

SILVISHROOMS: PREDICTING EDIBLE ECTOMYCORRHIZAL MUSHROOM PRODUCTIVITY

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ABSTRACT

The value of edible forest mushrooms harvested from the Pacific Northwest exceeds several hundred million dollars annually and provides self-employment income for various individuals and ethnic groups. Picking mushrooms has little impact on subsequent fruiting, but forest management critically influences their productivity because many edible mushrooms grow symbiotically with host trees. Landscape-scale silvicultural experiments are costly and have a limited range of inference; hence our goal is to develop quantitative models for predicting mushroom productivity under a broad range of stand conditions or alternate silvicultural choices. One purpose is to enhance the ability of managers and policy analysts to provide sustainable forest mushroom harvesting opportunities within the context of managing forests for wood fiber production. We outline a theoretical model of factors affecting edible ectomycorrhizal mushroom productivity, describe proposed research to quantify the model and incorporate economic analyses, and discuss how the model could be applied on scales ranging from stands to regions. The proposed research would expand on the goals of the Wood Compatibility Initiative by providing one of the first broadly applicable quantitative models of how silvicultural choices for wood production are likely to influence the productivity of a nontimber forest product.

KEY WORDS: Mushrooms, productivity, silviculture, economic, model.

INTRODUCTION

Edible mushrooms have been harvested from forests for as long as humans have foraged in woodlands, but in the later part of the 20th century, commerce in forest mushrooms became global, and annual international trade is now worth billions of U.S. dollars. A large portion of this trade is derived from the sporocarps (fruiting bodies) of fungi that grow symbiotically with trees by forming ectomycorrhizae (Figure 1), a nutrient and water exchange structure consisting of fine tree roots and an enclosing sheath of fungal tissue. Ectomycorrhizal (EM) fungi act as an extended fine root system for trees and, in return, they obtain carbohydrates from host tree photosynthesis. These carbohydrates

are one reason that EM fungi can fruit copiously each year if weather is favorable. Depending on the species, sporocarps of EM fungi can be mushrooms that fruit above ground or truffles that fruit below ground. Well-known edible EM fungi include chanterelles, matsutake, boletes, and truffles. Some edible EM fungi occur in the tropics and in inoculated plantations in the Southern Hemisphere, but most grow in temperate and boreal forests of the Northern Hemisphere with tree species in the Pinaceae and Fagaceae. Work is underway to cultivate edible EM fungi in plantations (Hall et al. 1998), but inoculation and establishment of most EM species has proven difficult (Danell 1994). Even if widely cultivated, forest mushrooms are likely to remain a viable commercial product for the foreseeable future.

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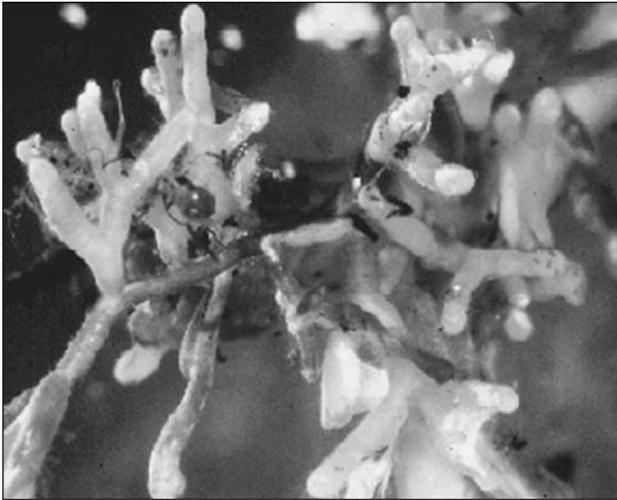


Figure 1—Chanterelle ectomycorrhizae. Photo by Eric Danell.



Figure 2—Young stand thinning operations in chanterelle habitat.

Table 1—Discounted present net worth in perpetuity for chanterelles and Douglas-fir timber under two timber harvest regimes on Site Index 130 lands (base age 50 years) on the Olympic Peninsula, Washington

Types and amounts	50-year rotation - no commercial thinning	80-year rotation - commercial thinning at ages 35 and 55
U.S. dollars per hectare per year ^a		
Chanterelles (2 kg ha ⁻¹ yr ⁻¹)	29	34
Chanterelles (5 kg ha ⁻¹ yr ⁻¹)	73	86
Chanterelles (20 kg ha ⁻¹ yr ⁻¹)	292	343
Douglas-fir timber	8,420	7,049

^a Values are adjusted to year 2000 values. Multiply by 0.4 to obtain U.S. dollars per acre per year. See Pilz et al. (1998) for assumptions inherent in this analysis.

