europe) was commonly used for this popular edible in western North America until recent research demonstrated it to be a distinct species found only in western North America. Name changes can also result from moving a species into a different genus. For instance, we will discuss the recent move of some *Cantharellus* species into the genus *Craterellus*. Current molecular techniques of DNA and protein analysis provide supporting evidence for both of these examples, and more scientific names undoubtedly will be altered as the techniques are more widely applied. Readers are referred to the *International Code of Botanical Nomenclature* (Greuter and others 2000) for information on the highly complex rules that govern scientific name changes. Appendix 1 lists currently accepted scientific names, their authors (cited authorities), dates of publication for names or name changes, earlier scientific synonyms, and references. For brevity and clarity, throughout the text we abbreviate the genus *Cantharellus* with "*C*.," *Craterellus* with "*Cr*.," *Gomphus* with "*G*.," and *Polyozellus* with *"P."*

Common names—Because common names are quite variable, we have carefully selected names (listed in appendix 1) that do not overlap among species. *Cantharellus cibarius* has long fame as the "golden chanterelle [of Europe]," although it likely grows elsewhere too. We call *C. cibarius* either simply "the golden chanterelle" or "European golden chanterelle" where needed to clearly distinguish it from the golden chanterelle of the Pacific Northwest. We use the term "Pacific golden chanterelle" (coined by Redhead and others 1997) for *C. formosus* because it reflects the species distribution along the west coast of North America. In this publication we also introduce the term "craterelle" to distinguish species in the genus *Craterellus* from "true chanterelles" in the genus *Cantharellus*.

Common names can be influential. Oregon is one of only two states[2] in the United States to recognize a state mushroom. The catchy common name "Pacific golden chanterelle," its popularity as a good edible, and its importance in commerce motivated the legislature in 1999 to select *Cantharellus formosus* as the Oregon state mushroom.

Unfamiliar terms—Because many of our readers might not be acquainted with the technical language used to discuss fungi, we define or discuss potentially unfamiliar terms in the text or in footnotes the first time the word is used. We also include a brief

[2] Minnesota's state mushroom is the morel, *Morchella esculenta*.

glossary for readers who prefer to skip sections and might have missed the definition. Comprehensive definitions can be found in *Dictionary of the Fungi* (Kirk and others 2001).

Chanterelles Around the World

What Are Chanterelles?

The term "chanterelle" is used for a variety of edible, and highly prized mushrooms with ridges (instead of gills) on the underside of the cap. Mushrooms are the reproductive structures (fruitbody or sporocarp) of certain fungi, and in the case of chanterelles, the fungus lives in the soil and derives its carbohydrate nutrition from a symbiotic mycorrhizal association with fine tree roots (Smith and Read 1997). The word "chanterelle" is derived from the Greek "kantharos" meaning "cup," "goblet," or "drinking vessel," a reference to their funnel-like shapes (Persson and Mossberg 1997). As the species name for the European golden chanterelle, "*cibarius*" is derived from the Latin word for "food," the combined species name, *Cantharellus cibarius*, quite appropriately translates as "cup of food." Indeed most chanterelles are highly prized for their flavor and can be safely collected and consumed because they are easily identified (Moser and Jülich 2000).

Four genera, *Cantharellus*, *Craterellus*, *Gomphus*, and *Polyozellus*, are commonly referred to as "chanterelles" because their spore-bearing surfaces appear similar without magnification. The fertile or spore-bearing surface of mushrooms is called the hymenium. The chanterelle hymenium can be smooth, wrinkled, veined, or ridged, but never forms bladelike gills (as in mushrooms like *Agaricus*) or tubes (as in *Boletus*). Most chanterelles have spore-bearing ridges that typically extend from the edge of the cap (pileus) well down the tapered stems (stipes). Chanterelles can be brittle, fleshy, or leathery, but they are never woody in texture. Morphological characters that distinguish these genera are listed in table 1. Appendix 2 provides a technical description of the genus *Cantharellus*, the "true chanterelles."

North American Chanterelles

Over 40 species of chanterelles and chanterelle-like mushrooms (in all four chanterelle genera) are currently recognized in North America. Common host trees include pine, fir, spruce, Douglas-fir, hemlock, and oak (see app. 1 for species names). Seven prominent edible species occur in the forests of the Pacific Northwest (here defined as southeastern Alaska, British Columbia, Washington, Oregon, northern California, Idaho, and western Montana): the Pacific golden chanterelle (*C. formosus*), the white chanterelle (*C. subalbidus*), the rainbow chanterelle (*C. cibarius* var. *roseocanus*), the winter craterelle (erroneously called *Cr. tubaeformis*—see further discussion below), the horn of plenty (*Cr. cornucopioides*), pig's ears (*Gomphus clavatus*), and the blue chanterelle (*Polyozellus multiplex*). Although these chanterelles differ in abundance and distribution, and not all are commercially collected, all are popular edibles. East of the Rocky mountains, field guides most commonly discuss the following edible species: the golden chanterelle (*C. cibarius*), the red or cinnabar chanterelle (*C. cinnabarinus*), the smooth chanterelle (*C. lateritius*), the small chanterelle (*C. minor*), the black craterelle [originally "chanterelle"] (*Cr. cinereus*), the black trumpet or horn of plenty (*Cr. cornucopioides*),[3] the flame-colored craterelle [chanterelle] (*Cr. ignicolor*), the autumn craterelle [chanterelle] (*Cr. tubaeformis*), the fragrant craterelle [chanterelle] (*Cr. odoratus*), the fragrant black trumpet (*Cr. foetidus*), and the pig's ear gomphus (*G. clavatus*).

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[3] See the Pacific Northwest chanterelle species description for *Cr. cornucopioides* concerning *Cr. fallax* and recent taxonomic revisions.

Table 1—Morphological characters differentiating the cantharelloid genera *Cantharellus*, *Craterellus*, *Gomphus*, and *Polyozellus*

Genus	*Cantharellus*	*Craterellus*	*Gomphus*	*Polyozellus*
Order	Cantharellales	Cantharellales	Phallales	Thelephorales
Family	Cantharellaceae	Cantharellaceae	Gomphaceae	Thelephoraceae
Habit	Single stems often solid (sometimes fused)	Single stems often hollow	Single to multiple stems	No stem to multiple stems from the same base
Texture	Fleshy, firm	Leathery, brittle	Fleshy, firm, chunky	Somewhat leathery
Colors	Usually bright: orange, yellow, red, or white	Dark (brown or black) tones often present; some are yellow	Orange, red, purple, or tan with white flesh	Dark bluish purple to black exterior and flesh
Basidia [a]	Longitudinal nuclear spindles during meiosis	Longitudinal nuclear spindles during meiosis	Horizontal nuclear spindles during meiosis	Longitudinal nuclear spindles during meiosis
Spores	Ellipsoid, smooth, walls colorless	Ellipsoid, smooth, walls colorless	Ornamented, walls yellowish, stain blue	Not quite spherical, warty, greenish in KOH

[a] Microscopic clublike structures where spores develop.

Sources include Bruns and others 1998, Dahlman and others 2000, Feibelman and others 1997, Hibbett and others 1997, Kirk and others 2001.

The two most commercially valuable and widely collected Pacific Northwest chanterelles are the Pacific golden and white chanterelles. Until recently, most collectors regarded Pacific golden chanterelles as simply larger forms of the golden chanterelle, *C. cibarius*. Nearly a century ago, however, American chanterelle specialists had begun to question whether the Pacific Northwest golden chanterelle was the same as *C. cibarius* (Redhead and others 1997). Murrill (1912), who made many collections in Pacific coastal forests observed, “I found it difficult to believe that this was the same plant I had seen so often in Europe and the eastern United States.” Thirty-five years later Smith and Morse (1947) also suggested that the western golden chanterelles differed from the eastern. In 1966, the British chanterelle specialist Corner named a new species, *Cantharellus formosus*, based on a collection he had made 30 years previously on British Columbia’s Vancouver Island. Although several other scientists (Norvell 1995, Petersen 1969, Thiers 1985, Tylutki 1987) believed this was the correct name for the commonly harvested golden chanterelle of western North America, popular field guides continued to refer to the Pacific golden chanterelle as “*C. cibarius*.” The resulting confusion led to both “*C. formosus*” and “*C. cibarius*” being listed in the United States government’s Northwest Forest Plan as survey and manage strategy 1 and strategy 3 fungi, respectively (USDA USDI 1994a,1994b; Castellano and others 1999). Partly in response to this error and partly to heighten public awareness to the fact that the Pacific golden chanterelle was not, in fact, *C. cibarius* of Europe, Redhead and others (1997) collected samples from several sites on Vancouver Island near the area where Corner had originally collected *C. formosus*. By comparing the descriptions and DNA data from these and other collections (Danell 1995, Feibelman and others 1994), they were able to establish *C. formosus* as the correct scientific name and proposed the common name “Pacific golden chanterelle” (plate 2).

In the same publication, Redhead, Norvell, and Danell also named and described the newly recognized rainbow chanterelle (*C. cibarius* var. *roseocanus*), associated with Sitka spruce on the coast and Engelmann spruce at higher elevations in the Cascade Range, but not found in pure stands of Douglas-fir or hemlock. The rainbow chanterelle has since been observed to fruit in pure stands of lodgepole (shore) pine on the Oregon Coast.[4] (*C. formosus* also grows in spruce forests, but has not yet been confirmed as an ectomycorrhizal associate of pines.) Citing preliminary DNA evidence that showed it to be closely related to the European golden chanterelle, the authors named the rainbow chanterelle as a variety of *C. cibarius*. If further evidence warrants, the rainbow chanterelle might later be elevated to the status of a distinct species.
More species of chanterelles are likely to be described in the Pacific Northwest. Other DNA research (Dunham and others 1998, Feibelman and others 1994) indicates there might be two or more intermingling species of golden chanterelles in the Douglas-fir and western hemlock forests of the Oregon Cascade Range (and possibly elsewhere). One yet-to-be named chanterelle that appears genetically distinct differs only slightly in color and stature from *C. formosus*.[5] Similarly, one or more[6] distinct species of golden chanterelles are thought to grow with oaks in California. For instance, specimens fruiting under oaks in Santa Barbara County were found to be genetically distinct from other known west coast chanterelles.[7] Although Smith (1968) originally described *C. cibarius* var. *pallidifolius* from Michigan, Thiers (1985) documented one collection growing with tanbark oak in Mendocino County, California. Analyses of DNA continue to probe the relationships among various North American and European species.[8]

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[4] Dunham, Susie. 2001. Personal communication. Ph.D. student, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752. Also, Danell, Eric. 2001. Unpublished DNA analysis. On file with: Museum of Evolution, Uppsala University, Norbyv.16, SE-752 36, Uppsala, Sweden.

[5] Dunham, S.; O'Dell, T.; Molina, R. [In review]. Analysis of nrDNA sequences and microsatellite allele frequencies reveals a cryptic chanterelle species *Cantharellus cascadensis* sp. nov. from the Pacific Northwest. On file with: Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752.

[6] Camacho, Francisco. 2001. Personal communication. Research assistant, Department of Environmental Science, University of California at Riverside, Riverside, CA, 92521.

[7] Dunham, Susie. 2000. Unpublished data. On file with: Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752. Collections courtesy of the late Helmut Ehrenspeck, Dibble Geological Foundation, Geological Sciences Department, University of California, Santa Barbara, CA 93106. Also, Danell, Eric. 2000. Unpublished DNA analysis. On file with: Museum of Evolution, Uppsala University, SE-752 36, Uppsala, Sweden. Collections from N. California, courtesy of John Donoghue, Northwest Mycological Consultants, 702 NW 4th St., Corvallis, OR 97330.

[8] Danell, E.; Camacho, F.; Liston, A. [and others]. [In preparation]. RFLP and sequencing of rDNA ITS of the ectomycorrhizal edible mushrooms *Cantharellus cibarius*, *C. pallens*, *C. formosus* and *C. subalbidus*. On file with: Museum of Evolution, Uppsala University, Norbyv.16, SE-752 36, Uppsala, Sweden.

Craterelles or “horns of plenty” (*Craterellus*) are the thinner cousins of true chanterelles (*Cantharellus*), and most scientists place both genera in the same order (Cantharellales) and family (Cantharellaceae) (Dahlman and others 2000, Hansen and Knudsen 1997, Kirk and others 2001, Pine and others 1999). Distinctions between these genera are currently being revised, however, and several species have recently been moved from the genus *Cantharellus* to the genus *Craterellus*. During the last century, craterelles were distinguished from true chanterelles based on the presence or absence of clamp connections[9] on the hyphae, whether the stem is hollow or solid, and the presence or absence of yellow carotenoid pigments (table 1) (Corner 1966, Donk 1964, Fries 1874, Jülich 1984, Patouillard 1900, Pegler and others 1997, Petersen 1971b, Romagnesi 1995, Watling and Turnbull 1998). Recent DNA analyses support *Cantharellus* and *Craterellus* as separate and independent (Dahlman and others 2000, Feibelman and others 1997, Pine and others 1999) but do not confirm visible characters as consistently useful for differentiating the two genera. For instance, despite their small size, rubbery consistency, and hollow stem, both the autumn craterelle (*Cr. tubaeformis*) and flame-colored craterelle (*Cr. ignicolor*) were previously treated as true chanterelles in the genus *Cantharellus* because both have clamp connections and carotenoid pigments like chanterelles. Analyses of DNA (Bruns and others 1998, Dahlman and others 2000, Feibelman and others 1997, Hibbett and others 1997), however, clearly support inclusion of both species in the genus *Craterellus*, along with the yellow-footed chanterelle (now *Cr. lutescens*), the horn of plenty (*Cr. cornucopioides*), and the wavy capped chanterelle (now *Cr. undulatus*). Hollowness of the stem is now considered the most useful feature for distinguishing these genera in the absence of a microscope or DNA probes. Even this character might not turn out to be entirely consistent, however, as the solid-stemmed *C. melanoxeros* could be a craterelle. Time and further DNA analyses will tell.

Smith and Morse (1947) and Smith (1968) distinguished between two western and two eastern craterelles (as chanterelles) using the names *C. tubaeformis* and *C. infundibuliformis*. Redhead (1979) noted that Smith used inconsistent features to distinguish the pairs of species in eastern versus western North America, and also that the name *C. infundibuliformis* was unavailable, because it is considered to be synonymous with *C. tubaeformis*. Smith and Morse (1947) and Redhead (1979) have both suggested that the western species on rotten logs requires a distinct name, but further studies of original collections are also needed. Dahlman and others (2000), using molecular data, likewise suggested that the Pacific Northwest winter craterelle is a distinct species differing from *Cr. tubaeformis* of Europe and eastern North America. In this publication, we use the name *Craterellus neotubaeformis* nom. prov.[10] for our western winter craterelle because the group of mycologists who are working on this species wish to incorporate a link to the old name. More information about Fries’ distinctions among *C. tubaeformis*, *C. infundibuliformis,* and the yellow-foot chanterelle *C. lutescens* (all listed as *Cantharellus*) can be found in Donk (1969), Petersen (1979), Kuyper (1990), and Redhead and others (2002).

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[9] Distinctive microscopic structures.

[10] “Nom. prov.” is an abbreviation for the Latin term “nomen provisorium” meaning “provisional name.” It is used to reserve a species name while the description is being prepared for official publication.

The genus *Gomphus* is more distantly related to *Cantharellus* than is *Craterellus*. Although superficially similar to true chanterelles, this genus is placed in its own family, the Gomphaceae, and a different order, the Phallales. Analyses of DNA (Bruns and others 1998, Hibbett and others 1997, Humpert and others 2001, Pine and others 1999, Villegas and others 1999) now confirm a close relationship between *Gomphus* and other genera formerly placed in the Clavariaceae family (for example, coral fungi—*Ramaria*, club coral fungi—*Clavariadelphus*, and fairy clubs—*Clavaria*) as well as other members of the Phallales such as stinkhorns (*Phallus* species). Unlike the other three chanterelle genera, *Gomphus* contains both edible and inedible species. Of the four *Gomphus* species found in western North America, only the pig's ear gomphus (*Gomphus clavatus*) is considered a safe edible. Inedible species include the scaly vase chanterelle (*G. floccosus*), Kauffman's gomphus (*G. kauffmanii*), and Bonar's gomphus (*G. bonarii*). See the key for Pacific Northwest species and the description of *Gomphus clavatus* (page 30) for information on how to recognize the nonedible *Gomphus* species.

Polyozellus is a genus that contains only one species. The edible and choice blue chanterelle (*P. multiplex*) was originally described as a *Cantharellus* species because its veined hymenium and fleshy texture resemble those of true chanterelles. W.A. Murrill (1910) placed this species into its new genus, and subsequent research (Imazeki 1953) confirmed that *P. multiplex* is only very distantly related to the true chanterelles. *Polyozellus* is now (Kirk and others 2001) placed in the Leathery Earth Fan family (Thelephoraceae) and order (Thelephorales) along with other fungi characterized by dark rough angular spores and the production of thelephoric acid (Hibbett and others 1997). We include it because it appears similar to chanterelles, has long been called a chanterelle, and is edible.

Although not considered chanterelles, the club corals (*Clavariadelphus* species) and hedgehog mushrooms (*Hydnum* species) have been regarded as chanterelle relatives (Corner 1957, 1966; Donk 1964; Persson and Mossberg 1997; Petersen 1971b). Although Reijnders and Stalpers (1992) concluded that *Hydnum* was not closely related to chanterelles, more recent DNA evidence indicates otherwise (Hibbett and others 1997). Hibbett and Thorn (2000) note that whereas the club corals belong to the same order and family as *Gomphus*, hedgehogs belong to the same clade (DNA-based group of related fungi) as chanterelles and craterelles.

Because all chanterelles are only distant relatives of gilled fungi, our knowledge of genetics and physiology derived from research on gilled fungi might not be fully applicable to chanterelles. This is important to keep in mind as we later discuss the biology and ecology of chanterelles.

Global Distribution and History of Use

About 90 species in the genera *Cantharellus* and *Craterellus* have been described worldwide. The total number differs according to authors and how they define species (Corner 1966, Dahlman and others 2000, Danell 1994a, Eyssartier and Buyck 2000, Feibelman and others 1997, Pegler and others 1997, Persson and Mossberg 1997, Watling and Turnbull 1998). Well over 70 species of true chanterelles have been described thus far, and many more are yet to be named. They are found on every continent that has forests with ectomycorrhizal host trees. Impressive chanterelle mycotas exist in southeastern and eastern Asia, Japan, Africa, Australia, and Central and South America. Chanterelles are especially appreciated in Europe and North America. The large number of common names listed in table 2 illustrates the worldwide popularity of this highly prized edible. Table 3 shows the global distribution of species discussed in our text.