Table 2—Return from timber and American matsutake for three management and productivity scenarios

Products	Alternative 1: timber harvest and 100% increase in matsutake productivity	Alternative 2: timber harvest, constant matsutake productivity	Alternative 3: no timber harvest; constant matsutake productivity
U.S. dollars per hectare per year ^a			
Timber	1,317	1,317	0
Matsutake (50% harvest cost)	1,537	1,145	1,145
Matsutake (90% harvest cost)	434	358	358

^aAdjusted to year 2000 U.S. dollars.
See Pilz et al. (1999) for assumptions inherent in this analysis.

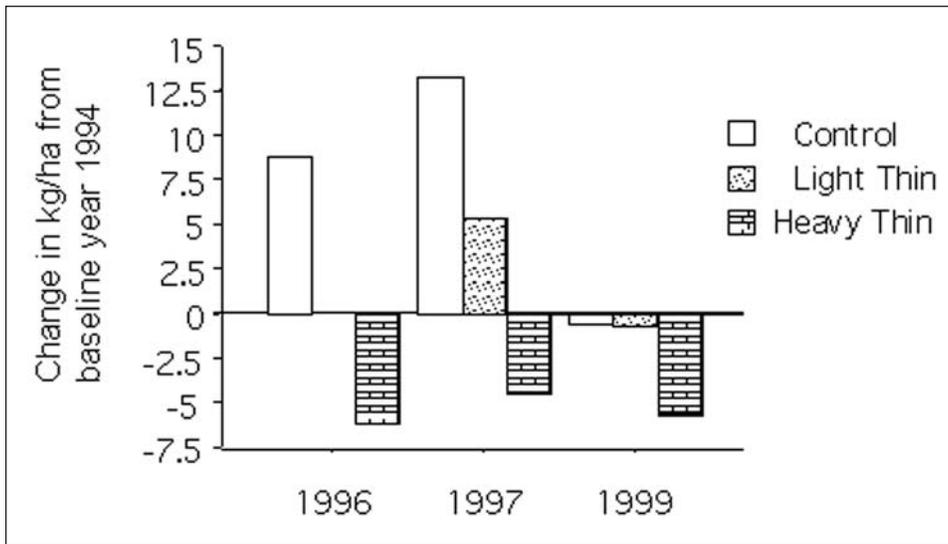


Figure 3—Change in chanterelle productivity for 3 of 4 years after thinning young Douglas-fir stands.

The increase in harvesting of forest mushrooms and truffles has engendered concerns about whether the harvest is sustainable. Egli et al. (1990) and Norvell (1995) suggest that picking mushrooms per se has no discernable impact on subsequent fruiting in small areas over periods of a decade or two. Pilz and Molina (1998) have described a three-pronged regional research and monitoring program for tracking potential long-term or broad-scale mushroom harvest impacts in the forests of the Pacific Northwestern United States. Here we describe in detail our pursuit of the research component of this regional program.

Sustaining appropriate forest habitat is essential for sustaining associated EM mushroom crops. Ectomycorrhizal fungi exhibit varying degrees of specificity for arboreal host species; the tree species growing in a stand dictate the range of associated fungi that can occur in the stand. Clearcutting a forest interrupts the fruiting of edible EM fungi for 1 to 3 decades as the new stand becomes established. Although mushroom productivity is still poorly understood, we are starting to acquire knowledge about how site conditions (soil fertility or climate), stand conditions (age, density, or growth rate) and management activities (commercial thinning or fertilization) affect mushroom productivity over time, and how mushroom values compare to timber or other resource values. Because many mushroom crops are harvested from the same forests that are managed for timber or other forest products and amenities, forest managers need a better understanding of how their choices will influence the size and value of mushroom crops if they are to optimally manage for multiple resource values (Table 1 and 2).

Biological, ecological, and physiological research has provided hypotheses for the influence of factors affecting mushroom productivity. For instance, the young stand thinning and diversity study on the Willamette National Forest in Oregon (Figure 2) is an example of a silvicultural experiment, replicated across a national forest landscape, that has shown dramatic declines in chanterelle fruiting for up to 4 years following heavy thinning (Figure 3). Nevertheless, testing landscape-scale hypotheses with replicated sets of stand treatments is expensive, and inferences derived from the results are limited to the forest types where the experiments were conducted. Development of a quantitative ecosystem process model that predicts mushroom productivity over a broad range of forest types, stand conditions, and site factors is much more cost-effective and broadly applicable approach. Fortunately, we believe that a confluence of scientific advances in carbon allocation modeling and immunoassay techniques has made development of such a model possible.

CENTRAL HYPOTHESIS (See Figure 4 for definitions and acronyms)

Average (5 to 10 years) site productivity of selected edible EM mushroom species can be predicted by two factors:

- 1 The amount of net primary productivity (NPP) allocated below ground by EM trees in a forest stand.
- 2 The occupancy of that site or stand by the fungus of interest.

- **Gross primary productivity (GPP):** Total quantity of carbon fixed through photosynthesis in the form of carbohydrates or other metabolic compounds.

- **Net primary productivity (NPP):** Net quantity of carbon available to the tree or its mycorrhizal fungus partners for growth or other functions after subtracting the amount used for tree respiration (maintenance metabolism). NPP is a relatively constant 47%, of gross primary productivity across a wide range of forest types and conditions.

- **Belowground allocation:** The proportion or amount of net primary productivity that the tree allocates for large structural roots, fine feeder roots, and mycorrhizal symbionts.

- **Fruiting potential:** The maximum productivity that is possible on a given site in a given year if weather is favorable for mushroom development during the fruiting season.

- **Average site productivity:** The average mushroom productivity (kg per ha per yr) of a site over 4 to 10 years. This variable provides a mean of expressed fruiting potential by averaging across years with variation in weather patterns during the fruiting seasons. Conversely, 4 to 10 years is a sufficiently short interval so that natural changes in stand conditions should not unduly interfere with deriving correlations for our model.

- **Site occupancy:** The percentage of potential habitat that is occupied by the edible EM fungal species of interest relative to competing ectomycorrhizal (EM) fungi as measured by the percentage of EM root tips colonized by the species of interest or by the spatial extent of its mycelium.

Figure 4—Definitions and acronyms.

CARBON ALLOCATION MODELING

One scientific development that makes our proposed model possible is the recent development of a simplified carbon allocation model. The acronym 3PG stands for physiological principles predicting growth. It is a generalized forest carbon allocation model, Landsberg and Waring (1997), that works with any forest biome and can be run as an Excel¹⁰ spreadsheet by practicing foresters given a few days of training. The model uses relatively simple and readily available inputs such as species growth tables, latitude, aspect, weather records, edaphic variables, stand age, and stand density to derive monthly estimates of gross primary productivity, carbon allocation, and stand growth. The model has the capacity for specifying thinning regimes, although the function needs further refinement. In recent iterations, the 3PG model has been linked to satellite

imagery of canopy photosynthetic capacity to model forest growth across landscapes (Coops et al. 1998). Intended as a practical management tool, the model is under constant revision to incorporate new research data, simplify application, and broaden its usefulness. Belowground processes and allocation are one of the least developed aspects of this model, and our envisioned research will contribute to the model's development and range of applicability. Web sites discussing the model and current applications are listed in the acknowledgment section.

Various factors are known to influence the allocation of carbon below ground. For instance, trees are known to allocate a larger proportion of their NPP below ground on infertile sites than on fertile sites (Perry 1994). Much of this allocation goes to mycorrhizal fungi to enhance their ability to obtain nutrients. This is true of old forests, and

¹⁰ The use of trade or firm names in this publication is for the reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

- **Modify rotations, thinning densities, thinning intervals, or tree species selection to retain or enhance mushroom productivity in forests predominantly managed for timber production.**
- **Manage stands in areas with convenient access for mushroom picking to enhance long-term mushroom production.**
- **Lengthen rotations or refrain from harvesting timber in areas identified as having low timber value and high mushroom productivity.**
- **Manage stand conditions to promote mushroom production in forests not intended for timber production (for example, carbon sequestration).**
- **Provide continuous mushroom harvesting opportunities across watersheds, land ownerships, or bioregions as the mosaic of forest conditions and age classes shifts across the landscape.**
- **Maintain mushroom harvesting opportunities in the coming centuries by anticipating the shifts in forest biomes as they respond to global warming or other human caused factors.**

Figure 5—Potential applications for predicting how environmental factors, stand conditions, and forest management choices influence the size and value of mushroom crops.

of boreal or high-elevation forests growing on cold soils; under these conditions, nutrients are often tightly bound in accumulated organic matter; hence trees allocate more carbon to mycorrhizae to access the scarce nutrients, especially nitrogen. Drought-related stress also can influence below-ground carbon allocation when trees provide more carbohydrates to roots and mycorrhizae to obtain scarce water. In some cases, drought-related stress can be influenced by tree size because tall trees experience greater hydraulic resistance moving water to a more distant canopy, and small trees might not fully exploit available soil water (Pothier et al. 1989).