Table 2—Worldwide vernacular names of chanterelles (*Cantharellus cibarius* sensu lato[a])

Name	Meaning	Language
Agerola	from Girolle	Catalonian
Amarillo	yellow	Spanish, local—Hidalgo, Mexico
Anzutake	apricot mushroom	Japanese
Baina		Basque
Bolet cabriter		Catalonian
Cabrilla		Spanish, local—Segovia, Spain
Camagroc		Catalonian
Canarinhos	canary bird chicken	Portuguese
Cantarela	from chanterelle	Spanish, local—La Rioja and Navarra, Spain
Cantarelos	from chanterelle	Portuguese
Capo gallo	cock crest, head	Italian
Carn de gallina	chicken meat	Spanish
Chanterelle		French, English
Chevrette	small goat	French
Corneta	trumpet	Spanish, local—Hidalgo, Mexico
Crête de coq	cock crest	French
Csirke gomba	chicken mushroom	Hungarian
Dooierzwam	egg yolk mushroom	Dutch
Dotterpilz	egg yolk mushroom	German
Duraznillo	name of a sweet tropical fruit	Spanish, local—Texcoco, Mexico
Eierschwamm	egg mushroom	German
Euskera ziza hori		Spanish, local
Finferlo	see Pfifferling	Italian
Finferli	see Pfifferling	Italian, local—South Tyrol, Austria
Galbiori	yellowish one	Romanian
Galletto	young rooster	Italian
Gallinace	chicken	French
Gallinaccio	chicken	Italian
Galuschel	yellow ear	German
Gelbhähnel	yellow chick	German
Gelbling	yellowing	German
Ginestola		Catalonian
Ginesterola	From the yellow *Genista* plant	Catalonian
Girola	from girolle	Spanish, local—La Rioja and Navarra, Spain
Girolle	girer = twist	French
Gullsvamp	golden mushroom	Swedish, local—Småland, Sweden
Hanekam	cock crest	Dutch
Harilik kukeseen	common cock mushroom	Estonian
Hasenöhrlein	little hare ear	German

Table 2—Worldwide vernacular names of chanterelles (*Cantharellus cibarius* sensu lato[a]) (continued)

Name	Meaning	Language
Hed Kamin Yai	large Kamin mushroom	Thai
Huangzhi-gu	yellow cape jasmine mushroom	Chinese
Hühnling	chick	German
Jaunette	little yellow	French
Jidanhuang	egg yolk	Chinese
Jiyou-jun	chicken fat mushroom	Chinese
Kantarel	from chanterelle	Danish, Dutch
Kantarell	from chanterelle	Swedish, Norwegian
Kantarella	from chanterelle	Icelandic
Kantarelli	from chanterelle	Finnish
Keltasieni	yellow mushroom	Finnish
Keltavahvero		Finnish
Kkue-kko-ri beosus	nightingale mushroom	Korean
Kuratko	chick	Czech
Kurka		Polish
Lekazina		Basque, local
Lisitjka	fox mushroom	Russian
Liska	fox mushroom	Czech
Mãozinhas	baby hands	Portuguese
Membrillo	name of a sweet tropical fruit	Spanish, local—Texcoco, Mexico
Niwl gomba	hare mushroom	Ancient Hungarian
Orecina	little ear	Italian (dialect)
Oreille de lièvre	hare’s ear	French
Oreja de liebre	hare’s ear	Spanish
Picornell		Spanish, local—Balearic Islands, Spain
Pfifferling	Pfeffer = pepper	German
Q^{h}ale másinċe·	tree? = mushroom	Kashaya, Kashaya Pomo tribe, Northern California
Rebozuelo	Woman’s dress	Spanish, common in Europe and South America
Reheling		German
Rehfüsshen	deer’s foot	German
Roka gomba	fox mushroom	Hungarian
Rossinyol	nightingale	Catalonian
Rubito	little blond	Spanish, local
Sal-gu beosus	apricot mushroom	Korean
Saltzaperretxiko	sauce mushroom	Basque
Seta amarilla		Spanish, local
Seta del brezo		Spanish, local—Soria, Spain
Seta de San Juan	St. John’s mushroom	Spanish, local—Segovia, Spain
Sisa lekaxin		Basque

Table 2—Worldwide vernacular names of chanterelles (*Cantharellus cibarius* sensu lato[a]) (continued)

Name	Meaning	Language
Susa		Spanish, local
Txaltxatua		Basque
Ull de perdiu	partridge eye	Catalonian
Urri-ziza	golden mushroom	Basque
Vaqueta	small cow	Catalonian
Vingesvamp	wing mushroom	Danish, local
Wisogolo		Swahili
Xingjun	apricot mushroom	Chinese
Xochilnanácatl	flower mushroom	Nahuatl, Valle de México, Mexico
Yumurta mantari	egg mushroom	Turkish
Ziza horia	yellow mushroom	Basque, Spain and France

[a] "Sensu lato," Latin for "in a broad sense," is used after species names to indicate that the definition of a species is being interpreted broadly or loosely in a particular context. It is abbreviated "s.l.," an abbreviation we use throughout the manuscript.

Table 3—Worldwide distribution of the chanterelle species we discuss

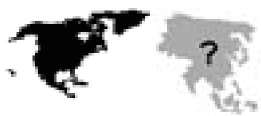
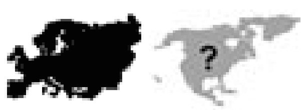
Species	Continent(s)	Distribution
C. appalachiensis		East coast of North America (similar chanterelle reported in India)
C. atrolilacinus		Costa Rica, Guatemala?
C. cibarius		Circum-Atlantic in the Northern Hemisphere, also North Africa, Himalayas, and Thailand[a]
C. cibarius var. *amethysteus*		Europe, Southern United States?
C. cibarius var. *roseocanus*		Pacific Northwest near coast
C. cinnabarinus		Southeastern United States, West Indies, Central and South America, and Japan
C. concinnus (= *C. cibarius* var. *australiensis*)		Australia, New Guinea, and New Zealand

Table 3—Worldwide distribution of the chanterelle species we discuss (continued)

Species	Continent(s)	Distribution
C. congolensis		Tanzania, Burundi, Congo, and Senegal
C. formosus		Pacific Northwest
C. friesii		Europe
C. lateritius		Eastern North America and Costa Rica
C. longisporus		Tanzania, Madagascar
C. melanoxeros	 	Europe; also reported in Malaysia, Singapore, and Indochina
C. minor	 	Eastern United States; reported from Japan, Thailand, and New Guinea
C. ochraceoravus		Australia
C. pallens		Europe, with hazels, oaks, and spruce
C. platyphyllus		Tanzania, Madagascar
C. pseudocibarius		Tanzania, Burundi, Congo, and Cameroon
C. pudorinus		Malaysia, Singapore, and Indochina
C. subalbidus		Pacific Northwest

Table 3—Worldwide distribution of the chanterelle species we discuss (continued)

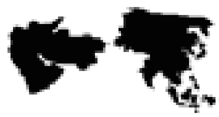
Species	Continent(s)	Distribution
C. subcibarius		Pakistan, India, China, Malaysia, Japan, and Philippines
C. symoensii		Eastern Africa
Cr. boyacensis		Columbia, Costa Rica, and Central to South America
Cr. cinereus		Eastern North America and Europe, in broadleaf forests
Cr. cornucopioides (= *Cr. fallax*)		North, Central, and South America, Europe, Asia, and Japan, in broadleaf forests
Cr. costaricensis		Costa Rica
Cr. ignicolor		Eastern North America
Cr. lutescens		Eastern North America, Europe
Cr. neotubaeformis nom. prov.		West coast of North America
Cr. odoratus		North America, Malaysia, Singapore, and Indochina
Cr. tubaeformis		Europe, Asia, and North America in coniferous forests
Cr. undulatus		Europe and North America, with hazels and oaks

Table 3—Worldwide distribution of the chanterelle species we discuss (continued)

Species	Continent(s)	Distribution
G. bonarii		Northern and western North America
G. clavatus		West coast of North America, Europe, Pakistan, India, and Japan; likely pan-hemispheric
G. floccosus		Northern and western North America
G. kauffmanii		Pacific Northwest and southern Appalachians; rare
P. multiplex		Northern and montane North America, Japan

Note: See appendix 1 for prior names and synonyms.

[a] Species with distributions spanning several continents, such as *C. cibarius*, might actually consist of two or more locally unique species that will be differentiated with future research.

Europe—Currently, 10 species of chanterelles are widely recognized in Europe. The golden chanterelle (*C. cibarius*) is the primary commercial species. Other species that occur throughout Europe are the blackening chanterelle (*C. melanoxeros*), the horn of plenty (*Cr. cornucopioides*), the black craterelle (*Cr. cinereus*), the autumn craterelle (*Cr. tubaeformis*), and the yellow foot (*Cr. lutescens*). The orange chanterelle (*C. friesii*) and the amethyst chanterelle (*C. cibarius* var. *amethysteus*) have a more southern distribution, and the European pale chanterelle (*C. pallens*) and the wavy-capped chanterelle (*Cr. undulatus*) are primarily ectomycorrhizal associates of hazels and oaks. Uncertain species include a single collection of *C. borealis* (Petersen and Ryvarden 1971) and the recently described *C. pseudominimus* and *C. romagnesianus* (Eyssartier and Buyck 1999b).

The Dutch herbalist Lobelius (1581) was the first to mention chanterelles in the European literature. The Belgian botanist Clusius (1601), who traveled extensively and wrote the first scientific monograph on fungi, cited German “Reheling” and Hungarian “Niwl Gomba” as local common names for the golden chanterelle. The existence of these old vernacular names suggests that Europeans ate chanterelles in medieval times. French language and traditions influenced much of medieval Europe, so the name “chanterelle” and the practice of eating chanterelles likely spread from France to other parts of Europe. The Swedish naturalist Linnaeus (1747) noted that “chantarellen” were common edible mushrooms, but used the scientific name *Agaricus chantarellus* for the golden chanterelle (Linnaeus 1755). The Swedish scientist Elias Fries, now regarded as the “father of mycology” for his pioneering work on fungal taxonomy, coined the current scientific name for the golden chanterelle, *Cantharellus cibarius*, in his *Systema Mycologicum* (Fries 1821–32). Persson and Mossberg (1997) discuss the early history of chanterelle research in greater detail and reproduce original illustrations.

Traditionally, Germanic and Anglo-Saxon Europeans have been regarded as mycophobic (afraid of fungi or eating mushrooms), whereas Slavic, Finnish, and Latin peoples are considered mycophilic (fond of fungi). The latter have a long tradition of mycophagy (eating fungi) dating back to Roman times (Ainsworth 1976, Pegler and others 1997). There are many colloquial names for chanterelles in Catalonian and Italian (table 2) that reflect a long tradition of using them for food. In contrast, few local names exist for chanterelles in mycophobic England and Sweden. Once wealthy Britons discovered chanterelles in the early 1880s, however, they became fashionable and were served at banquets and state occasions (Pegler and others 1997). The popularity of chanterelles continues to grow throughout Europe.

Africa—In Africa, 20 species, such as *C. congolensis*, *C. longisporus*, and *C. pseudocibarius* (Corner 1966), were described decades ago. More recent literature further explores their taxonomy and use (Buyck 1994; Buyck and Eyssartier 1999; Buyck and others 1996, 2000; Eyssartier and Buyck 2001a; Härkönen and others 1995). Chanterelles are found in many tropical African countries such as Burkina Faso (Sanon and others 1997), Burundi (Buyck 1994), Guinea-Congo (Buyck and others 1996), Madagascar (Eyssartier 1997, Eyssartier and Buyck 1999a), Senegal, (Thoen and Ba 1989), Zaïre [now Democratic Republic of the Congo] (Eyssartier 1997, Thoen and Ba 1989), and Zambia (Bordeaux 1996). Local tribes often seek them avidly (Rammeloo and Walleyn 1993) and vernacular names are diverse (Buyck 1994). Many tribes use "wisogolo" (Swahili for chanterelle) for all *Cantharellus* species (Härkönen and others 1995). In the rainy season, chanterelles are picked in the "miombo" forests that stretch across Africa south of the Congo Basin rain forest. These chanterelles are often sold in quiverlike baskets made of coconut leaves for the equivalent of $2.25 per pound.

On a 1998 expedition to Tanzania, author Eric Danell, Bart Buyck (Paris Museum of Natural History), and Dr. Kivaisi's staff (University of Dar es Salaam) encountered 12 chanterelle species, including 2 new to science. During their visit, Ngoto, a Zaramo tribesman from Kisarawi collected the red kilogoro (*C. platyphyllus*), the black *C. congolensis* (plate 3), and the yellow *C. pseudocibarius*. The pungent *C. symoensii* from eastern Africa tastes somewhat bitter, but when cooked with sugar it becomes delicious.

Asia—Chanterelles similar to *C. cibarius*, and the close relative *C. subcibarius*, are reported from Pakistan, India, China, Thailand, Malaysia, Japan, and the Philippines. Many Thai chanterelles fruit in ectomycorrhizal *Dipterocarpus* forests during the rainy season (May–October). *Craterellus cantharellus* (now *C. lateritius*) is reported from Thailand[11] (Jones and others 1994), and *C. ianthinus*, *C. pudorinus*, and *Cr. odoratus* occur in Malaysia, Singapore, and Indochina (Corner 1966, Nuhamara 1987, See and others 1995). Chanterelles are an important ingredient in Thai cuisine. In Chiang Mai (northwestern Thailand), *C. minor* is picked by farmers in mixed bamboo and teak

[11] Nopamornbodi, Omsub. 1996. Personal communication. Researcher, Soil Microbiology Research Group, Division of Soil Science, Department of Agriculture, Chatujak Bangkok 10 900, Thailand.

forests, and then sold at local markets for $0.55 per pound (Jones and others 1994). By contrast, local residents regard chanterelles that fruit during the July monsoon season in India's Goa territory as inedible. Chanterelles resembling *C. appalachiensis* and *C. lateritius* are reported from India's Uttar Pradesh province (Dhancholia and others 1991). In the Himalayas, *C. cibarius* s.l.[12] occurs under spruce, oak, and pine,[13] and Watling and Abraham (1992) reported *C. cibarius* from Kashmir where it is widespread and grows under Himalayan spruce.

Indirect evidence suggests that the Chinese have used mushrooms for 6,000 years. The first Chinese mycota (reference guide) was written in 1245 A.D. (Yun-Chang 1987). Chamberlain (1996) suggests that the Chinese are so familiar with mushrooms that few poisonings are reported. In some provinces, chanterelles are called jiyou-jun (Hall and others 1998) meaning "chicken-oil-mushroom."[14] In Yunnan, chanterelles are picked in the mountains and sold locally for the equivalent of less than $1.00 per small basket, a price considered quite expensive. Small specimens are preferred for their texture. Tibetan women who collect *C. cibarius* s.l., serve them for breakfast together with other mushrooms, dumplings, tea, and fried yak cheese (Chamberlain 1996). Chanterelles are also used medicinally in China to prevent night blindness, alleviate skin dryness, and keep mucous membranes moist (Pegler and others 1997).

Australia—We do not know whether Australian aborigines used chanterelles, although *C. cibarius* var.[15] *australiensis* grows with Eucalyptus forests in Australia, New Guinea, and New Caledonia.[16] Eyssartier and Buyck (2001b) review 17 possible Australian chanterelle species and conclude only 3 are true chanterelles (*C. ochraceoravus* Grgurinovic, *C. concinnus* Berk (= *C. cibarius* var. *australiensis*), and *C. viscosus* Berk). In New Guinea, the Beangi people of the Morobe Province do eat chanterelles, but declining sales at local markets suggest waning popularity (Shoeman 1991). Some small chanterelle species are also native to New Zealand, but no records exist of their traditional use by the Maori.

Central and South America—Several *Cantharellus* species, including *C. cibarius* s.l. and the red chanterelle (*C. cinnabarinus*), have been reported from Central and South America, and the West Indies. Mushroom consumption seems to be an old tradition in this part of the world (Bandala and others 1997). In Mexico, the indigenous Nahuatl name "xochilnanácatl" means "flower mushroom," a reference to its fruity apricot smell

[12] See the footnote for table 2 or glossary for definition of "s.l."

[13] Reddy, M. Sudhakar. 1999. Personal communication. Researcher, Thapar Institute of Engineering and Technology, School of Biotechnology, P.O. Box 32, Patiala 147004, India.

[14] Zheng, Juxian. 2000. Personal communication. Ph.D. student, Department of Forest Mycology and Pathology, Swedish University of Agricultural Sciences, Box 7026, S750 07, Uppsala, Sweden.

[15] "Var." is an abbreviation for variety, which is used to connote "subspecies" in fungus names. Often used for geographically disjunct populations of a species or minor differences in taxonomic characters.

[16] Bougher, Neale. 1992. Personal communication. Researcher, Commonwealth Scientific and Industrial Research Organisation, Forestry and Forest Products, Private Bag, P.O. Box 5, Wembley, WA 6913, Australia.

(Gonzalez 1982). Local names in the Texcoco region, such as “membrillo” and “duraznillo,” are derived from Spanish terms for trees with sweet fruits. Chanterelles were among the edible mushrooms documented by Villareal-Ruiz (1994) in his ecological and silvicultural study near Veracruz. Harvesters collect chanterelles in the mountains, starting in early June, and bring them to the La Merced market in Mexico City. Common host trees are pines and evergreen oaks.

In 2000, Roy Halling of the New York Botanical Garden and author Lorelei Norvell collected *C. lateritius* and *C. cibarius* s.l. in oak forests of the Talamanca Mountains in Costa Rica. They also found a new chanterelle species previously collected by Halling (Halling and Mueller 2000, Mata 1999) that has been given the provisional name *C. atrolilacinus* Halling & Mueller nom. prov. Much further south, Spegazzini described three chanterelles from Argentina in 1909 (Farr 1973). *Craterellus* species are poorly known in Central and South America, but *Cr. tubaeformis*,[17] *Cr. cornucopioides* (discussed as *Cr. fallax*), *Cr. ignicolor,* and *Cr. undulatus*, have been reported along with *Cr. boyacensis* and *Cr. costaricensis* (Halling and Mueller 2000, Wu and Mueller 1995).

International Commerce

In 1992, Schlosser and Blatner (1995) reported the export market for the 515 metric tons of chanterelles collected in Oregon, Washington, and Idaho to be proportioned as follows: 30 percent Western United States, 14 percent Germany and France, 9 percent Canada, 27 percent to other European countries, and 20 percent to other international markets. Most chanterelles that are exported from the United States and Canada come from the Pacific Northwest, yet our exports constitute a relatively small proportion of international commerce. Watling (1997), Hall and others (1998), and Hall and Yun (2000) estimate global chanterelle commerce at about 200 000 metric tons (441 million lbs.), worth approximately $1.25 to $1.4 billion annually. By comparison, Schlosser and Blatner (1995) report the value of chanterelle exports from Idaho, Oregon, and Washington at $3.6 million in 1992. Similarly, Germany imported 5856 metric tons of chanterelles in 1996, but only 97 of those metric tons were from the United States and Canada (Weigand 2000). Although small in relation to world markets, our chanterelle exports make significant contributions to our regional economy and to the income of harvesters. The most salient feature of our position in global chanterelle commerce is that prices paid to local harvesters fluctuate widely in response to harvest quantities and seasons elsewhere. Although prices paid to harvesters in the Pacific Northwest fluctuate daily and seasonally, Blatner and Alexander (1998) report relatively stable annual average prices: $2.95 per pound in 1992, $4.00 per pound in 1994, $3.02 per pound in 1995, and $3.06 per pound in 1996. Rowe (1997) reports an average of $2.00 per pound in 1992, with a high of $8.00 per pound and a low of $1.25 per pound during the course of the season. The annual volume of Pacific Northwest chanterelle exports fluctuated during the 1990s, but no trend was apparent (Alexander and others 2002).

Declining production in parts of Europe (discussed later) and increasing consumer demand have recently improved market conditions for profitable importation of chanterelles from North America (Schlosser and Blatner 1995), Eastern Europe and the former Soviet republics (Weigand 2000), and Africa (Pegler and others 1997).

[17] Specimen collected in Guatemala by Roberto Flores, Biologist, Biologia Vegetal (Botanica) Facultad de Biologia, Campus de Espinardo, Universidad de Murcia, Avda Teniente Flomesta, nº 5, 30003 Murcia, Spain.

Germany is currently the largest chanterelle importer in Europe, followed by France and other western European countries (Alexander and others 2002). After trade relations improved in the early 1990s, the largest exporters to Germany became Poland, Lithuania, Belarus, Russia, and Latvia (Weigand 2000). Indeed, one Polish company, Omar Holding S.A., claims to export 500 to 700 metric tons of chanterelles around the world each year, an amount equal to the entire Pacific Northwest United States annual harvest. Using data compiled from EUROSTAT (the European Union's statistical information service), Tedder and others (2000) report 275 metric tons of chanterelles exported from North America to European Union countries in 1998, but Poland, Romania, Bulgaria, Lithuania, Belarus, Russia, Ukraine, Montenegro, and Turkey supplied 14 765 metric tons. Imports from Asia and Africa will likely compete with European and North American crops as international trade networks continue to expand. For instance, two Swedish companies are developing networks for importing chanterelles from Zimbabwe and Tanzania, and Pegler and others (1997) report that some African chanterelles are already being sold in England and France. Japan also imports chanterelles; *C. cibarius* from France has sold for over $100 per pound in the Nishiki market in Kyoto.

Many countries that import or export chanterelles also have local, regional, and national chanterelle markets. Citing statistics from the Agricultural Marketing Service, Fruit and Vegetable Division, U.S. Department of Agriculture, Haugen (2001) reports U.S. wholesale market prices for chanterelles to be $22 per pound in Dallas, Texas, and to range between $4.50 and $11.25 per pound in San Francisco during the most recent autumn fruiting season (September through November 2001). Although the United States might not import many chanterelles, starting in 2004, fresh mushrooms imported into the United States and sold in retail markets will need to have the country of origin labeled (Farm Security and Rural Investment Act of 2002).

In Sweden, in 1993, about 50 metric tons of golden chanterelles were sold in local markets. Swedish chanterelles retail for about $10.00 per pound. Harvesters can either market their chanterelles directly to consumers for $6.00 per pound or sell in bulk to wholesalers for about $0.80 per pound. Up to $555 (5,000 SEK[18]) per person of annual income from mushroom, berry, and cone picking is tax free, so a family of four can earn up to $2,220 per year tax free from the harvest of such nontimber forest products. Because Swedish forests produce about 450 to 2500 metric tons of fresh chanterelles annually and at least 40 percent of the population picks mushrooms at least once a year, Kardell and others (1980) surmised that large quantities are consumed without ever reaching the market. Indeed, many Europeans enjoy harvesting their own mushrooms as much as eating them. There is even a book on training dogs to find chanterelles (Hallgren and Hansson-Hallgren 1990).

When the Pacific golden chanterelle (*C. formosus*) was first exported to Europe from the Pacific Northwest, it was mistakenly called *C. cibarius*. This misnomer caused confusion among mushroom dealers and mycologists, who recognized differences between the two chanterelles (Danell 1995, Norvell 1995, Redhead and others 1997).

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[18] SEK (Swedish krona) is the abbreviation for Swedish currency stipulated by the International Organization of Standardization. The Swedish krona is also abbreviated Skr by the International Monetary Fund. Exchange rates vary daily; so all prices converted from non-United States currencies to dollars are approximate. These calculations were conducted December 11, 2002, when the exchange rate was 1 US$ = 9.01323 SEK.

Some European canning companies chose not to use the Pacific chanterelle because they discerned a difference in texture from the golden chanterelle of Europe (Danell 1994a). Consequently, Swedish canning companies imported about 90 metric tons of golden chanterelles from Eastern Europe in 1993. Europeans pay less for the white chanterelle of the Pacific Northwest than for the Pacific golden chanterelle because the Pacific golden chanterelle more closely resembles the golden chanterelle collected in Europe. In spite of these factors, Alexander and others (2002) state that prices for Pacific Northwest chanterelles remain nearly double what importers pay for chanterelles from Eastern Europe.

Although customer preferences can be fickle, they also can be modified with education and advertising. Certainly our Pacific Northwest white chanterelle is a good candidate for an educational marketing campaign in Europe because it is hefty, relatively abundant, and flavorful. As consumers continue to experiment with new products, other chanterelle species are likely to be marketed internationally. For instance, *Cr. tubaeformis* is considered inedible in Poland and deemed rather small to bother picking in the United States, but its popularity in Sweden is increasing because it tastes similar to the golden chanterelle, fruits abundantly, and is easily preserved by drying. Craterelles are appreciated as much as chanterelles in many parts of Europe (Dahlman and others 2000), and some species are commercially harvested in the Pacific Northwest as well (Arora 1999, de Geus 1995, Molina and others 1993, Schneider 1999). The black color of the horn of plenty (*Cr. cornucopioides*) deters consumption by some, but in Sweden and France it is considered a delicacy. British mycologist Cooke called it "…an excellent addition to the table" (Pegler and others 1997), and Arora (1986) says "…its flavor is superb and its potential unlimited." Other chanterelles such as the blue chanterelle and pig's ear gomphus are harvested for local or specialty markets in the United States but are not currently sold internationally in large quantities.

Understanding Chanterelles

As mushroom consumption increased in Europe during the middle of the 19th century (Ainsworth 1976, Persson and Mossberg 1997), so did interest in cultivating mushrooms other than the button mushroom (*Agaricus bisporus*). The complex symbiotic association between chanterelles and trees made cultivation a difficult challenge, however. In order to sustain natural crops of chanterelles in the forest and develop cultivation techniques, more knowledge was needed about the origin, biology, ecology, physiology, and chemistry of chanterelles. In this section we explore what is known about chanterelles as organisms. Although much of this information derives from research in Europe, we review it as a starting point for understanding Pacific Northwest chanterelles.

Chanterelle Evolution

Chanterelles belong to a group of fungi called Basidiomycetes, members of the phylum Basidiomycota (Alexopoulos and others 1996), a taxonomic category of fungi that also includes gilled fungi and boletes (among others). Recent protein analysis suggests that Basidiomycetes branched off from other fungi about 1.2 billion years ago during the Precambrian era (Heckman and others 2001), but the first undisputed fossils of land plants and fungi do not appear until the Ordovician period 480 to 460 million years ago. Fossils of mycorrhizae in 400-million-year-old Rhynie chert lend credence to the theory that mycorrhizae facilitated the colonization of land by vascular plants (Hibbett and others 2000). Evolutionary theorists suggest that as woody plant debris accumulated during the Carboniferous era, a variety of Basidiomycete species evolved the ability to produce enzymes that decompose cellulose and lignin (recalcitrant compounds in wood that simpler microorganisms find difficult to decompose). Mycologists believe that saprobic (decomposer) basidiomycete fungi evolved symbiotic ectomycorrhizal associations with tree roots during the Jurassic era (213 to 144 million years ago) when pines first appeared (Allen 1991, Pirozynski and Hawksworth 1988). Although genetic analyses suggest mycorrhizal fungi diverged 130 million years ago (Berbee and Taylor 1993), the oldest actual fossil of an ectomycorrhizal root tip is 50 million years old (Selosse and Le Tacon 1998), and the oldest gilled mushroom (preserved in amber) is about 90 to 94 million years old (Hibbett and others 1995). Pegler and others (1997) speculate that chanterelles are more primitive than gilled fungi (also subject to revision), but regardless of their actual antiquity, chanterelles have had ample time to colonize every continent except Antarctica and to differentiate into the several genera and numerous species now found worldwide.

Morphology and Physiology

A chanterelle individual is composed of a network of microscopic hyphae (one-cell-wide fungal filaments). Collectively, a network of hyphae is called a mycelium, and a chanterelle individual may be referred to as a mycelial colony. What we call chanterelle mushrooms are in fact the fruitbodies of a chanterelle mycelial colony (equivalent to fruits of green plants). Fruitbodies of basidiomycete fungi develop into a variety of forms, such as truffles, conks, or, in the case of chanterelles, mushrooms. Chanterelle fruitbodies begin as dense clots of mycelium that form primordia (miniature mushrooms that have the potential to grow to full size under favorable conditions). Fruitbodies have a layer of fertile tissue called the hymenium (in chanterelles, the ridges found under a cap and down the stem) that in turn generates microscopic reproductive structures (basidia in this case) where spores are produced and released.

Fungi are not photosynthetic; hence they must obtain their food from other living or dead organisms. Chanterelles live symbiotically with host trees, colonizing the fine roots of trees and forming structures called mycorrhizae (literally “fungus-roots”). Although all chanterelles are thought to be mycorrhizal, this has not been experimentally confirmed with all the species of the four genera called chanterelles. Chanterelle hyphae also permeate the surrounding soil, absorbing water and minerals that they translocate to host trees. In return for greatly extending the tree’s effective root system, the tree provides chanterelles with carbohydrates that are needed for growth and reproduction. Chanterelles form a type of mycorrhizae called ectomycorrhizae (plate 4), the prefix ecto- referring to a fungal sheath or mantle that forms around the root tips of a host tree (Smith and Read 1997). Chanterelles can form long-lived mycelial colonies (Jahn and Jahn 1986) if their tree partners continue to provide nutrition. Chanterelle ectomycorrhizae are not distinctive under field conditions; thus they were not well described until they were created under sterile laboratory and greenhouse conditions (plate 5) (Danell 1994a, 1994b; Danell and Camacho 1997).

Soils and Host Trees

Chanterelles grow in a wide variety of soils, but little is known about how chanterelles colonize field soils because their mycelium is diffuse and individual hyphae do not aggregate to form easily visible structures other than the mushrooms. The golden chanterelle grows best in well-drained forest soils with low nitrogen content and a pH range of 4.0 to 5.5 (Danell 1994a, Jansen and van Dobben 1987). In eastern North America and southern California, chanterelles associate with oak, beech, birch, and various conifers growing on a variety of soils derived from limestone, glacial till, sedimentary rock, or weathered granite. In the Pacific Northwest, chanterelles generally associate with Douglas-fir, hemlock, spruce, fir, and pine growing predominantly on volcanic, sedimentary, metamorphic, or sand dune soils.

Chanterelles have a very broad host range. One species alone, the golden chanterelle, has been reported to form mycorrhizal associations with trees in 14 genera: *Abies*, *Betula*, *Carpinus*, *Castanea*, *Corylus*, *Eucalyptus*, *Fagus*, *Picea*, *Pinus*, *Populus*, *Pseudotsuga*, *Quercus*, *Shorea*, and *Tsuga* (Danell 1999). However, because the name *C. cibarius* has been misapplied to what is likely a group of similar species around the world, this broad host range is more appropriately bestowed on the genus *Cantharellus* as a whole. Certain chanterelle species or varieties are thought to associate only with specific tree genera. For instance, the rainbow chanterelle (*C. cibarius* var. *roseocanus*) in the Pacific Northwest appears to associate only with spruce (Redhead and others 1997) or pine (see footnote 4). Similarly, in pure culture synthesis trials, Danell (1994b) noted that one strain of *C. cibarius* colonized spruce and pine roots, but not birch even though chanterelles fruiting under the different tree genera could not be distinguished by DNA analysis.

Fruiting

Chanterelles always fruit[19] in association with host trees. In forest plantations, chanterelles will begin to fruit when the trees are 10 to 40 years of age, depending on the climate and growth rate of the host trees (Danell 1994a, 1994b). Although chanterelles tend to fruit most abundantly in young or mature stands, they also occur in older forests. Love and others (1998), who interviewed harvesters on Washington's Olympic Peninsula, speculate that in dry years, stands with abundant, well-rotted, coarse woody debris might have better chanterelle crops than stands lacking this feature because more soil moisture is retained by the rotted wood. Chanterelles fruit abundantly in tree plantations, but not in nurseries unless specifically cultivated (Danell 1994a, Danell and Camacho 1997, O'Dell and others 1992). Chanterelle hunters in the Pacific Northwest commonly report disproportionate numbers of chanterelles fruiting along the edges of old logging roads or log skid trails, but potential explanations remain speculative.

Production can vary greatly from year to year and site to site. Among the many factors influencing chanterelle abundance in any given year, weather patterns are very important. Dahlberg (1991) suggests that warm spring weather promotes fruiting by encouraging rapid mycelial growth and abundant nutrient storage. In Oregon, a long-term chanterelle study conducted by Oregon Mycological Society members found a significant correlation between warm summers and chanterelle abundance (Norvell 1995, Norvell and Roger 1998). Reijnders (1963) notes that rain during primordia formation supplies moisture needed for cell elongation and mushroom growth. High soil humidity during the fruiting season also allows mushrooms to continue growing without drying out (Kasparavičius 2000). Chanterelle mushrooms grow slowly (2 to 5 cm per month) and persist for an average of 44 days and occasionally more than 90 days (Largent and Sime 1995, Norvell 1995), longer than many gilled mushrooms (Weber 2001), so consistently high humidity might be especially important in their development.

Insects and Parasites

Long-lived mushrooms, such as chanterelles, need to discourage hungry insects or animals, lest they be eaten before they can disperse their spores. Some chanterelle species are rarely infested with insects in spite of the 120 species of flies reported to feed on mushrooms (Hackman and Meinander 1979). One Finnish study found that

[19] Although "fruit" is technically a misnomer when applied to fungi, "fruiting" and "fruitbodies" are widely used in the mycological literature.

less than 1 percent of golden chanterelles were infested with larvae, compared to 40 to 80 percent of other mushroom taxa (Hackman and Meinander 1979). On the other hand, pickers report occasional heavy larval infestations in *C. lateritius* in the Southeastern United States, and wormy chanterelles have been documented in the Midwest (Smith 1949) and Great Smoky Mountains (Lacy 1984). Considering that most mushrooms and toxic plants are eaten by at least some adapted insects, it is surprising that neither the European nor the Pacific golden chanterelles become heavily infested during their long period of fruiting (Danell 1994a, Kälin and Ayer 1983, Norvell 1992b). Chemists Pang and Sterner (1991) and Pang and others (1992) suggest that insecticides might be formed in response to predation, but the compounds described have never been tested on insects. Slugs and snails also prefer other mushrooms, or even cannibalism, to chanterelles (Frömming 1954, Rangel-Castro 2001, Worthen 1988). North and others (1997) reported wildlife consuming more chanterelles than other mushrooms. Mammals, such as squirrels, sheep, wild boar, and moose are known to eat chanterelles (Danell 1994a, Fogel and Trappe 1978, Grönwall 1982). Contrary to these published reports, Pacific Northwest harvesters rarely report significant competition from wildlife such as deer, elk, and bear. Similarly, the authors have noted very little animal consumption of Pacific Northwest chanterelles in their field studies (Pilz and others 1998b), except in very dry years.[20]

Both fungi and viruses are known to parasitize chanterelles. Overholts (1929) reported the small gilled mushroom, *Entoloma parasiticum* (cited as *Claudopus subdepluens* in the original publication) growing from chanterelles. *Entoloma pseudoparasiticum* fruits exclusively on chanterelle hymenia (Noordeloos 1992). Helfer (1991) reported *Hypomyces odoratus* (a relative of the parasitic but edible lobster mushroom *Hypomyces lactifluorum*) growing as a parasite on *C. cibarius*. *Hypomyces semitranslucens* attacks *Cr. tubaeformis,* and the wilt fungus *Verticillium lecanii* infects *Cr. lutescens* (reported as *Cr. aurora*). Viruses occasionally cause growths on chanterelle caps, often affecting whole clusters (Blattny and Králík 1968). Other malformations might be caused by mutations in the chanterelle itself.

Reproductive Strategy

Many mushroom species produce large flushes of mature spores over a period of a week or two. This relatively rapid spore maturation and release might be an evolutionary adaptation to swift consumption of the mushroom by insects or mammals. Saprobic (decomposer) mushrooms that decay limited substrates, such as logs, might also release large quantities of spores to increase the probability of establishing new colonies before their nutritional sources are depleted. Chanterelles, by contrast, produce a continuous supply of slowly maturing spores over a period of a month or two. Spore development is less regular (Maire 1902), spore germination rates are low (Fries 1979), and the total number of spores released over the lifespan of the chanterelle is comparatively small (Danell 1994a).

Nevertheless, given that chanterelles can dissuade fungivores (organisms that eat fungi), form long-lived colonies, produce long-lived fruitbodies, and repair tissue at wound sites (Danell 1994a), their reproductive strategy of long-term, low-level spore

[20] Norvell, Lorelei; Roger, Judy. 2000. Unpublished data. Oregon Mycological Society chanterelle study. On file with: Pacific Northwest Mycology Service, LLC, 6720 NW Skyline Boulevard, Portland, OR 97229-1309.

dispersal appears to be effective (Danell 1994a). For example, in Denmark, chanterelles are now found in reforested regions of Denmark even though virtually the entire country was deforested two centuries ago.[21] Chanterelles are also harvested from plantations of nonnative trees in Scotland (Dyke and Newton 1999).

In spite of what we do know; questions of how, when, and under what condtions chanterelles thrive and reproduce remain among the most important gaps in our understanding of how to sustain chanterelle populations in perpetuity. In particular, we need basic research on spore dispersal and germination, conditions conducive to establishment and persistence of chanterelle colonies, population genetics, physiological interactions with arboreal hosts, and competition with other fungi.

Chemistry, Nutrition, and Health

> "Not only this same fungus [the chanterelle] never did any harm, but it might even restore the dead."
>
> —L. Trattinnick, Essenbarre Schwamme (nineteenth century). Quoted in Benjamin (1995), p. 68

The health effects of chanterelles, as with any complex natural food, can be expected to vary. For instance, Grüter and others (1991) state that chanterelle extracts have a weak mutagenic effect on bacteria, although less so than extracts from the button mushroom (*Agaricus bisporus*). Conversely, Grüter and others (1990) showed that *Cr. cornucopioides* extracts, in association with bacteria, inhibited the mutagenic action of aflatoxin (a highly carcinogenic mold toxin commonly found in peanuts) and benzopyrene (a compound in cigarette smoke). In his section on the medicinal effects of *C. cibarius*, Hobbs (1995) cites the *Icones of Medicinal Fungi from China* (Ying and others 1987) as asserting that chanterelles increase resistance to certain diseases of the respiratory tract and inhibit the growth of sarcoma.

Bicyclic carotenoids are the compounds responsible for the yellow color of many chanterelles (Arpin and Fiasson 1971, Gill and Steglich 1987, Mui and others 1998). Common in green plants, where they act as antioxidants, ultraviolet protectors, and pigments, these chemicals are rare in mushrooms (Gill and Steglich 1987). The golden chanterelle and *C. minor* both contain beta-carotene and small amounts of other carotenoids (Gill and Steglich 1987). Vitamin A, synthesized from beta-carotene, (Jensen and Salisbury 1984) is essential for good night vision (Stryer 1988), a fact that might explain the use of chanterelles by Chinese herbalists to treat night blindness. Carotenoids found in the pink-red *C. cinnabarinus* and the orange *C. friesii* are composed almost entirely of canthaxanthin, a pigment also found in salmon and flamingo feathers (Gill and Steglich 1987). Canthaxanthin is reported to protect human tissues from oxidative damage (Chen and Tappel 1996) and is sold as an antioxidant.

Carotenoids mediate responses to light in some fungi (Carlile 1970). Danell (1999) noted that chanterelles fruiting in a greenhouse grew toward a stationary light source. Perhaps this phototropic response promotes stem elongation for better spore dispersal. European and Pacific golden chanterelles are usually pale until after they emerge from moss or litter layers and become exposed to light. Chanterelles contain high levels of vitamin D (Mattila and others 1994), a vitamin synthesized from ergosterol when

[21] Svendsen, Ditte. 1998. Personal communication. Chief Forest Officer, State Forest District of Thy, Danish Forest and Nature Agency, Ministry of the Environment. Søholtvej 6, Vester Vandet, DK-7700 Thisted, Denmark.

tissues are illuminated. Chanterelle vitamin D concentrations vary considerably, but remain high even when the mushrooms are dried and stored for up to 6 years (Rangel-Castro and others 2002c). With inadequate dietary sources, humans can suffer vitamin D deficiencies during the dark winters in high latitudes because we synthesize it in our skin in response to sunlight. Next to cod liver oil, chanterelles are one of the most concentrated natural dietary sources of vitamin D, and are certainly an excellent choice for vegetarians. High vitamin D concentrations also might play a role in chanterelle ultraviolet protection and resistance to insect predation (Rangel-Castro 2001).