Most factors that limit tree growth also increase the proportion of NPP allocated below ground. It is possible that mushroom productivity will be significantly correlated with a simple integrative measure of growth constraints such as site index (the ratio of tree height to age), and this hypothesis also will be tested. Our hypothesis states, however, that mushroom productivity is correlated with the amount (kg per ha per yr) of NPP allocated below ground, not the proportion. Because NPP is a relatively constant fraction of gross primary productivity (GPP), the quantity of NPP allocated below ground is a function of GPP as well as the proportional allocation of NPP. In other words, although growth constraints cause trees to allocate a greater proportion of their food resources below ground, they have less available food to begin with because they are growing more slowly.

One of the more important questions we will address with our research is how the quantity of food available to mycorrhizal fungi varies across gradients of site fertility, soil temperatures, and stand age.

Of the NPP allocated below ground, the proportion allocated to large structural roots is about 25% of the NPP allocated to stem wood. The remainder is available for fine roots and mycorrhizae. Although carbon allocation patterns are relatively well known for most structural and functional components of tree growth and metabolism, the allocation and use of NPP among fine roots and mycorrhizae is not yet well quantified. Likewise, we have little information about how EM fungi compete for arboreal photosynthates or how various species of EM fungi allocate acquired carbon to growth, metabolism, function, or the production of sporocarps. Because so little quantitative information exists about carbon allocation in this realm, we start with two simplifying assumptions: (1) the amount of carbon each EM species obtains from trees in the stand will be correlated with site occupancy of that EM species, and (2) site occupancy will be correlated with average site productivity for each EM species. Although we expect these correlations to be robust, we also expect parameter values for the correlations to vary between fungus species.

Several species of chanterelles (*Cantharellus* species, Figure 6) and matsutake (*Tricholoma* species, Figure 7) will be the first EM species modeled because they are



Figure 6—Chanterelle (*Cantharellus formosus* Corner).



Figure 7—American matsutake (*Tricholoma magnivelare* (Peck) Redhead).

among the most widely collected and traded mushrooms in international commerce, and both are widely distributed in temperate and boreal forests of the Northern Hemisphere (Bergius and Danell 2000; Danell 1999). They occur in sufficient abundance to facilitate site selection and to reliably sample. We have used these species for comparative evaluations of mushroom and timber values, so economic analyses can be readily extrapolated to mushroom and timber productivity estimates derived from our model.

METHODS

Estimating Site Occupancy

We envision the application of several alternate or complementary techniques for estimating the occupancy of a site or stand by the EM fungus species of interest, namely immunoassays of ectomycorrhizal root tips derived from soil cores, olfactory surveys of matsutake mycelia in mineral soil horizons, and the spatial distribution of sporocarps in a stand.

In collaboration with Dr. Eric Danell, we anticipate contracting with immunoassay development companies to develop monoclonal antibody reagents (Miller et al. 1988; Neuner-Plattner et al. 1999) that will allow us to quickly assay the percentage of ectomycorrhizae in stands colonized by the edible mushroom species of interest. Immunoassays for chanterelles will be designed for specificity to the genus *Cantharellus* because all the species in the genus are edible and commercially collected. For matsutake we plan to develop reagents specific to methyl cinnamate (Yajima et al. 1981), the unique odor molecule produced by the several species of *Tricholoma* that are harvested as “matsutake” around the world.

Successful development of immunoassay reagents for chanterelles and matsutake will provide useful tools for sampling stands for potential mushroom productivity even when the mushrooms are not fruiting. They also can be used to verify fungal persistence in plantations of trees inoculated with these species.

Chanterelle mycelia grow diffusely in the soil, so directly estimating their mass or volume is not currently feasible. Matsutake mycelia, however, grow in dense mats near the surface of the mineral soil, and the mats exude the distinctive odor of matsutake. Charles LeFevre, as a part of his graduate thesis, has developed, tested (Figure 8), and refined olfactory sampling procedures for estimating the areal extent of matsutake mycelia in a forest stand.

As a backup to both of these approaches to estimating site occupancy, we plan to sample mushroom productivity by using many systematically located small plots. The percentage of plots that are occupied by either chanterelles or matsutake will give us a less direct, but we hope still useful, estimate of the site occupancy for each species.

Field Sites

We plan to select field sites that cover the range of climatic and edaphic conditions that we hypothesize are important to mushroom productivity. Factors driving site selection will include:

- At least some fruiting of chanterelles or matsutake so that productivity and site occupancy can be estimated.
- High fertility versus low fertility soils.