The nutrient value (dry weight basis) of mushrooms is high compared to many vegetables (Bano and Rajarathnam 1988). Protein content has often been overestimated, however, because analyses based on total nitrogen content include nondigestible chitin in the cell walls (Danell and Eaker 1992). Analyses based on amino acid content reveal that *C. cibarius* contains approximately 10 percent protein by dry weight (Danell and Eaker 1992). Fruiting bodies of *C. cibarius* have also been analyzed for levels of carbohydrates (Laub and Lichtenthal 1985), lipids (Aho and Kurkela 1978, Daniewski and others 1987), minerals (Vetter 1993), vitamins (Leichter and Bandoni 1980, Mattila and others 1994), and sterols (Kocór and Schmidt-Szalowska 1972). Additional mineral analyses of Pacific chanterelles from the Olympic Peninsula are shown in table 4.

Mushrooms are known to accumulate and concentrate toxic metals (Gast and others 1988, Obst and others 2001, Seeger 1982, Stijve 1993), a pertinent health concern for those who eat chanterelles from polluted areas. Grzybek and Janczy (1990) found that lead and cadmium levels in *C. cibarius* were lower than those in other edible species from the same site. Likewise, golden chanterelles collected in northern Europe accumulated less radioactive cesium-137 from the 1986 Chernobyl nuclear accident than many other species of edible mushrooms (Danell 1994a). It is possible that some heavy metals in fungi might not threaten human health, however, because Schellmann and others (1984) showed that cadmium and copper bind strongly to the indigestible cell walls. Chanterelles collected from the relatively less polluted natural environments of the Pacific Northwest might enjoy commercial advantages if their wholesome origin is emphasized.

The vernacular names listed in table 2 reflect the pleasant fruity smell of chanterelles. The olfactory compounds responsible for the chanterelle’s distinctive aroma are still unknown, but volatile chemicals found in highest concentrations thus far include octenols (responsible for the characteristic “mushroom” smell), caproic acid, acetic acid, and octa-1.3-dien (Breheret 1997, Buchbauer and others 1993, Pyysalo 1976). Chanterelles are especially prized for this fruity or apricot aroma and their nutlike taste with peppery overtones (Czarnecki 1986, Czarnecki and Wallach 1995), flavors best retained by cooking fresh chanterelles in butter, oil, water, or wine (Persson and Mossberg 1997). Canning, or lightly sautéing and then freezing, are popular means of preserving chanterelles, but dried chanterelles are usually chewy or rubbery when reconstituted (Fischer and Bessette 1992). Opinions differ about the relative flavor of different chanterelle species. Generally, young moist chanterelles seem to be more flavorful than older, rain-soaked specimens. Savvy cooks add apricots or apricot juice when preparing older, wet chanterelles.

Although chanterelles are generally considered one of the safest wild edible mushrooms, idiosyncratic allergic-type reactions have been reported to the North American Mycological Association’s poison registry (Benjamin 1995). Gerber (1989) states that consuming large quantities of chanterelles without chewing them properly can cause

Table 4—Mineral nutrient analysis of *C. formosus* fruiting bodies (bulked samples) from six sites on the Olympic Peninsula, Washington

Element (measure[a])	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Phosphorus (%)	0.64	0.052	0.6	0.64	0.81	0.42
Potassium (%)	5.23	4.85	4.54	5.39	6.12	3.19
Calcium (%)	.04	.04	.04	.03	.07	.04
Magnesium (%)	.12	.11	.12	.12	.17	.06
Sodium (%)	.01	.02	.02	.02	.07	.01
Manganese (ppm[b])	28	47	92	25	85	29
Copper (ppm)	30	39	27	30	34	15
Boron (ppm)	<1.0	<1.0	<1.0	<1.0	<1.0	<1.0
Zinc (ppm)	81	83	74	70	90	40
Selenium (ppm)	<4.0	<4.0	<4.0	<4.0	<4.0	<4.0
Sulfur (ppm)	1127	986	959	1038	1397	635
Carbon (%)	45.7	45.8	44.3	46.8	43.3	45.4
Sulfur (%)	.10	.09	.09	.09	.12	.07
Nitrogen (%)	3.18	3.98	3.06	3.23	3.89	2.67

[a] All but the last three values were derived from an inductively coupled plasma (ICP) spectral analysis after wet (hydrogen peroxide and nitric acid) digestion in a microwave oven. The last three values were derived from a LEUCO-CNS Analyzer. Nitrogen reflects total nitrogen, not the fraction in amino acids.

[b] ppm = parts per million by dry weight.

Data provided by Kermit Cromack, Jr., Department of Forest Science, Oregon State University, Corvallis, Oregon.

intestinal distress, and Persson and Karlsson-Stiber (1993) report that consuming *Cr. tubaeformis* with alcohol might in rare cases cause negative reactions. As with all wild mushrooms, chanterelles should be positively identified, cooked well, and sampled in small amounts when eaten for the first time. Lastly, Lehrer and others (1986) report that 5 percent of those with respiratory allergies are sensitive to chanterelle spores.

Human Impacts

The production and harvest of several chanterelle species have declined in parts of Europe during the past several decades (Arnolds 1985, 1995). For instance, the number of locations where chanterelles fruit in the Netherlands has decreased by 60 percent in 20 years (Arnolds 1988, 1991, 1995; Jansen and van Dobben 1987). Chanterelles have not been the only mushrooms affected. By the early 1990s, red lists of endangered and threatened mushroom species were being compiled throughout Europe (Arnolds 1992, 1995; Bendiksen and Høiland 1996; Deutsche Gesellschaft fur Mykologie e. V. 1992; Gärdenfors 2000; Kreisel 1990; Larsson 1997; Lizon 1993, 1995; Redhead 1997a). Air pollution (Gulden and others 1992), short timber rotations, clearcutting, depletion of forest soil litter layers (Arnolds 1990, Bendiksen 1994), and excessive mushroom harvests are some of the reasons suggested for this declining abundance of edible forest mushrooms.

Air pollution has certainly compromised forest health in parts of industrialized Europe. Whether the harm is caused by damaged foliage or polluted soils, the tree and its symbiotic partners (the mycorrhizal fungi) are both likely to suffer (Jansen 1991). Because the chanterelle mycelium usually grows in the upper 5 to 10 cm of the soil (Danell 1994b), it is readily exposed to air pollution deposits. Wallander and Nylund

(1992) showed that excess nitrogen can decrease fungal biomass, and Nohrstedt (1994) and Menge and Grand (1978) observed fewer mushrooms fruiting after fertilization trials. Arnolds (1988) suggested that excessive soil acidification resulting from sulfur or nitrogen deposits could alter the mobility of numerous toxic and essential elements. Removal of litter layers containing high amounts of nitrogen might restore chanterelle productivity in some cases (Arnolds 1991, Baar and Kuyper 1993, de Vries and others 1995), but removal of litter layers or coarse woody debris also diminishes habitat for saprobic forest fungi and wildlife populations.

Clearcut timber harvesting has the potential to shrink or eliminate chanterelle patches (mycelial colonies) by removing their carbohydrate supply, disturbing protective moss layers, or liberating toxic levels of nitrogen (Wallander and Nylund 1992). Prompt reforestation might allow established chanterelle patches to persist if planted tree seedlings form mycorrhizae with the chanterelle mycelium before its food reserves from the previous host trees are depleted. Analyses of DNA could determine the origin of chanterelles that fruit in recently regenerated stands. Such research would provide insights about the relative importance of spore dispersal versus persistent mycelial colonies for restoring chanterelle productivity in new stands.

As the decline in mushroom production in Europe became evident, some people suggested implementation of mushroom harvest restrictions (Ebert 1992, Jansen 1990). Several researchers, however, have found that picking has no negative impact on subsequent chanterelle fruiting (Arnolds 1991, Danell 1994a, Egli and others 1990, Jahn and Jahn 1986, Norvell 1995, Norvell and Roger 1998, Norvell and others 1996). Egli and others (1990) did report that intense trampling of study plots depressed fruiting, but they speculated the effect was temporary and resulted from crushed chanterelle primordia because fruiting returned to previous levels after the trampling treatments ceased.

Arnolds (2001) reported that many macrofungi fruited abundantly in the Netherlands in the summer of 2000, including species such as chanterelles that were previously noted to be in serious decline. Possible reasons include exceptionally favorable weather conditions and reduced acid rain and nitrogen deposition as pollution controls begin to take effect.

Regardless of the causes, less local fruiting and continued high demand have created a significant import market in western European countries. Depressed natural production in affected forests also has reinvigorated chanterelle cultivation research, but chanterelles have proven to be difficult to culture artificially.

Cultivation

Mushroom harvesters often spread old mushrooms around hoping to establish new patches by dispersing spores, but the efficacy of this well-intentioned practice remains unconfirmed. Scientists and entrepreneurs intent on establishing new chanterelle colonies need more reliable methods. One approach is to isolate the fungus of interest, grow it in pure culture, and then inoculate the mycelium onto tree seedlings that lack other mycorrhizae (Danell 1994a, 1994b, 1999; Danell and Fries 1990). Once such inoculated seedlings develop mycorrhizae, tree nurseries and their customers must be able to confirm the identity of the mycorrhizal fungus to ensure that contaminant fungi did not become established. Further, to demonstrate that this method will eventually lead to chanterelle-producing plantations, scientists must demonstrate that the inoculated mycorrhizae will persist on the seedlings after they are outplanted into soils where many competing mycorrhizal fungi already exist. Finally, in order to justify the expensive inoculation procedures, they must show that any chanterelles that ultimately fruit in these plantations are genetically derived from the original inoculated fungal strain, not naturally established colonies.

One reason chanterelles have been so difficult to cultivate is the presence of bacteria and other foreign microorganisms within the sporocarp tissues (Danell and others 1993). Bacteria, mainly fluorescent *Pseudomonas* but also *Streptomyces*, *Xanthomonas*, and *Bacillus*, are present in millions per gram of fresh weight (Danell and others 1993). Presumably these bacteria are incorporated in fungal tissues during primordium formation (Danell 1994a, Danell and others 1993), and grow actively between the cells without harming the mushroom (Danell and others 1993). Analyses show that amino acids, organic acids, and sugars released by chanterelles serve as a likely nutrient source for the bacteria (Rangel-Castro 2001, Rangel-Castro and others 2002a). Garbaye and others (1990) have noted beneficial interactions between bacteria and other mushrooms, and Rainey (1991) described the role of *Pseudomonas* during fruiting of the button mushroom. Rangel-Castro (2001) and Rangel-Castro and others (2002b) discuss the possibility that chanterelle mycelia obtain nitrogen indirectly by exuding enzymes that are used by associated bacteria to break down organic matter and then reabsorbing the resultant nitrogen-containing breakdown products. Regardless of their function, bacterial contamination has plagued all who have tried to culture chanterelles (Ballero and others 1991, Itävaara and Willberg 1988, Schouten and Waandrager 1979, Straatsma and others 1985). When chanterelle tissue is transferred to nutrient media, bacteria from the chanterelles grow more quickly than fungal hyphae, thus precluding subsequent isolation of uncontaminated chanterelle hyphae. Recently, Dutch scientists used an antibacterial nutrient media formulation (Fries 1979) to grow and isolate pure chanterelle mycelium from chanterelle tissues (Straatsma and van Griensven 1986, Straatsma and others 1985).

Genetically identifiable chanterelle strains are needed to positively verify culturing and inoculation success. Polymerase chain reaction (PCR), restriction fragment length polymorphisms (RFLP), and DNA sequencing are recent techniques used to check the identity of specific strains (Glick and Pasternak 1998). Many interesting studies on chanterelle physiology bear repeating with genetically identified cultures because sometimes even the species of an isolated strain was difficult to verify before the advent of DNA analysis (Ballero and others 1991, Doak 1934, Garza-Ocañas 1991, Hattula and Gyllenberg 1969, Pachlewski and others 1996, Riffle 1971, Siehr and others 1969, Strzelczyk and others 1997, Sugihara and Humfeld 1954, Torev 1969, Volz 1972). For instance, DNA analysis has shown that a chanterelle strain kept at the American Type Culture Collection (ATCC) was previously incorrectly identified (strain M83= NRRL 2370=ATCC 13228CBS 155.69).[22]

Once pure chanterelle strains have been isolated, they must be grown into sufficient quantities to inoculate seedlings. Chanterelle mycelia grow very slowly in pure culture (plate 6), a trait common to ectomycorrhizal fungi lacking their tree partner. At the optimal temperature of 20 °C, the growth rate on modified Fries medium (Straatsma 1998, Straatsma and van Griensven 1986) is 0.5 millimeters per day (Danell 1994a). After sufficient pure culture chanterelle inoculum is obtained, ectomycorrhizae are formed by inoculating the roots of aseptically grown tree seedlings. Doak (1934),

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[22] Stalpers, J.A. 1994. Personal communication. Researcher, Centraalbureau voor Schimmelcultures, Fungal Biodiversity Center, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.

Garza-Ocañas (1991), and Moore and others (1989) report successful chanterelle ectomycorrhiza formation by using standard and Straatsma's techniques. To facilitate rapid and routine seedling inoculation, Danell (1994a, 1994b) refined previous specialized techniques (Jentschke and others 1991, McLaughlin 1970) and demonstrated the importance of elevated carbon dioxide levels to chanterelle ectomycorrhiza formation (Magnusson 1992, Straatsma and Bruinsma 1986, Straatsma and others 1986). In addition to supplemental carbon dioxide, other critical elements of Danell's technique include: sterile inoculation chambers, aseptically germinated tree seedlings, continuous gas exchange through microporous filters, a dilute fertilizer and glucose solution vacuum-flushed through a quartz sand rooting substrate, and a computer to control the lights and the pumps for gas and nutrient exchanges (plate 7). Within 8 to 12 weeks, Swedish *C. cibarius* ectomycorrhizae can be reliably produced on the root systems of Scots pine, Norway spruce, and even North American ponderosa pine by using this method. No Pacific Northwest chanterelle has yet been successfully inoculated onto native tree species.

Danell planted some of his inoculated seedlings into pots in a greenhouse in order to investigate the persistence of artificially inoculated chanterelle ectomycorrhizae. During the next several months, chanterelle ectomycorrhizae became more abundant on well-colonized seedlings, although some newly emergent or noncolonized root tips developed ectomycorrhizae with common greenhouse contaminant fungi. In 1996, the first artificially cultivated chanterelles (plate 8) unexpectedly fruited from the drainage holes of these pots when the seedlings were only 16 months old and 0.5 meters tall (Danell and Camacho 1997). Analyses of DNA confirmed that the chanterelles were identical to the original inoculated strain of mycelium. No obvious environmental conditions triggered the fruiting; the greenhouse environment was relatively uniform, and fruiting occurred in April, June, and November. The chanterelles were not directly attached to the tree roots, but emerged from the top of the pot and from drainage holes, and then grew toward lamps that provided supplemental light. Although the strain used for inoculation was free of bacteria, all the chanterelles that grew in the greenhouse did contain bacteria. Why chanterelles fruited with seedlings in a greenhouse but natural populations of chanterelles only fruit with older trees remains a matter of speculation, but Danell (1994a) discusses the difficulties of spore reproduction in the field and postulates that the mycelium requires a level of carbohydrate saturation to fruit.

The relatively low market value of chanterelles (compared to truffles or matsutake, for instance), combined with the high costs of producing inoculated seedlings, suggests that greenhouse culture of chanterelles is unlikely to be profitable even if chanterelles fruit within 1 year of inoculation. Instead, plantations of inoculated seedlings might provide additional chanterelle crops as the trees mature (Danell 1997). Hall and Yun (2000) suggest that less valuable ectomycorrhizal mushrooms, such as chanterelles, might be better suited as secondary crops in forests managed for timber than in tree plantations predominantly intended for mushroom cultivation. Regardless of the primary management goal for inoculated plantations, the expense of inoculating seedlings in pure culture might be partially circumvented by planting nonmycorrhizal seedlings in close proximity to inoculated trees, thus allowing the selected strains of chanterelles to spread under nursery or plantation conditions (Danell 1999).

In June 1998, Danell outplanted 600 Scots pines inoculated with the golden chanterelle in 24 locations in southern Sweden. The experimental chanterelle orchards consist of tree seedlings planted 1.5 meters apart. At a mycelial growth rate of 15 centimeters per year in southern Sweden (Danell 1994a), identical mycelium from all the inoculated seedlings should theoretically fuse and fully occupy the soil habitat within 5 years. Annual sampling of ectomycorrhizae in these plots will determine the persistence and growth of the inoculated chanterelle strain. Whether chanterelles fruit on young seedlings in these field plots, as they did in the greenhouse, will be especially interesting.

Inoculated seedlings could either be sold to individuals hoping to create their private chanterelle patches or to entrepreneurs seeking to establish commercial chanterelle plantations. In France, Robin Nursery in Saint-Laurent-Du-Cros, sells tree seedlings inoculated with other species of edible ectomycorrhizal fungi. Established truffle orchards, grown from inoculated seedlings, are producing truffles in Europe and elsewhere (Chevalier and Frochot 1997, Giovannetti and others 1994, Hall and others 1998), and outplanting trials with *C. cibarius* on Scots pine have begun in Sweden (Danell 2001).

Lacking prior experience, prediction of chanterelle productivity in inoculated plantations is speculative at best, but some production seems probable. Careful site selection for favorable soil conditions will improve the likelihood of success. Nitrogen fertilization should be avoided, but irrigation might speed tree growth or improve chanterelle productivity in dry climates or in dry years.

The quantity, diversity, and competitive vigor of other resident ectomycorrhizal fungi are likely to be among the most important factors influencing potential chanterelle production in a plantation of artificially inoculated trees. In a review of truffle plantations in France, Chevalier and others (2001) report production of 8 to 46 $kg \cdot ha^{-1} \cdot yr^{-1}$ and note that one of the factors favoring successful truffle orchards is planting trees inoculated with truffle ectomycorrhizae into areas where only endomycorrhizal plants, such as grass, previously grew. Plantations also can be established in areas of the Southern Hemisphere where there are no ectomycorrhizal host plants, hence no competing native ectomycorrhizal fungi. One striking example of mushroom productivity in an exotic plantation has been reported from mountainous regions of Ecuador. There pines, unintentionally inoculated in the nursery with the edible slippery jack (*Suillus luteus*), were planted in native grasslands that lacked ectomycorrhizal fungi. Using different assumptions, Hedger (1986) reported a dry weight production of 569 to 1138 $kg \cdot ha^{-1} \cdot yr^{-1}$, Horton (1997) estimated 104 to 227 $kg \cdot ha^{-1} \cdot yr^{-1}$, and Chapela and others (2001) estimated 81 to 174 $kg \cdot ha^{-1} \cdot yr^{-1}$. Because these are dry weight biomass values, even the lower estimates are ten times greater than most fresh weight biomass estimates of ectomycorrhizal mushroom productivity (all species combined) in native temperate forests. Although these large estimates were extrapolated from seasonal samples, the assumption that a uniformly moderate climate allowed fruiting for 9 months of the year was derived from observations by local mushroom processors. If efforts to establish chanterelles in plantations in the Southern Hemisphere eventually succeed (Hall and others 1998), fresh crops from these countries would have the competitive advantage of being available during the off-season in the Northern Hemisphere. On the other hand, widespread introduction of ectomycorrhizal fungi into ecosystems that lack these fungi might pose the risk of extirpating native species or disrupting the food webs of native ecosystems. For instance, Wang and others (1997) state that until more research is conducted on the potentially semi-pathogenic nature of the Japanese matsutake (*Tricholoma magnivelare*), New Zealand and Australia are unlikely to allow importation for fear of harming pine plantations that support local timber industries. Nonnative ectomycorrhizal fungi will only invade an ecosystem if appropriate host trees also are present.

Pacific Northwest Chanterelles

Species Descriptions

In the following pages, we provide an identification key to ten chanterelle species and five look-alikes. The users can skip to key choice five if they are sure the specimen is in one of the four genera we discuss as chanterelles. Note that three of the four species of *Gomphus* are not considered edible. After the key, we describe in more detail seven prominent edible species (in alphabetical order by scientific name)—the rainbow chanterelle (*C. cibarius* var. *roseocanus*), the Pacific golden chanterelle (*C. formosus*), the white chanterelle (*C. subalbidus*), the horn of plenty (*Cr. cornucopioides*), the winter craterelle (*Cr. neotubaeformis* nom. prov.), pig's ears (*G. clavatus*), and the blue chanterelle (*P. multiplex*). Scientific names are those currently most accepted among mycologists. Scientific names are accompanied by the name of the authors who first validly published each species, followed by the publication date. These authorities and dates also correspond to citations in our "Literature Cited" section. Occasionally species were first described in one genus and later moved to another. In these cases, the name of the author who first described the species is placed in parentheses, followed first by the name of the author who placed the species into the current genus, and then by the date of the publication that combined that species and genus. The first common name that we list reflects our attempt at consistent and non-overlapping usage; other frequently used common names follow. Important features for distinguishing among similar chanterelle species are highlighted in bold type. The discussions of similar mushrooms are meant to assist the novice at becoming familiar with look-alike specimens they might encounter, but other similar mushrooms are likely to occur outside the Pacific Northwest. Always positively identify each mushroom before eating it, then cook the mushrooms thoroughly and start by consuming small amounts. Even "safe edibles" such as chanterelles can cause allergic reactions in some individuals. These descriptions are not meant as a definitive identification guide. If you are uncertain, seek additional information and advice. Table 5 lists popular field guides with additional photographs, keys, and descriptions for each species, and table 6 provides technical references.

Key to Pacific Northwest Chanterelles, Chanterelle-Like Mushrooms, and Look-Alikes

1. Underside of cap covered with soft, toothpick-like spines; fruitbody creamy to pale orange; resembling chanterelles only until turned over [orange hedgehogs] .... ***Hydnum repandum*, *H. umbilicatum***, & allies

1. Underside of cap with gills, wrinkles, ridges, or nearly smooth **2**

- **2.** Hymenium (spore-producing surface) consisting of true bladelike gills; gills thick, distant, unforked, orange to smoky gray from black spores; cap thick fleshed, orange, woolly [woolly pine spike] .... ***Chroogomphus tomentosus***

- **2.** Hymenium consisting of folds, wrinkles, ridges, or gills; if gilled, gills thin, crowded, and repeatedly forking **3**

3. Hymenium consisting of crowded, forked, very thin gills that are easily scraped off the underside of the cap **4**

3. Hymenium consisting of relatively shallow arching ridges, blunt folds, or wrinkles that are not easily scraped off the underside of the cap **5**

- **4.** Gills pallid to dingy yellow or browner, often staining reddish brown; spore print yellowish to reddish brown; taste sour or bitter [poison pax, brown chanterelle] .... ***Paxillus involutus*** [**POISONOUS**], ***P. vernalis*** & allies

- **4.** Gills brilliant to pastel orange, not staining; spore print white; taste bland [false chanterelle] ....***Hygrophoropsis aurantiaca***

5. Hymenium shallow veined, purple to violet colored when young (later dull ochre or tan); cap thick fleshed, often slightly off-center; stem not hollow; overall shape resembling a sow's ear [pig's ear gomphus] .... ***Gomphus clavatus***

5. Hymenium variously colored (including sooty or bluish black) but not distinctly purple or violet when young; with or without hollowed stems; trumpet-, fan-, vase-, or bun-shaped **6**

- **6.** Fruiting bodies blackish, bluish black, or sooty gray over all **7**

- **6.** Fruiting bodies white, creamy, pinkish, orangish, yellowish, reddish, or tan colored **8**

7. Cap trumpet shaped, yellow, brown, or gray, but typically very dark brown to black; hymenial folds smooth to unevenly lightly wrinkled, ash gray, brownish, salmon or rose-tinged, rarely yellow; stem gray, brown, or black; flesh relatively thin and tough; occasionally entire mushroom yellow with only stem base black; stem hollow [horn of plenty] .... ***Craterellus cornucopioides***

7. Cap fan shaped, deep blue black to purple; hymenial veins frosted with a heavy gray bloom; stem short, solid [blue chanterelle] .... ***Polyozellus multiplex***

8. Stem a hollow, puckered tube, dirty orange yellow; cap orange brown, convex to funnel shaped; hymenial ridges distinct, yellow orange at first, becoming lilac brown with age, stem base long remaining orange; usually on crumbly brown rotted wood or peaty soil [winter craterelle] .... ***Craterellus neotubaeformis*** nom. prov.

8. Stem either solid or short and not tubular **9**

9. Cap (and fruitbody) deeply vase shaped becoming slightly trumpet shaped, when mature often larger than a man's hand; cap surface very scaly to crumbly-scaly [*Gomphus*] **10**

9. Cap convex to depressed; cap surface smooth or with small, more or less flattened scales [chanterelles] **12**

10. Fruitbody large, fleshy-meaty; funnel-shaped cap cap tan to brown (no orange tones) with large woolly-felty scales that curve back toward or detach and fall into a pile of debris at the bottom of the funnel [Kauffman's gomphus] .... ***Gomphus kauffmanii***

10. Fruitbody similar, but with orange colors present and with scales not as readily breaking off and falling into the funnel **11**

11. Hymenial ridges deep, relatively close; cap bright rusty orange; hymenium and stipe yellowish to ochraceous [woolly or scaly vase chanterelle] .... ***Gomphus floccosus***

11. Hymenial ridges shallow, distant; cap salmon to foxy orange; hymenium and stipe cream to tan [Bonar's gomphus] .... ***Gomphus bonarii***

12. Fruitbody whitish overall (pallid, cream, ivory, or buff) [white chanterelle] .... ***Cantharellus subalbidus***

12. Fruitbody distinctly pigmented (yellow, gold, pink, ochre, orange) **13**

13. Hymenium usually paler than cap, pale yellow orange with a subtle to intensely pinkish cast; cap yellow orange beneath a thin brownish cuticle that (in dry weather) lifts into small appressed scales (squamules); flesh staining immediately yellow when bruised [Pacific golden chanterelle] .... ***Cantharellus formosus***

13. Hymenium rarely paler than cap, deep orange yellow with no to little pinkish cast; young cap covered with a pink or yellow pink "frost" (especially at the margin), lacking brown tones and always smooth; flesh not staining immediately yellow when bruised [rainbow chanterelle] .... ***Cantharellus cibarius* var. *roseocanus***

Scientific name—*Cantharellus cibarius* var. *roseocanus*[23] Redhead, Norvell, and Danell 1997

Common name—Rainbow chanterelle

Edibility—Choice

Description—Mushrooms up to 12 cm across, usually much smaller, **bright yellow orange overall**, cap usually bright orange yellow overall but margin covered with a thin pinkish bloom (possibly obscured when rain soaked); hymenium ridged, more or less brilliant orange yellow, as intensely colored as or darker than the cap, running from the cap edge well down the stem; stem usually relatively short solid, light yellow; flesh firm and fibrous, **bruising sparingly and very slowly**, with damaged areas noted as darker patches in older specimens; odor fruity apricotlike (slightly stronger than *C. formosus*). Spore print orange yellow. Under the microscope: basidiospores ellipsoid, smooth, colorless (6)[24] 7.5 to 10 (11.3) × 4.5 to 5.5 μm; clamp connections abundant in all tissues.

Range and habitat—The rainbow chanterelle is native to the region and apparently restricted to temperate western spruce and pine forests. The species has been confirmed from Oregon, Washington, and British Columbia, and likely also occurs in California (Steiger 1997). Rainbow chanterelles are ectomycorrhizal with Sitka spruce and shore pine along the coast and Engelmann spruce in the mountains. It generally fruits from August through October in old forests.

Similar mushrooms—Unlike the Pacific golden chanterelle, the rainbow chanterelle has a smooth cap that lacks closely appressed scales even when young, exhibits no immediate yellow staining when bruised, and has a darker spore print. The bright orange yellow ridges of the rainbow chanterelle lack a pinkish cast, so that any pink coloration is generally restricted to the outer cap margin. The intense pinkish coloration found in certain young or dry Pacific golden chanterelles, on the other hand, is found only on the hymenium.

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[23] The authors conservatively named this chanterelle as a variety of *C. cibarius* because the available genetic data were preliminary. Subsequent research might indicate it merits the status of a separate species.

[24] When values for size are given in parentheses, they represent outlier values that are occasionally encountered.

Scientific name—*Cantharellus formosus* Corner 1966

Common names—Pacific golden chanterelle, golden chanterelle, yellow chanterelle

Edibility—Choice

Description—Mushroom often big, up to 14 cm across, brightly colored with **dull orange to brown-orange cap** and stem; hymenium (fertile spore-bearing surface) deeply ridged, pale orange yellow and often with a pink cast, and running from the cap edge well down the stems; cap surface frequently with small closely adhering, slightly darker scales particularly visible in dry weather; flesh firm and fibrous, when bruised, at first yellowing slowly, eventually darkening to a dull ochre; **odor faint**, fruity, apricotlike, more noticeable in drier fresh specimens; taste mildly peppery when raw. Spore print yellowish white. Under the microscope: basidiospores ellipsoid, smooth, colorless, 7.2 to 9.2 × 4.7 to 6.1 µm; clamp connections abundant in all tissues.

Range and habitat—The Pacific golden chanterelle is native to western North American temperate coniferous rain forests. Collections have been reported from California, Oregon, Washington, and British Columbia under hemlock, Douglas-fir, and spruce. It is ectomycorrhizal and fruits from midsummer through late fall in young to old forests.

Similar mushrooms—As discussed in the section on Pacific Northwest chanterelles, a variety of very similar undescribed species of golden chanterelles likely exist in western North America. Macroscopic (visible without magnification) characters tend to overlap among these species depending on size, age, growing conditions, and moisture status of the specimens. Fortunately, they are all good edibles.

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Nonchanterelles frequently cited as look-alikes in field guides include the woolly pine spike (*Chroogomphus tomentosus*), the false chanterelle (*Hygrophoropsis aurantiaca*) and some *Clitocybe* species. These species, however, have bladelike gills rather than ridges underneath the caps, and even though the gills might be thick (woolly pine spike) or fork like the ridges on chanterelles, they are distinct from the flesh of the cap or stem. Orange hedgehogs (*Hydnum repandum* and *Hydnum umbilicatum*) also can be easily mistaken for the Pacific golden chanterelles when viewed from a distance or from above. Hedgehogs have white stems and a spore-bearing surface that consists of white to orange spines rather than ridges. Hedgehogs are choice commercially harvested edibles.

Although bearing scant resemblance to chanterelles, the poison pax (*Paxillus involutus*) is sometimes called the "brown chanterelle." This dull yellow brown mushroom (with yellow to olive crowded gills that run down the stem, stain brown, and separate readily from the cap) has been eaten in Europe (especially Poland) for centuries. Unfortunately, this common urban mushroom causes the rare "Paxillus syndrome" (immune hemolytic anemia) (Benjamin 1995) and has been implicated in a number of deaths. The toxins can accumulate in susceptible consumers over long periods of time with little effect, and then the next meal can cause sudden illness or death.

Scientific name—*Cantharellus subalbidus* Smith and Morse 1947

Common name—White chanterelle

Edibility—Choice

Description—Mushrooms up to 14 cm across, relatively compact, **cream to ivory colored overall**; cap generally darkening to a pale buff color when old or water soaked, entire mushroom becoming dark orange or rust color when very dry; hymenium of generally well-separated and long ridges, extending from the cap well down the solid stem; flesh firm, dense, cream colored, and slowly staining dull yellow when handled; **odor pleasant**, in fresh specimens reminiscent of apricots (contrary to Smith and Morse's original description); taste usually peppery when raw. Spore print white. Under the microscope: basidiospores ellipsoid, smooth, colorless, 7 to 9 × 5 to 5.5 µm; clamp connections abundant in all tissues.

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Range and habitat—White chanterelles, apparently mycorrhizal with Douglas-fir and hemlocks, are endemic to coastal and montane forests of California, Oregon, Washington, and British Columbia. They commonly fruit in late summer and early fall in mature to old forests.

Similar mushrooms—After harvest, white chanterelles can be confused with Pacific golden chanterelles because with handling the whites tend to yellow and darken, and the goldens lose color as they dry. Additionally, in the forest, golden chanterelles are sometimes pale to almost white when sheltered from light under duff or debris. Among chanterelles that might also be mistaken for white chanterelles are an unnamed British Columbia species that is very similar to the European pale chanterelle, *C. pallens* (Redhead and others 1997), and another reported by Thiers (1985) as *C. cibarius* var. *pallidifolius* from under tanbark oaks in California.

Scientific names—*Craterellus cornucopioides* Persoon 1825


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Craterellus fallax A.H. Smith 1968 and *Cr. konradii* Bourdot & Maire, previously treated as separate species, are now considered synonyms by Dahlman and others (2000). *Craterellus konradii* was the name previously given to the yellow form of this species.

Common names—Horn of plenty (*Cr. cornucopioides*), also known as the trumpet (or angel) of death and black chanterelle. The names black trumpet and deceptive horn of plenty are used to refer to *Craterellus fallax* when that species is viewed as distinct. The names angel of death and trumpet of death belie the fact that these mushrooms are choice and highly prized edibles: here "death" refers not to any toxic qualities but rather the somber dark brown to black color of the mushrooms.

Edibility—Arora (1991) describes this species as delicious and the most flavorful of the "chanterelles." They are highly prized in Europe but not eaten in Japan.

Description—Mushroom up to 6 cm across, **trumpet to funnel shaped**, thin, tough, hollow; caps sometimes yellow, brown, or gray, but typically very dark brown to black, inner top surface slightly feltlike and outer surface smooth; **hymenium slightly wrinkled (not ridged)**, ash-gray, brownish, salmon or rose-tinged, rarely yellow; stem gray, brown, or black; flesh relatively thin and tough; occasionally entire mushroom yellow with only stem base black; odor pleasant; taste mild when raw. The white spore print of *Cr. cornucopioides* has been used to distinguish it from the yellow/salmon-tinged spore print of *Cr.* fallax when they are recognized as separate species. Under the microscope: basidiospores off-round to ellipsoid, smooth, colorless, (7) 11 to 15 (20) × (5) 7 to 11 µm; clamp connections absent.

Range and habitat—Horns of plenty tend to grow in scattered groups or close clusters, often arising from a common base in humus or mineral soil. They are ectomycorrhizal with coniferous and deciduous trees (Dahlman and others 2000, Molina and others 1993). Although relatively common in eastern North America and abundant in the coastal regions of central to northern California, horns of plenty are uncommon north of southern Oregon. Redhead (1997a) cites only one unconfirmed report of *Cr. cornucopioides* (from a Vancouver Island foray) in his coverage of macrofungi in British Columbia. The horn of plenty fruits during the same cold weather as the winter craterelle—beginning in late fall in southern Oregon and continuing on into early winter and late spring in California.

Similar mushrooms—The horn of plenty is a relatively distinctive mushroom not easily confused with any other, except perhaps the blue chanterelle, *Polyozellus multiplex*. The clustered blue chanterelle is dark blue to gray violet (instead of brown or black) and is never hollow.

Scientific name—*Craterellus neotubaeformis* nom. prov.[25]

Previously misapplied names include *Cantharellus tubaeformis* Fr. : Fries 1821 and *Cantharellus infundibuliformis*, (Scopoli) Fries 1838.

Common names—Winter craterelle (previously called the winter chanterelle); outside of western North America it is also known as the autumn, funnel, or trumpet chanterelle.

Edibility—Edible and highly favored by some

Photo by David Pilz

Description—Mushroom **small, up to 5 cm across**, texture pliable; caps dark brown to brownish orange ochre with down-turned margin and **depressed center**, depression sometimes deep and continuing into the hollow stem, surface frequently scurfy with uneven short fibers or fine scales; hymenium of shallow, forked ridges, pale orange yellow to yellow gray or pale lilac brown; stems hollow, brilliant to dull orange yellow; odor and taste not distinctive when raw. Spore print white to yellow. Under the microscope: basidiospores slightly off-round to ellipsoid, smooth, colorless, 9 to 11 × 6 to 10 µm; clamp connections abundant in all tissues.

Range and habitat—Relatively common and abundant in moist coniferous rain forests of the Pacific Northwest from Alaska to northern California, winter craterelles are usually found scattered to clustered on well-decayed wood (illustrated in the species photo), or sometimes in soil and humus, near the roots of living trees and around stumps. Winter craterelles generally fruit November to May. *Craterellus neotubaeformis* nom. prov. was recently confirmed as a mycorrhizal species (Jonsson and others 2000, Trappe 2001).

Similar mushrooms—Novices might mistake the darker young forms of the false chanterelle (*Hygrophoropsis aurantiaca*) or other similarly colored mushrooms with gills that continue down the stem (such as *Chrysomphalina chrysophylla* or *Hygrocybe* species) for the winter chanterelle. All of these look-alikes, however, have bright orange, thin gills rather than ridges.

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[25] As noted in the section on North American chanterelles, Dahlman and others (2000) suggest that what has been called *Cr. tubaeformis* in the Pacific Northwest is a different species from the true *Cr. tubaeformis* from Europe. The provisional name used here incorporates this prior name to provide a link.

Scientific name—*Gomphus clavatus* (Persoon : Fries) Gray 1821

Common name—Pig's ear gomphus

Edibility—Good to choice when young, but frequently larval infested when old or in warmer weather. (Although the three other *Gomphus* species discussed in the "Similar Mushrooms" section below—*G. floccosus*, *G. kauffmanii*, and *G. bonarii*—are quite meaty and eaten by some, they have been known to cause digestive upsets and are not recommended edibles.)

Description—Mushroom up to 15 cm tall and across, yellow to olive-tan with violet tones, fleshy, club to peg shaped; cap initially purple-tinged and irregularly convex, later upturned and ruffled at the margin, smooth to slightly feltlike; hymenium of purple to lavender shallow wrinkled folds that extend almost to the stem base; stem relatively wide and solid; flesh firm, white to buff; taste not distinctive when raw and odor mild. Spore print color ochre to dark olive buff. Under the microscope, basidiospores long ellipsoid, warty-ornamented, yellow brownish, (9) 10 to 16 (17) × (4) 4.5 to 7 (7.5) µm; clamp connections abundant in all tissues.

Range and habitat—Solitary to clustered (often in arcs or circles) in rich soil and humus. The pig's ear gomphus is ectomycorrhizal with conifers and occurs from northern California to Alaska, and east (through the northern states and Canadian provinces) to the Atlantic. It is also found in Europe and Asia.

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Similar mushrooms—Although Arora (1991) notes that young clublike specimens are somewhat similar to club coral fungi, the pig's ear is not readily confused with other fungi. Smith and Morse (1947) originally noted a similarity with *Cr. pseudoclavatus*, a species that lacks clamp connections and apparently has been collected only once in northern California (Thiers 1985). The pig's ear gomphus lacks the hairy to scaly caps with deeply depressed to hollow centers characteristic of the three scaly vase *Gomphus* species found in North America (all of which also lack purplish folds and clamp connections). The common woolly or scaly vase chanterelle (*G. floccosus*) (plate 9) has a heavily to moderately scaly, bright to rusty orange cap. The less common Kauffman's gomphus (*G. kauffmanii*) and Bonar's gomphus (*G. bonarii*) are also characterized by having large, coarse to woolly scales. Kauffman's gomphus produces mushrooms with pale yellow brown to buff-colored caps (no red or orange tones present) and ochre- to cinnamon-colored spore "folds," whereas Bonar's gomphus grows in dense clusters, has orange buff, salmon, or foxy orange caps, dingy cream to tan shallow folds, and produces smaller basidiospores.

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Scientific name—*Polyozellus multiplex* (Underwood) Murrill 1910

Common name—Blue chanterelle, blue clustered chanterelle, black chanterelle (in Alaska)

Edibility—Good to choice

Description—Mushroom up to 15 cm across, fleshy, dark purple to deep blue black; caps slightly roughened and dry, often occurring in clusters above stems that are frequently fused; hymenium of shallow forked veins often extending down the stems, dark violet black to blue purple when fresh, becoming a paler gray violet when dried; flesh tough and somewhat brittle, dark purple; odor faintly pungent, taste mild and not distinctive when raw. Spore print white. Under the microscope, basidiospores ornamented with low bumps, colorless, 4.5 to 9 × 4.5 to 8 µm; tissues turn greenish black in potassium hydroxide; clamp connections present.

Range and habitat—Relatively rare and, in the Pacific Northwest, restricted to old coniferous forests from California's Humboldt County north to Alaska. Ectomycorrhizal with fir and Sitka spruce in British Columbia. The blue chanterelle is also found in the Rocky Mountains south to New Mexico and east to Maine at higher latitudes. It might be common in some areas. *Polyozellus multiplex* is also known from Japan (Imazeki 1953).

Similar mushrooms—The dark bluish black to purple color and clustered growth form make the blue chanterelle distinctive and not easily confused with any other mushrooms. *Craterellus cinereus* var. *multiplex*, although similar, is browner in color and has ellipsoid, smooth basidiospores; the pig's ear gomphus is fleshier, a much paler violet, and has much larger, roughened, ellipsoidal basidiospores.

Table 5—North American field guides treating two or more Pacific Northwest chanterelle species

	C. formosus **Pacific golden chanterelle**	***C. subalbidus*** **white chanterelle**	***Cr. neotubaeformis*** **nom. prov. winter craterelle**	***Cr. cornucopioides*** **horn of plenty**	**(= *Cr. fallax*)[a] black trumpet**	***G. clavatus*** **pig's ear gomphus**	***P. multiplex*** **blue chanterelle**
Arora 1986	*K, C	C	*C	C	D	C	C
Arora 1991	*C[b]	C	*C	C		C	C
Bandoni and Szczawinski 1976		B				*B	
Barron 1999			*C	C		C	C
Bessette and Sundberg 1987	*C		*C		C		C
Bessette and others 1997			*C[c]		C	D	
Biek 1984		K	*K	K, B		K	
Castellano and others 1999	C[d]						C
Castellano and others 2003		K, C	*K, C			K, C	K, C
Courtenay and Burdsall 1982			*C	C			
Evenson 1997							
Glick 1979		B	*B	B		B	B
Groves [and Redhead] 1979			K, C			K, C	K, C
Kibby 1992		C	C[c]		C		C
Lincoff 1981	*C	C	*C		C	C	C
McKenny and others 1987		C	*C			C	C
McKnight and McKnight 1987			*C	C		C	C
Miller 1978	*K, C	K	*C[c]	K, C		K, C	K
Miller and Miller 1988		*C	*C	C		C	
Molina and others 1993	*C	* C		C			
Orr and Orr 1979	K, C			D	K, C		
Persson and Mossberg 1997	C	C	*C	C	D	C	
Phillips 1991		C	*C		C	C	
Schalkwijk-Barendsen 1991			*C	D	*C		
Smith 1949	*K, C		*C[c]	*C		*K, C	* K, C
Smith 1975	*K, C	K, C					
Smith and Weber 1980					*K, C	* K, C	K, C
Weber and Smith 1985			*K, C		*K, C		

Note: Many field guides use previous scientific names or alternate common names. Consult appendix 1 for cross-references.
Legend: * = Entry in field guide listed under a previous scientific name or alternate common name, D = written description only, K = key provided, C = color photo or painting, B = black and white photo or drawing.

[a] Now considered the same species as *Cr. cornucopioides*, but listed in table 5 because most field guides treated them separately.

[b] The chanterelle shown on page 2 of Arora's (1991) mushroom guide is likely one of the yet undescribed (unnamed) California species.

[c] Eastern North American species (autumn craterelle). See discussion of *Cr. tubaeformis* and *neotubaeformis* nom. prov. in the "North American Chanterelles" section and under the species description for our western winter craterelle.

[d] Accuracy of color rendition best in Pilz photo.

Photo by David Pilz

Plate 1—Pacific golden chanterelles for sale at Pike Street Market in Seattle, Washington.

Photo by Lorelei Norvell

Plate 2—Closeup view of *Cantharellus formosus*, the common Pacific golden chanterelle. For at least 80 years, the name "*C. cibarius*" was misapplied to this Pacific Northwest native, which is, in fact, a unique species.

Photo by Eric Danell

Plate 3—Chanterelles exhibit a striking range of color variations and climatic adaptations. Pictured here is the black *C. congolensis* that grows in the Congo Basin in African countries such as the Democratic Republic of the Congo, Burundi, Tanzania, Malawi, and others.

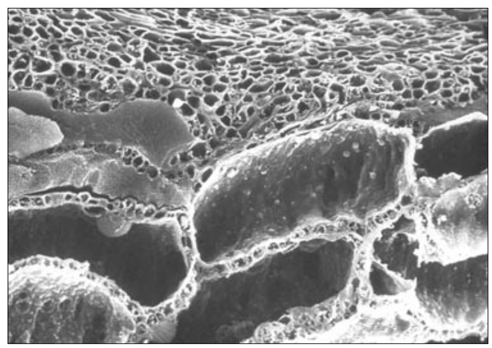

Photo by Eric Danell

Plate 4—Cross section of a *Cantharellus cibarius*/*Picea abies* mycorrhiza. The thin tubes on top are transected chanterelle hyphae, building up the yellow mantle. The big root cells belong to the spruce root. Scanning electron micrograph, 1900×.

Photo by Eric Danell

Plate 5—*Cantharellus cibarius*/*Pinus sylvestris* mycorrhizae grown in pure culture.

Photo by Eric Danell

Plate 6—*Cantharellus cibarius* mycelium growing on a special antibacterial agar in a petri plate.

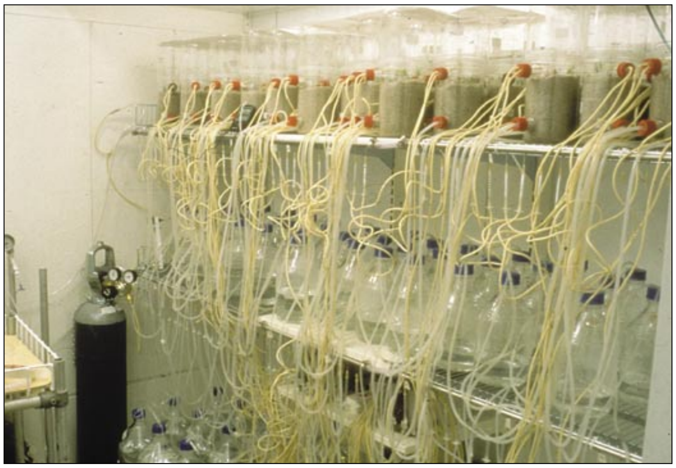

Photo by David Pilz

Plate 7—Danell's elaborate laboratory setup for inoculating pine roots with chanterelle mycelium in pure culture.

Photos by Eric Danell (closeup inset) and © Wes Colgan (potted seedling)

Plate 8—The first chanterelle ever to fruit from a pure culture inoculation. Oregon State University greenhouse, Corvallis, OR, June 1996.

Photo by Daniel Luoma

Plate 9—*Gomphus floccosus*, woolly or scaly vase chanterelle. One of the more common nonedible species of *Gomphus* that looks similar to chanterelles.

Photo by David Pilz

Plate 10—A basket of chanterelles collected on the Gifford Pinchot National Forest and for sale at a mushroom buying shed in Randle, Washington.

Photo by David Pilz

Plate 11—Field crew members Rita Claremont, Shannon Cleary, and Doni McKay mapping a chanterelle patch to study the effects of stand thinning.

Table 6—Taxonomic and technical research papers[a] on Pacific Northwest chanterelles

	C. formosus	*C. cibarius* var. *roseocanus*	*Cr. subalbidus*	*Cr. neotubaeformis* (and *Cr. tubaeformis*)	*Cr. cornucopioides* (and *Cr. fallax*)	*G. clavatus*	*P. multiplex*
Murrill 1910							T
Mounce and Jackson 1937							D, B
Shope 1938							D, B
Smith and Morse 1947	*D[b]		T, B	*K, D		*K, D, B	*K, D, B
Imazeki 1953							M
Corner 1966	T, K, W		K, D	*K, D	K, D, W	K, D, W	
Smith 1968				*K, D, B	*K, D, B, W	*K, D, B	
Peterson 1969	D[b]						
Peterson 1971a					D	D, K, C	
Peterson 1971b						D	
Peterson 1973						D	
Peterson 1975					D, C		
Bigelow 1978				*K, D, B	D, B	D, B	
Peterson 1979				*K, D, C	D, C		
Smith and others 1981			K, D	*K, D	K, D	K, D, B	K, D, B
Thiers 1985	K, D		K, D	*K, D	K, D	K, D	K, D
Tylutki 1987	K, D		K, D, B	*K, D		K, D, B	K, D
Feibelman and others 1994	G		G	G	G		
Largent 1994	*E						
Danell and others 1995	G	G	G				
Largent and Sime 1995	*E						
Hibbett and others 1997				G		G	
Redhead and others 1997	D, K, B, G	T, K, B, G	K, G				
Bruns and others 1998				G		G	
Bergemann and Largent 1998, 2000	E						
Pine and others 1999				G	G		
Dahlman and others 2000	G		G	G	G		

Note: Consult appendix 1 for previous synonyms.

Legend: * = Discussed under a previous scientific name or alternate common name, T = type description (description of the specimen upon which the species is named), D = description, K = key provided, C = color photo, W = watercolor painting, B = black and white photo or drawing, M = morphological analysis (including nongenetic chemical tests), G = genetic (DNA) analyses, E = ecology or fruiting substrate discussed.

[a] Listed in chronological order to reflect evolving species concepts.

[b] Early discussions of *C. formosus* in western North America.

Management and Research in the Pacific Northwest

Commercial Harvest

Evidence that Native Americans ate chanterelles is scarce. Although it is possible that ethnographers simply neglected to ask about mushrooms or tribes were reluctant to reveal all their cultural traditions and foods, many North American tribes (referred to as First Nations in Canada) seem to ignore or disdain mushrooms as food (Kuhnlein and Turner 1991). Turner and others (1990) do, however, document the consumption of chanterelles by the Thompson Indians, a Salish-speaking tribe in southern interior British Columbia. Goodrich and others (1980) also report that the Kashaya Pomo, whose homeland is in northern Sonoma County, California, were known to bake chanterelles on hot rocks.

European Americans have harvested chanterelles for personal use ever since they arrived in the Pacific Northwest. Chanterelles and other edible forest mushrooms supplemented the subsistence diets of settlers and several generations of their descendents[26] (Love and others 1998). Many regional mushroom clubs and mycological societies were also organized during the last century; their members eagerly collect chanterelles and other edible mushrooms for food and recreation (Brown and others 1985).

For many decades, recreational and subsistence mushroom harvesters found an abundance of mushrooms in nearby forests, but competition for those mushrooms changed markedly in the 1980s. As a result of litigation arising from the Endangered Species Act (ESA 1973), timber harvesting was dramatically curtailed on public lands managed by the U.S. Department of Agriculture, Forest Service (USDA-FS) and U.S. Department of the Interior, Bureau of Land Management (USDI-BLM). As a result, unemployed or part-time timber workers sought ways to supplement their incomes. Selling mushrooms came naturally to those who already had collected them for personal use and knew good harvest locations. Recent immigrants from Southeast Asia and Latin America also began harvesting mushrooms as international markets developed and demand increased. Love and others (1998) provide a thorough discussion of social, cultural, and economic aspects of chanterelle harvesting on Washington's Olympic Peninsula. Salient findings from their research include: (1) no one gets rich harvesting chanterelles, but many people seasonally supplement their incomes; (2) the low value and broad distribution of chanterelles encourage harvest by local residents rather than by traveling harvesters; (3) most recreational, commercial, and subsistence harvesters share an ethic of careful harvesting and an interest in sustaining harvest opportunities; (4) most harvesters understand the importance of forest management in maintaining productive chanterelle habitats.

The fact that harvester groups shared common interests was not immediately recognized. The emergence of large-scale commercial harvesting during the 1980s (plate 10) threatened many recreational harvesters who were disturbed by evidence that novice commercial harvesters disrespected both the chanterelles and their forest environment. They complained that commercial harvesters removed every mushroom in a patch, harvested small mushrooms before they matured, disturbed the forest floor to find young or hidden mushrooms, and littered. These problems gradually abated during the 1990s as landowners refined their harvest regulations and responsible commercial harvesters educated novices. Recreational harvesters came to realize that there are enough mushrooms for everyone, even if they had to search a little harder

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[26] Littke, Will. 1995. Personal communication. Forest Pathologist, Weyerhaeuser Company, Western Forestry Research, 505 N. Pearl St., Centralia, WA 98531.

or further, and that they shared many concerns with commercial harvesters, such as encouraging forest landowners to adopt sensible regulations and manage forests for mushroom habitat (Love and others 1998).

The early conflicts among harvester groups, and efforts of federal land management agencies to provide mushroom harvesting opportunities, provided much of the impetus for the research projects discussed later. These issues are not unique to the Pacific Northwest. The international market for edible forest mushrooms is creating local harvesting opportunities throughout all northern temperate forest regions. Interactions between harvesters and landowners differ widely depending on local traditions and land tenure, but global competition increasingly affects local prices and harvester profits. The Pacific Northwest chanterelle harvest cannot be adequately understood outside of this context, and conversely, Pacific Northwest management issues and research are internationally applicable.

Management Issues

Land tenure and management goals—Pacific Northwest forest lands include Native American reservation lands, national parks, national forests, USDI-BLM districts, state forests, state parks, county forests, corporate timberlands, and nonindustrial private timberlands. Consequently, forest management goals range from preservation through various multiple-use scenarios to industrial timber production. Although not all landowners have chanterelles on their property, each landowner category includes forests with chanterelles; therefore chanterelle-producing forests are subject to the full spectrum of management goals. Regardless of each landowner's primary objectives, the commercial mushroom harvest is an issue that almost all Pacific Northwest forest managers must face. Managing the chanterelle resource and its harvest entails many of the same issues as management of other edible mushrooms (Acker and Russell 1986, Amaranthus and Pilz 1996, de Geus and others 1992, Hosford and others 1997, Molina and others 1993, Pilz and others 1999, Redhead 1997b, Russell 1987) but differs in that chanterelles fruit in forests that span a larger geographic area than any other commercially collected mushroom in the Pacific Northwest. Additionally, commercial quantities of American matsutake (*Tricholoma magnivelare*) and western morel species occur predominantly on public lands, often in areas of low timber productivity or high elevation. Chanterelles, by contrast, fruit abundantly on both public and private lands, often in low-elevation forests that are highly productive for timber. The fact that chanterelles are so abundant and broadly distributed stimulates interest in their management among a wide range of stakeholders. For instance, the many cooperating landowners and volunteers in the Man and the Biosphere (MAB) chanterelle study on the Olympic Peninsula (Liegel 1998) exemplify this diversity of interest in chanterelles, their commercial harvest, and forest management activities that affect their abundance. The other research projects described in the next section also help illustrate the complex biological, ecological, silvicultural, social, and economic issues involved.

Northwest Forest Plan—Management of chanterelles in the Pacific Northwest United States has another interesting twist. The aforementioned Endangered Species Act litigation was resolved when the USDA-FS and USDI-BLM adopted management guidelines set forth in the Northwest Forest Plan, a product of President Clinton's 1994 Timber Summit (USDA and USDI 1994a, 1994b). A major goal was preservation of viable populations of species thought to depend on late-successional ("old-growth") forest habitats or structural legacy elements of old forests, such as large woody debris or snags. Two hundred and thirty-four species of fungi were included on the original survey and manage list, each allocated to one or more of four categories with different requirements for field surveys and management mitigations. Pilz and Molina (1996) discuss management issues and Castellano and others (1999, 2002) describe survey and manage fungus species. Some edible chanterelles were among the species listed, namely: *C. cibarius*, *C. formosus*, *C. subalbidus*, *Cr. tubaeformis* (*Cr. neotubaeformis* nom. prov.), *G. clavatus*, and *P. multiplex*. *Cantharellus formosus* and P. *multiplex* were placed in the highest priority survey category (strategy 1) because they were believed to be quite rare. At the time the list was created, mycologists erred on the side of caution and listed *C. formosus* as restricted to Corner's original collection site on Vancouver Island, British Columbia. Redhead and others (1997) subsequently reiterated the assertion by Petersen (1969), Thiers (1985), and Tylutki (1987) that *C. formosus* was really much more common, and demonstrated that the name should actually be applied to the common Pacific golden chanterelle found in all-aged forests throughout the Pacific Northwest. Revised guidelines for survey and manage species (USDA and USDI 2001) have recently been adopted, including procedures for removing or adding species. *Cantharellus cibarius* and *C. formosus* have been removed from the list, and *C. subalbidus*, *Cr. tubaeformis* (*Cr. neotubaeformis* nom. prov.), and *G. clavatus* are being reevaluated as more survey records are compiled. *Polyozellus multiplex*, on the other hand, is still considered uncommon and old-growth associated in the region. Newly identified chanterelle species might become objects of further surveys to evaluate their range, abundance, and habitats.

Harvesting impacts—One of the earliest concerns about commercial chanterelle harvesting was whether heavy harvesting would diminish subsequent fruiting. Although early research[27] with small-scale picking treatments applied to chanterelle patches does not support such a conclusion, the potential long-term or large-scale impacts of intensive commercial harvesting remain uncertain. Will harvesters bolster chanterelle reproduction and fruiting by spreading chanterelle spores and thus aiding the establishment of more colonies than would become established naturally? Or might they instead hamper chanterelle reproduction and fruiting by removing chanterelles before they disperse enough spores to replace colonies that die out? Such questions can only be addressed with long-term, broad-scale monitoring programs (Pilz and Molina 1998, 2002) or by a much better understanding of the reproductive biology, ecology, and population dynamics of chanterelles. Conducting statistically valid comparisons of chanterelle productivity across various forest habitats and alternate silvicultural regimes will further our understanding of how chanterelles respond to forest management decisions. Meanwhile, most interested parties agree on the importance of maintaining appropriate habitat to sustain chanterelles and their harvest.

Silviculture—Tree species composition, overall stand age, distribution of age classes, growth rates, and stand density can all influence chanterelle productivity because these factors affect the amount of energy (carbohydrates) allocated to mycorrhizal fungi by their host trees. Forest floor factors such as brush, debris, exposure, and soil compaction interact with weather patterns to create more or less favorable microenvironments for mushroom growth. Timber management activities routinely alter stand structure and forest floor conditions in Pacific Northwest chanterelle habitat; indeed, large areas of the region have been converted from old native forests to young timber plantations that often produce abundant chanterelles. When forests are managed for timber production by using clearcut harvesting, the intervals between clearcut log-

[27] See section on "Declining European Production."

ging are called timber rotations. Because chanterelles do not to fruit for the first 10 to 20 years of stand growth, conditions suitable for chanterelle fruiting exist for a greater portion of long rotations than of short rotations. For instance, if chanterelles start fruiting at 15 years of age in stands managed on a 45-year rotation, 66 percent of the rotation would be suitable for chanterelle production, but if the same stand were managed on a 75-year rotation, 80 percent of the rotation would be suitable for chanterelle fruiting. Stands managed for timber on longer rotations are often commercially thinned, and depending on the number, dominance, and species of the trees removed, temporary declines in chanterelle productivity levels are possible. Depending on the logging methods, frequent thinning can also result in more compacted soil than will infrequent thinning or clearcut harvesting. This is a concern for chanterelle productivity because compacted soils worsen conditions for the growth and development of ectomycorrhizae (Amaranthus and others 1996).

Even forests managed for preservation (such as parks) change over time, however, and will eventually be replaced after natural disturbances such as fire or windstorms. A better understanding of optimal chanterelle habitat conditions will provide forest managers with the knowledge needed to sustain or enhance chanterelle production while accomplishing primary management goals. On industrial timberlands, this could mean providing harvesting opportunities in conveniently located areas to promote favorable public relations with local communities or employees. On public lands managed for multiple use, modified thinning regimes or longer timber rotations could be used to augment chanterelle production in popular harvest locations. On lands managed for preservation or recreation (without timber harvests), understanding how forest conditions influence chanterelles could enable managers to determine human impacts on protected or rare chanterelle populations and regulate accordingly. Regardless of who owns the land, or what the management goals, a better understanding of the ecological relations between chanterelles and their forest habitats will be essential to sustaining chanterelle production and, eventually, to obtaining maximum production from artificially inoculated chanterelle plantations.

Recent Research

Recent Pacific Northwest chanterelle research encompasses taxonomy, population genetics, ecology, habitat modeling, harvesting methods and impacts, determinants of fruiting, productivity estimates, economic valuation, harvester sociology, and forest management activities. In this section we briefly describe some of these studies, cite available publications, and provide information for learning more about topics of particular interest. Describing ongoing research is problematic because citations are often lacking, research plans and personnel change, and we are not aware of all the research currently underway. Our intent is to portray the broad scope of current research devoted to chanterelles.

The Oregon Mycological Society (OMS) *Cantharellus* Project—In 1986, OMS members launched the first and oldest continuous chanterelle research and monitoring project in North America. Society members were concerned that chanterelles might decline in the Pacific Northwest, as had been noted in Europe. The research project was initiated by a small group of dedicated volunteers,[28] who approached the Mount Hood National Forest and City of Portland Water Bureau for permission to conduct a

[28] Frank Kopecky [Coordinator 1986-1988], Janet Lindgren, Lorelei Norvell [Project designer, Coordinator 1989–1991], and Maggie Rogers.

long-term chanterelle study in the Bull Run Watershed. The location, several miles behind locked gates and off limits to the general public, makes it one of the more secure mushroom study sites in the region.

The primary goal of the ongoing project is to determine whether harvesting chanterelles affects subsequent fruiting. Additional goals are to assess the impact of different harvest methods (pluck or cut), to correlate fruiting with weather patterns, and to inventory vegetation and other mushrooms on the 10 permanent study plots. The researchers have published methods and preliminary results in many publications (Norvell 1988, 1992a, 1992b, 1995; Norvell and Roger 1998; Norvell and others 1995, 1996; Roger 1998), and the study has been widely cited.

Thirteen years of data provide no evidence that plucking chanterelles has suppressed fruiting; indeed, the data suggest a slight stimulation of fruiting. Until 1999, no statistical correlation was noted between chanterelle productivity and harvest method, but since then a slight depression of chanterelle biomass and abundance has been detected in the "cut" plots relative to the pluck and control plots. Sixteen years of weather observations show a statistically significant positive correlation between chanterelle abundance and average summer temperature. A weaker correlation also exists with the amount of autumn rainfall. These results agree with similar studies (Bergemann and Largent 1998, 2000; Danell 1994a; Kotilova-Kubickova and others 1990; Ohenoja 1993; Straatsma and others 2001; Vogt and others 1992).

Since 1986, each chanterelle has been measured and flagged in place by using plastic sticks color coded by year. Casual observation of computer-generated maps and these highly clustered markers reveals that chanterelles generally fruit in the same spot year after year, the patches expanding only slightly as the forest ages. Slowly maturing chanterelles have persisted at the site for up to 90 days. Chanterelles in some of the plots consistently fruit earlier than others, perhaps in response to different microenvironmental conditions or as an expression of physiological differences between genetically unique mycelial colonies. From 1986 to 2001, 310 species of macrofungi (122 mycorrhizae, 119 soil saprobes, 61 wood saprobes or plant parasites, 8 fungal parasites) and 56 species of plants (40 vascular, 16 nonvascular) were recorded.

Opportunities for new studies have arisen from the long-term detailed data that have been collected. For instance, all harvested chanterelles have been dried and retained, and these voucher specimens are now undergoing DNA analysis to scrutinize colony size, interbreeding, and population diversity. Additionally, OMS is cooperating with Simon Egli[29] to correlate annual tree growth with chanterelle productivity, and then to compare the results with similar correlations derived from a long-term mushroom research site in Switzerland (Straatsma and others 2001). Educational applications also exist; given the detailed weekly mapping of every chanterelle location, each year's flux of fruiting patterns could be visually illustrated by making a short film clip with frames composed of weekly fruiting maps.

Notably, this study demonstrates that volunteers can make significant contributions to the advancement of scientific knowledge by conducting long-term research and monitoring activities. The OMS field mycologists and collaborating academic researchers

[29] Simon Egli, Researcher, Swiss Federal Institute for Forest, Snow and Landscape Research, Section Biodiversity, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

have donated expertise, materials, and over 7,000 hours of labor. The current OMS volunteer research team[30] continues to monitor the site every 2 weeks from May through December.

The MAB Chanterelle Study—Sponsored in part by the United Nations Man and the Biosphere (MAB) program, this 2-year study examined the biological, socioeconomic, and managerial aspects of chanterelle harvesting on the Olympic Peninsula of Washington. The study was reported as six articles in a special issue of *Ambio* (Liegel 1998).

Several aspects of the study are noteworthy. It was designed as an integrated, multidisciplinary study with the cooperation of stakeholders and landowners who represented almost[31] the full range of harvesting interests and forest management goals on the Olympic Peninsula (Liegel and others 1998a). The biological component documented the first nonbiased landscape-level estimates of chanterelle productivity (kilograms of fresh chanterelles produced per hectare per year) in the Pacific Northwest (Pilz and others 1998b). The first careful analysis comparing mushroom and timber values was derived from the typical chanterelle productivity values, local buying station prices for chanterelles, assumptions about harvester costs, and several timber management scenarios (Pilz and others 1998a). This was also the first sociological examination of the backgrounds, opinions, and concerns of recreational, commercial, and subsistence harvester groups, as well as the interactions among these groups and with landowners (Love and others 1998). The process of cooperative research improved communications among stakeholders and culminated in a public meeting to explore the meaning and usefulness of the research findings. Lastly, results were integrated across disciplines to develop management recommendations (Liegel and others 1998b) and to produce a university-level teaching case study about how to conduct integrated research and evaluate multidisciplinary sustainable forestry issues (McLain and others 1998).

Young Stand Thinning and Diversity Study (YSTDS)—Thinning young forest stands for timber production and other management goals is becoming increasingly common in the Pacific Northwest as planted trees grow together and become too dense for sustained vigorous growth. Thinning studies are expensive, but managers are interested in how their decisions influence wildlife, vegetation, stand development, and other forest products, such as chanterelles. In 1994, the Willamette National Forest (located in the central Cascade Range of Oregon) implemented a long-term cooperative[32] research project to examine how a variety of young stand thinning regimes and silvicultural treatments could be used to produce timber, enhance biological diversity, and speed the development of old-growth stand structure. Chanterelle

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[30] Adrian Beyerly, Mel Brink, Janet Lindgren, Kathy Patrick, Judy Roger [Coordinator 1992 to present].

[31] Unfortunately Native American tribal interests and lands were not included.

[32] Cooperators include Oregon State University, the Pacific Northwest Research Station (U.S. Department of Agriculture, Forest Service), the Cascade Center for Ecosystem Management, and Evergreen State College, WA. More information may be found on the Internet at http://www.fsl.orst.edu/mycology/youngstndthin/Yss.html.

mushroom productivity was included as an environmental response variable to examine the impact of thinning on recreational harvesting opportunites and their availability as nontimber forest products.

Four study sites (blocks of replicate stands) were chosen on the Blue River, McKenzie, and Middle Fork Ranger Districts. At each site, chanterelles were sampled in three 50-year-old stands: control stands (no thinning, 615 trees per ha), lightly thinned stands (270 residual trees per ha), or heavily thinned stands (125 residual trees per ha). Prethinning productivity was obtained for all 12 stands in 1994 to improve interpretation of the relative changes in productivity among stands after thinning. Control stands were sampled every following autumn (except 1998) through 2001. Postthinning chanterelle productivity was sampled in the thinned stands in the autumns of 1996, 1997, 1999, and 2001. Complete results will be published soon.[33]

Few published values exist for chanterelle productivity (reported here as fresh weight or numbers of fruiting bodies per hectare per year). Slee (1991), based on personal observations, estimated that 50 $kg \cdot ha^{-1} \cdot yr^{-1}$ [34] was possible in some Scottish forests. The MAB chanterelle project noted values from 0.076 to 21.947 $kg \cdot ha^{-1} \cdot yr^{-1}$ (1 to 1180 $chanterelles \cdot ha^{-1} \cdot yr^{-1}$), averaging 2.520 $kg \cdot ha^{-1} \cdot yr^{-1}$ (305 $chanterelles \cdot ha^{-1} \cdot yr^{-1}$).[35] In the YSTDS, chanterelle production across all the sites and years sampled ranged from 0 to 33.5 $kg \cdot ha^{-1} \cdot yr^{-1}$ (0 to 2251 $chanterelles \cdot ha^{-1} \cdot yr^{-1}$). Average production across all control stands for the 6 years they were sampled was 9.785 $kg \cdot ha^{-1} \cdot yr^{-1}$ (432 $chanterelles \cdot ha^{-1} \cdot yr^{-1}$). Importantly, almost all the stands sampled in the MAB project and the YSTDS were selected without prior knowledge of whether chanterelles grew in the stands or not, and the sample plots were delimited without prior knowledge of where chanterelles might fruit within the stands; hence these productivity values are unbiased landscape-level estimates of typical chanterelle productivity in Pacific Northwest forests. In the year immediately following thinning, productivity in lightly thinned stands was about 33 percent of controls and in the heavily thinned stands about 10 percent of controls, but fruiting appears to be rebounding after 7 years.

Selected patches of chanterelles and nearby ectomycorrhizal trees also are being mapped to examine how chanterelle fruiting patterns might shift in response to the removal of some adjacent host trees (plate 11). A few of these patches also have been sampled for genetic relatedness of the mushrooms (see “Taxonomy and genetics” below).

Bureau of Land Management fungal diversity studies—Since 1998, PNW Mycology Service and USDI-BLM Salem District researchers have conducted two concurrently running 5-year fungal diversity studies in Oregon’s Coast Range (Norvell

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[33] For more information, contact Randy Molina, Pacific Northwest Research Station (U.S. Department of Agriculture, Forest Service), 3200 SW Jefferson Way, Corvallis, OR 97331. Information is also available on the Internet at http://www.fsl.orst.edu/mycology/youngstndthin/Yss.html.

[34] See “English Equivalents” at the end of the text for conversions to “pounds per acre” or “numbers per acre” values.

[35] One of the highly productive chanterelle sites in this study had weight data, but not count data; therefore average chanterelle weights cannot be validly derived from these productivity values.

2000a, 2000b; Norvell and Exeter 1999, 2002a, 2002b, 2002c).[36] The Benton County density management study was designed to investigate species richness of ectomycorrhizal fungi in adjacent 65-year-old Douglas-fir stands undergoing five different thinning regimes: nonthinned control (420 trees per ha), three thinning intensities (300, 200, and 100 residual trees per ha), and a clearcut (no residual trees). The Pacific golden chanterelle, winter craterelle, and pig's ear gomphus were among 219 ectomycorrhizal mushroom species identified during 1998–2001. Preliminary post-thin (2000–2001) data show surprisingly early reestablishment of pretreatment (1998–1999) chanterelle fruiting patterns. Abundance was depressed in the heavily thinned stand, however, and only two chanterelles were obtained from the end of a clearcut transect within 20 m of live trees.

Chanterelles were also among 284 mycorrhizal species identified from the Polk County chronosequence study. The 1998–2001 data from 25-year-old, 55-year-old, and 150-year-old Douglas-fir/hemlock stands show that Pacific golden and white chanterelles fruit in both young and old-growth stands, whereas the winter craterelle has been collected only from the old-growth stand. Given the abundance of craterelles in the 65-year-old Benton County stands, however, their absence in this study's 50-year-old stand might simply be coincidental.

Other thinning studies—We know of four additional unpublished field assessments that examined chanterelle fruiting responses to stand thinning in the Pacific Northwest. Consistently, stand thinning does not eliminate chanterelle fruiting. Although reductions in fruiting after thinning are highly variable, general trends suggest that the more ectomycorrhizal host trees removed, the greater the reduction in fruiting and the longer the dip in production seems to last.

Ecological studies—One of the most thorough sets of studies to describe habitat and fruiting conditions for *C. formosus* (as *C. cibarius*) and *C. subalbidus* was conducted in northern California.[37] Researchers have documented and analyzed (1) correlations between the environment and fruiting (Largent 1994); (2) plant associations, stand characteristics, fruiting seasons, fruitbody lifespans, and spore production (Largent and Sime 1995); (3) plant associations and stand characteristics of montane Pacific golden and white chanterelle habitats (Steiger 1997); and (4) site-specific silvicultural and soil variables (Bergemann and Largent 2000). Among their many findings, they noted the long lifespan of chanterelle sporocarps, lengthy fruiting seasons, long periods of sporulation, *C. subalbidus* occurring on higher pH soils and in areas of deeper duff than *C. formosus* sites, and the preference of *C. formosus* for soils with low exchangeable acidity.

Taxonomy and genetics—We described earlier taxonomic research in our introduction to chanterelles, but much work continues. New insights continue to emerge as characters revealed through DNA analysis are used to refine taxonomic distinctions that were originally based on morphological characters alone. The Northwest Forest

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[36] For more information, contact author Lorelei Norvell or botanist Ronald Exeter, Salem District Office, U.S. Department of the Interior, Bureau of Land Management, 1717 Fabry Road SE, Salem, OR 97306. Information is also available on the Internet at http://www.pnw-ms.com.

[37] Professor David Largent (and graduate students), Humboldt State University, 1 Harpst Street, Arcata, CA 95521-4957.

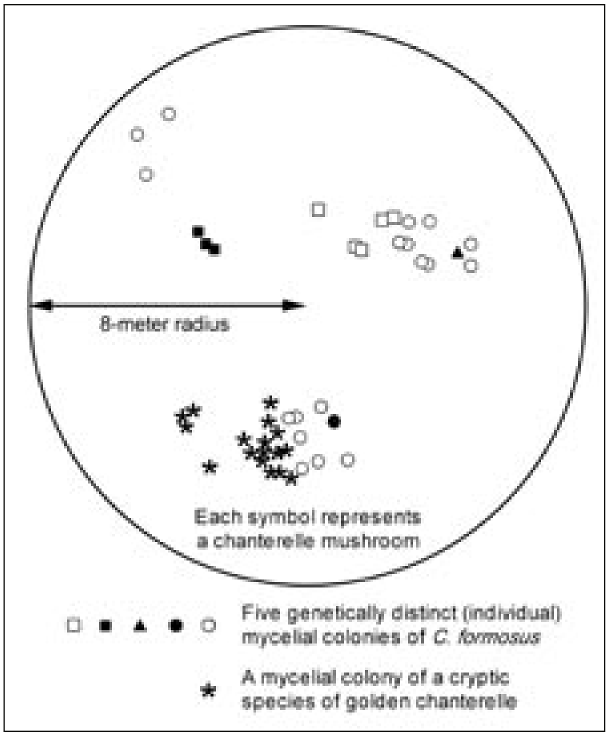

Figure 1—Genetic diversity of chanterelles fruiting in proximity (results of DNA analysis by Susie Dunham, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752).

Plan has funded many of the recent taxonomic, habitat, and distribution studies of *Cantharellus*,[38] *Craterellus*,[39] and *Gomphus*[40] species in the Pacific Northwest because clear species distinctions are required to judge whether a listed fungus actually requires old-growth forest habitat.

In addition to applying DNA analyses to species distinctions, researchers are using similar techniques to understand genetic variation and interbreeding dynamics within chanterelle populations. For example, figure 1 illustrates the genetic diversity found in one chanterelle patch measuring only 16 m in diameter. University of Washington researchers[41] are investigating spatial and temporal variation in the genetic diversity of chanterelle colonies on the Olympic Peninsula and how that diversity might respond to chanterelle harvesting.

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[38] Susie Dunham and Kelly Collins, Ph.D. students, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752.

[39] Matt Trappe, Ph.D. student, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752.

[40] Admir Giachini, Ph.D. student, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752.

[41] Rusty Rodriguez, Researcher, Biological Resources Division, U.S. Department of the Interior, Geological Service, Seattle, WA 98115 and Professor Joseph Ammirati, Department Chair, Department of Botany, University of Washington, Box 355325, Seattle, WA 98195-5325.

Habitat modeling—We use the term "model" to denote a conceptual or mathematical representation of our knowledge about the natural world. Although often designed as predictive tools, models also clarify the importance of what we already know, how items of information relate to each other, and what information still needs to be acquired to make predictions that are accurate enough to be useful. The Northwest Forest Plan has fostered habitat modeling research to predict where chanterelles are likely to occur and what habitat attributes are important for their reproduction and growth. Cantharelloid fungi were selected as prototypes for efforts to model the habitat requirements of other old-growth-associated fungi because chanterelles range from common and widespread (*C. formosus*) to rare and found only in old forests (*P. multiplex*). Chanterelle habitat information has been derived from published literature, herbarium records, research, and new surveys (Dreisbach and others 2002).

For instance, *Cr. tubaeformis* (*Cr. neotubaeformis* nom. prov.) is a survey and manage species typically found fruiting from well-rotted coarse woody debris, a structural component of old-growth forests that can be found in young stands if logs are left after logging or remain after stand replacement disturbances such as fire. Although recently confirmed as a mycorrhizal species, the winter craterelle also has been confirmed as a close associate of well-decayed coarse woody debris (Trappe 2001). Mass spectrometry of C^{13}/C^{12} isotope ratios suggests that the winter craterelle obtains carbohydrates from decomposition as well as from its mycorrhizal association with live trees (Hobbie and others 1999, 2001; Trappe 2001). Paired sets of old and young stands with high and low levels of coarse woody debris are being surveyed in the Coast and Cascade Ranges of Oregon to test potential association with coarse woody debris for survey and manage fungus species other than the winter craterelle.[42] Chanterelles are frequently encountered on these survey sites and will be included in a habitat model that predicts the likelihood that a given species will occupy habitat with known levels of coarse woody debris.

A frequent criticism of academic or government research is that scientists too often disregard the expertise of skilled harvesters who are keen observers of variation in mushroom characteristics, preferred mushroom habitats, ideal stand conditions, and environmental factors that induce fruiting. Obtaining, evaluating, and publishing such data, however, can be challenging. Many harvesters hesitate to share information they have worked long and hard to accumulate, particularly when scientists have neglected to acknowledge or compensate them for information they previously shared. In addition, harvester information is often intuitive or anecdotal, and sometimes contradictory. In spite of these difficulties, "expert" models can be designed that combine qualitative information (expert opinions of scientists or harvesters) with quantitative data (field surveys). Such models use rules and probability-based decision trees to calculate the likelihood of resulting predictions. For example, the probability that a particular species of chanterelle would occur in a habitat with certain features could be predicted. The models might be interactive, responding to queries submitted by users. Alternately, data about the probability of occurrence could be fed into geographic information system databases to produce maps of probable distributions. Probability of chanterelle

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[42] Efrén Cázares-Gonzalez, Assistant Professor, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752 and Tina Dreisbach, Interagency Regional Mycologist, Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331.

occurrence then could be combined with productivity estimates to predict landscape or regional abundance. Much of this work remains developmental, but such models will help planners evaluate the chanterelle resource, especially in the context of large-scale multiple-resource management plans.

Future Research

Taxonomy, augmented by DNA analysis, will remain an essential underpinning of all chanterelle studies. Until clear taxonomic classifications, habitat preferences, and distributions are developed for chanterelle species, other investigations will be hampered by ignorance of the precise organism being studied. How chanterelles have evolved and dispersed over geologic time will become more apparent as genetic and physiological research begins to explain adaptations to changing habitats and hosts. In combination with studies of population dynamics and reproductive strategies, such research will better equip us to sustain viable chanterelle populations despite mounting human pressures such as habitat degradation or increased harvesting.

Equally essential to sustainable harvests is a monitoring program that evaluates potential large-scale, long-term changes in chanterelle populations or productivity. Declines in edible mushroom productivity in Europe and Japan were only documented after several decades had passed and fruiting had decreased so much the change became obvious. Because widespread mushroom harvesting, discernible pollution, and intensive forest management are more recent phenomena in the Pacific Northwest than in Europe, we have an opportunity to evaluate chanterelle productivity before major changes occur. By initiating a statistically valid regional monitoring program (Pilz and Molina 1998) with tested and standardized sampling protocols, small changes should be detectable earlier than was the case in Europe and Japan. The monitoring program could be frugal, but it must be long term.

Habitat quality and available food are critical factors affecting the range and abundance of any species. Predicting how forest management activities influence the quantity and quality of future chanterelle habitat will allow managers to plan for continuous chanterelle harvesting opportunities as the mosaic of forest conditions shifts across the landscape through time. Future research, still in the planning stages (Pilz and others 2002), is designed to investigate how silvicultural conditions of a stand (tree species composition, stand age, size class distribution, stand density, tree species dominance, growth rates) interact to determine the quantity of carbohydrates allocated underground to ectomycorrhizal fungi for their growth and fruiting. Sample estimates of the percentage of chanterelle ectomycorrhizae in a stand (relative to ectomycorrhizae of other fungi) could then be used to calculate the proportion of such carbohydrates that are available specifically to chanterelles for their growth and fruiting. Efforts are underway to develop monoclonal antibody marker systems that would facilitate quick quantification of chanterelle ectomycorrhizae for this purpose. Although annual productivity is strongly influenced by seasonal weather patterns, this approach will allow managers to predict how their silvicultural choices affect multiyear average chanterelle productivity.

Chanterelles will be harvested from forests for the indefinite future, but efforts to grow them in plantations likely will also proceed apace. As humanity seeks more resources from a fixed or shrinking forest land base, intensive multiple-resource management and domestication of additional species are often-used strategies that already are being applied to chanterelles. Chanterelles are harvested from a spectrum of habitats that range from natural native forests to intensively managed exotic timber plantations. Chanterelles can, and will be, intentionally encouraged in all these types of habitats because humankind has learned to appreciate their aesthetic, culinary, and commercial values. Knowledge about the interactions between chanterelles, their ectomycorrhizal tree hosts, and the habitats where they grow will be useful in any context where chanterelles are managed, cultivated, or harvested.

Many aspects of chanterelle research and management are likely to remain interdisciplinary and cooperative. As this publication has illustrated, the topic of chanterelles is multifaceted and the list of interested parties is long. Only a comprehensive and inclusive approach can do the subject justice, to say nothing of the organisms themselves.

Closing Remarks

> "Suitable for cooking."
> —Linnaeus, *Flora Oeconomica*, 1748

Carl von Linné was, intentionally or not, a master of understatement. Nevertheless, few North Americans or Swedes ate mushrooms 250 years ago when the founder of modern taxonomy was developing his system of botanical nomenclature. Since then, the reputation of chanterelles as safe, vitamin rich, and delicious mushrooms has flourished globally as cultures interact, people migrate, and trade expands. The economic and culinary future appears bright for chanterelles. Abundant, widely distributed, and highly valued, chanterelles are a resource more resilient and sustainable than many other natural products that humans harvest, sell, and use. Edible forest mushrooms are increasingly being integrated into forest management plans wherever they occur. Commercial harvesters, distributors, retailers, chefs, consumers, subsistence harvesters, recreational harvesters, members of mycological societies and mushroom clubs, artists, scientists, foresters, environmentalists, and the general public all have a common interest in guaranteeing the perpetual availability of chanterelles. Working together, we can enjoy them for a long time to come.

Glossary

See Kirk and others (2001) for a complete glossary of mycological terms.

basidia—Microscopic clublike structures that form on the hymenium of fungi in the Basidiomycetes and are the site of meiosis and spore development.

basidiospores—Spores (for sexual reproduction) produced on basidia by fungi in the Basidiomycetes.

clade—A group of organisms (regardless of taxonomic ranking) that evolved together through time. Recent DNA analyses frequently delineate clades of genetically similar fungi that include some species that were previously placed (based on morphological distinctions) in dissimilar genera, families, and orders.

clamp connections—Distinctive microscopic structures that form a secondary bridge or connection between two adjacent hyphal cells. Found only, but not always, in fungi of the class Basidiomycota.

ectomycorrhiza—A type of mycorrhiza where the fungus covers the root tip with an outer ("ecto") mantle of hyphae, penetrates between the outer cells of the root tip, but does not penetrate into the root's cells. Ectomycorrhizae (plural) are common with trees in temperate forests and with fungi that produce mushrooms and truffles.

fungivore—An organism (typically animals, insects, or mollusks) that eats fungi.

hymenium—Spore-bearing surface of a mushroom. The hymenium can take the form of gills (as in button mushrooms), ridges (as in chanterelles), tubes (as in boletes), or other structures.

hyphae—One-cell-wide filaments of cells that constitute the "body" of multicellular fungi and converge to form structures such as mycorrhizae or mushrooms.

mycelium—A web of hyphae that colonizes a substrate such as soil or decaying organic matter. Sometimes used in reference to a "colony" of a fungus individual.

mycology—The study of fungi.

mycophagy—Eating fungi.

mycophilic—Fond of fungi (especially eating them).

mycophobic—Fearful of fungi (especially eating them).

mycorrhiza—From Greek, "mykes" = fungus and "rhiza" = root. The structure formed when the mycelium of a fungus associates symbiotically with the roots of a plant. The fungus acts as the fine root system for the plant, providing it with water and mineral nutrients absorbed from the surrounding soil, and the plant in return provides the fungus with carbohydrates produced through photosynthesis. Mycorrhizae is the plural form commonly used in North America; mycorrhizas often is used elsewhere.

pileus—Mushroom cap.

saprobes, saprobic—Decomposers, decomposing.

sensu lato—Latin for "in a broad sense." The term is used after species names to indicate that the definition of a species is being interpreted broadly or loosely in that specific context. It is abbreviated "s.l." When "sensu" is used between a scientific name and a citation, it means taxonomic criteria or distinctions should be considered in the sense described in the publication.

stipe—Mushroom stem.

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English Equivalents

When you know:	Multiply by:	To find:
Microns, micrometers (µm)	0.000039	inches
Millimeters (mm)	0.039	inches
Centimeters (cm)	0.394	inches
Meters (m)	3.281	feet
Kilometers (km)	0.62	miles
Hectares (ha)	2.471	acres

Kilograms (kg)	2.205	pounds (lb)
Metric ton (t)	1.1023	short (US) ton
Metric ton (t)	2204.6	pounds
Kg per ha	0.8922	pounds per acre
Chanterelles per ha	0.404	chanterelles per acre
Celsius (°C)	1.8, then add 32	Fahrenheit

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Appendix 1—Common Names, Scientific Names, and Synonyms

We use unique common names in this text, but other common names (indented) overlap among some species. Only English common names are listed; common names might well exist in other languages. Additional common names do not necessarily correspond to the additional synonyms that are sometimes listed opposite under the scientific name. Entries are alphabetical by scientific name. Citations are provided for recent names or name changes. The currently accepted name is listed first. Synonyms follow, prefixed by an "=".

Common English names	Scientific names
***Cantharellus* (*C.*) species:**	
Chanterelles (inclusive or broad usage)	Species of the genera *Cantharellus*, *Craterellus*, *Gomphus*, and *Polyozellus*
true chanterelles	Species of the genus *Cantharellus* (Dahlman and others 2000)
Appalachian chanterelle	*C. appalachiensis* Petersen
none	*C. atrolilacinus* nom. prov. (Halling and Mueller 2000)
boreal chanterelle	*C. borealis* (Petersen and Ryvarden 1971)
golden chanterelle European golden chanterelle	*C. cibarius* Fr.
amethyst chanterelle wine-colored chanterelle	*C. cibarius* var. *amethysteus* Quél. = *C. amethysteus* (Quélet) Saccardo
American pale chanterelle	*C. cibarius* var. *pallidifolius* A.H. Smith
rainbow chanterelle	*C. cibarius* var. *roseocanus* (Redhead and others 1997)
cinnabar chanterelle red chanterelle	*C. cinnabarinus* Schw.
Australian chanterelle yellow chanterelle	*C. concinnus* Berk (Eyssartier and Buyck 2001b) = *C. cibarius* var. *australiensis* Cleland
none	*C. congolensis* Beeli
Pacific golden chanterelle Pacific chanterelle golden chanterelle yellow chanterelle	*C. formosus* Corner (Redhead and others 1997) (often erroneously called *C. cibarius* Fr., but not a synonym)
orange chanterelle	*C. friesii* Welw. & Curr.
none	*C. ianthinus* Corner
smooth chanterelle	*C. lateritius* (Berk.) Sing. = *Cr. cantharellus* (Schw.) Fr.
none	*C. longisporus* Heinem.
blackening chanterelle	*C. melanoxeros* Desm. = *C. ianthinoxanthus* (Maire) Kühner = *C. ianthinoxanthus* Corner
small chanterelle	*C. minor* Peck

Common English names	Scientific names
none	*C. ochraceoravus* Grgurinovic
European pale chanterelle	*C. pallens* Pilàt = *C. ferruginascens* Orton
none	*C. platyphyllus* Heinemann
none	*C. pseudocibarius* Hennings
none	*C. pseudominimus* (Eyssartier and Buyck 1999b)
none	*C. pudorinus* Corner
none	*C. romagnesianus* (Eyssartier and Buyck 1999b)
white chanterelle	*C. subalbidus* A.H. Smith & Morse
none	*C. subcibariu*s Corner
none	*C. symoensii* Heinemann
none	*C. viscosus* Berk
***Craterellus* (*Cr.*) species:**	
none	*Cr. boyacensis* Singer
black craterelle black or gray chanterelle	*Cr. cinereus* (Pers. : Fr.) Persoon = *C. cinereus* Pers. : Fr.
none	*Craterellus cinereus* var. *multiplex* (Smith) Smith 1968 = *Cantharellus cinereus* f. *multiplex* Smith 1953
horn of plenty fairy's loving cup trumpet of death black chanterelle	*Cr. cornucopioides* (L. : Fr.)Pers. = *Cr. konradii* Bourdot & Maire (yellow variety)
black trumpet horn of plenty deceptive horn of plenty angel of death trumpet of death	= *Cr. fallax* Smith
none	*Cr. costaricensis* Wu
fragrant black trumpet	*Cr. foetidus* Smith
flame-colored craterelle flame-colored chanterelle	*Cr. ignicolor* (Peters.) (Dahlman and others 2000) = *C. ignicolor* Peterson
yellow foot [craterelle] yellow-stemmed chanterelle	*Cr. lutescens* (Fr.) Fr. = *C. lutescens* Fr. = *C. aurora* (Batsch) Kuyper = *C. xanthopus* (Pers.) Donk
fragrant craterelle fragrant chanterelle	*Cr. odoratus* Schw. = *C. odoratus* (Schw.) Fr.
none	*Cr. pseudoclavatus* Smith

Common English names	Scientific names
winter craterelle winter chanterelle	*Cr. neotubaeformis* nom. prov.
autumn chanterelle (British name) funnel chanterelle trumpet chanterelle	*Cr. tubaeformis* (Fr. : Fr.) Quélet = *C.tubaeformis* Fr. : Fr. = *C. infundibuliformis* (Scop.) Fr.
wavy capped craterelle wavy capped chanterelle	*Cr. undulatus* (Pers. : Fr.) Rausch = *Pseudocraterellus sinuosus* (Fr.) Corner = *Pseudocraterellus pertenuis* (Skovst.) Reid
***Gomphus* (*G.*) species:**	
Bonar's gomphus (a "scaly vase" chanterelle)	*G. bonarii* (Morse) Singer
pig's ear gomphus	*G. clavatus* (Pers.) S.F. Gray
scaly vase chanterelle wooly chanterelle	*G. floccosus* (Schw.) Singer = *C. floccosus* Schweinitz
Kauffman's gomphus (a "scaly vase" chanterelle)	*G. kauffmanii* (A.H. Smith) R.H. Petersen
***Polyozellus* (*P.*) species:**	
blue chanterelle black chanterelle	*Polyozellus multiplex* (Underwood) Murrill = *C. multiplex* Underwood
Other fungi:	
agaricus	*Agaricus* species
button mushroom	*Agaricus bisporus* (Lange) Imbach = *Agaricus brunnescens* Peck
boletes	*Boletus* species
woolly pine spike	*Chroogomphus tomentosus* (Murrill.) O.K. Miller
none	*Chrysomphalina chrysophylla* (Fr.) Clémençon
fairy clubs	*Clavaria* species
club and coral fungi	Clavariaceae family
club corals	*Clavariadelphus* species
various names for particular species	*Clitocybe* species
none	*Entoloma parasiticum* (Quel.) Kreisel = *Claudopus subdepluens* Fitzp.
none	*Entoloma pseudoparasiticum* Noordeloos
spreading hedgehog sweet tooth	*Hydnum repandum* L. : Fr. = *Dentinum repandum* (L. : Fr.) S.F. Gray
belly-button hedgehog	*Hydnum umbilicatum* Peck = *Dentinum umbilicatum* Peck

Common English names	Scientific names
waxy caps	*Hygrocybe* species
waxy caps	Hygrophoraceae
false chanterelle	*Hygrophoropsis aurantiaca* (Wulf. : Fr.) Maire
lobster mushroom	*Hypomyces lactifluorum* (Schw.) Tul. & Tul.
none	*Hypomyces odoratus* G.R.W. Arnold
none	*Hypomyces semitranslucens* G.R.W. Arnold
morel	*Morchella esculenta* (L.) Pers.
none	*Paxillus involutus* (Batsch) Fr.
stinkhorns	*Phallus* species
coral mushrooms	*Ramaria species*
slippery jack	*Suillus luteus* (L. : Fr.) S.F. Gray
Japanese matsutake Swedish matsutake	*Tricholoma matsutake* (Ito & Imai) Sing. = *Tricholoma nauseosum* (Blytt) Kytövuori (Bergius and Danell 2000)
American matsutake white matsutake pine mushroom tanoak mushroom	*Tricholoma magnivelare* (Peck) Redhead = *Tricholoma ponderosum* (Peck) Singer = *Armillaria ponderosa* Peck
Microorganisms:	
unicellular gram-positive aerobic bacteria	*Bacillus*
unicellular gram-negative aerobic bacteria	*Pseudomonas*
mycelial gram-positive aerobic bacteria	*Streptomyces*
wilt disease	*Verticillium lecanii* (Zimm.) Viégas
unicellular gram-negative aerobic bacteria	*Xanthomonas*
Trees:	
true firs	*Abies* species
birches	*Betula* species
miombo (forests)	Forests dominated by ectomycorrhizal trees of Caesalpiniaceae such as *Brachystegia, Julbernardia,* and *Isoberlinia* species
hornbeams	*Carpinus* species
chestnuts	*Castanea* species

Common English names	Scientific names
hazelnut, filbert	*Corylus* species
dipterocarp	*Dipterocarpus* species
eucalyptus	*Eucalyptus* species
beeches	*Fagus* species
tanbark oak, tan oak	*Lithocarpus densiflorus* (Hook. & Arn.) Rehder
spruces	*Picea* species
Norway spruce	*Picea abies* (L.) Karst.
Engelmann spruce	*Picea engelmannii* Engelm.
Sitka spruce	*Picea sitchensis* (Bong.) Carr.
Himalayan spruce	*Picea smithiana* (Wall.) Boiss
pines	*Pinus* species
lodgepole or shore pine	*Pinus contorta* Loudon var. *contorta*
ponderosa pine	*Pinus ponderosa* Laws
Scots pine	*Pinus sylvestris* L.
Cottonwoods, poplars	*Populus* species
Douglas-fir	*Pseudotsuga* species
coastal Douglas-fir	*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*
oaks	*Quercus* species
none	*Shorea* species (Dipterocarpaceae)
hemlocks	*Tsuga* species
western hemlock	*Tsuga heterophylla* (Raf.) Sarg.

Appendix 2—Description of the Genus *Cantharellus*

Based on the descriptions of Corner (1966), Dahlman and others (2000), Danell (1994a), Feibelman and others (1997), Pegler and others (1997), Petersen (1971b, 1973, 1985), and Smith and Morse (1947), *Cantharellus* can be described as an ectomycorrhizal homobasidiomycete genus, with terricolous, fleshy, solid, and long-lived but not perennial gymnocarpic sporocarps. The pileus has a sterile top, which distinguishes it from the Clavariaceae. The hymenium is either smooth or folded, with ridges on the stem and pileus. The gill-like ridges differ from true gills of the order Agaricales. The *Cantharellus* hymenium thickens as new basidia develop over the layer of older ones. By contrast, in the Agaricales the basidia form a monolayer. *Cantharellus* basidia are stichic (Juel 1916) and long, bearing long curved sterigmata. Spores are smooth, white or yellow, and of variable size. The number of spores per basidium varies between two and eight within the same carpophore (nuclear migration studied by Maire 1902). The haploid chromosome number in *C. cibarius* Fr. is 2 (Juel 1916). No cystidia are present. Hyphae are monomitic and clamp connections are present. The species studied so far within *Cantharellus* sensu Feibelman and others (1997) have large internal transcriber spacer (ITS) sequences (Danell 1994b, Feibelman and others 1997) 1400 to 1600 base pairs, and Danell and others [1] have revealed a sequence in the beginning of ITS1, which is unique to the genus *Cantharellus* sensu Feibelman and others (1997) (fig 1., GenBank #AF 044688, AF 044690, AF 044692, AF 044694).

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[1] Danell, E.; Camacho, F.; Liston, A. [and others]. [In preparation]. RFLP and sequencing of rDNA ITS of the ectomycorrhizal edible mushrooms *Cantharellus cibarius*, *C. pallens*, *C. formosus* and *C. subalbidus*. On file with: Museum of Evolution, Uppsala University, Norbyv.16, SE-752 36, Uppsala, Sweden.

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