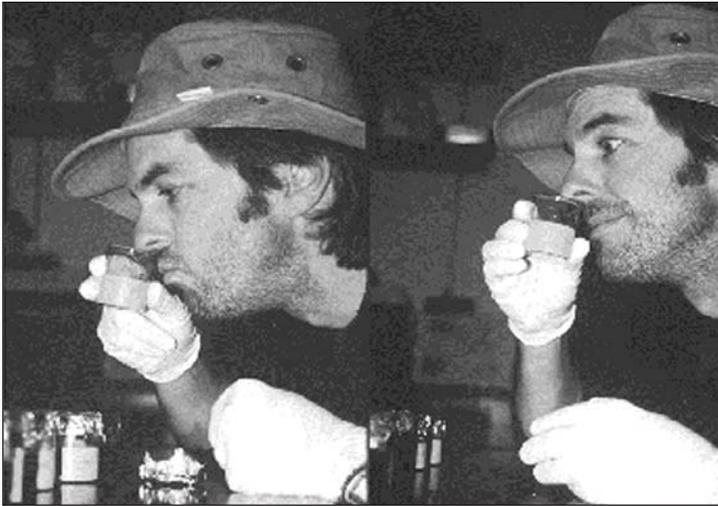


Figure 8—Tom Horton testing olfactory methods for detecting *Tricholoma magnivelare* mycelium in soil.

- Temperate versus cold (boreal or alpine) climates.
- Forests with tall trees versus forests with short trees.

In addition to sampling *C. formosus*, *C. subalbidus*, and *T. magnivelare* on sites in the Pacific Northwest, *C. cibarius* and *T. nauseosum* (syn. *T. matsutake*) will be sampled on sites in Sweden to broaden the applicability of the model to coniferous forest biomes throughout the Northern Hemisphere. Actual carbon budgets will be calculated for each site, annual mushroom productivity will be averaged over 4 or more years, and site occupancy estimated. The amount of carbon allocated below ground to fine roots and mycorrhizae will be modified by the percentage of occupancy of chanterelles or matsutake and then correlated with average mushroom productivity recorded on the site. The correlations we develop and the predictions of our resulting model will be tested on other sites where long-term mushroom productivity estimates already exist. For example, the young stand thinning and diversity study has 12 stands where chanterelle productivity has been sampled for more than 5 years. We also have at least nine other sites in the Pacific Northwest where 2 or more years of chanterelle or matsutake productivity have been sampled and where the model's predictions could eventually be tested.

FUTURE ITERATIONS

Current iterations of the 3PG model are designed to work with forest stands of a single tree species and uniform age. Given that the most abundant fruiting of chanterelles and matsutake often occurs in young stands, early versions

of our modified model might be most applicable to recently regenerated forest stands that have timber production as one of their goals. Future revisions of the 3PG model are likely to incorporate multiple tree species of nonuniform age. Our aim is to use tree species ratios (host/nonhost tree species for each EM fungus) and dominance by those tree species (photosynthetic capacity) to modify our predictions of the amount of carbon allocated to the mushroom species of interest. These versions of the SilviShroom 3PG model would then be more applicable to natural or diverse forest stands.

Our core modeling efforts will not provide estimates of the fruiting potential of a stand in any given year, only multiyear averages. Physiological evidence exists, however, that seasonal weather patterns likely influence the amount of carbon allocated below ground immediately prior to and during the mushroom fruiting season. If the effects of weather patterns on seasonal carbon allocation are further elucidated, the information might provide a means for predicting fruiting potential in a given year. We will test this hypothesis with actual carbon allocation budgets developed for each stand in the study.

Economic Valuation

Timber values are thoroughly understood, but mushroom values are harder to estimate and most attempts are relatively recent (Alexander et al. 2002; Pilz et al. 1998, 1999). Preliminary analyses illustrated in Tables 1 and 2 include many economic assumptions about mushroom prices and harvester costs, but they also include uncertain assumptions about how timber management choices affect

mushroom productivity. Coupling analyses of mushroom values with predictions of mushroom productivity under different forest management scenarios will allow managers to better evaluate resource tradeoffs and synergies.

Scaling from Stands to Landscapes

Evaluating commercial mushroom crops and their values at the scale of landscapes would enable planners or policy analysts to anticipate how regional mushroom crops might be influenced by changes in climate, pollution, exotic forest pests, forest age class distributions, timber management regimes, or land-use patterns. Satellite sensing of canopy conditions to use in scaling the 3PG model to landscape estimates of mushroom productivity will be ineffective, however, unless we better understand the range and habitat preferences of the modeled mushroom species. After the core modeling research is underway, we plan to survey mushroom experts (mycology club members, agency botanists, and commercial mushroom harvesters) about the habitat preferences of commercially harvested mushroom species. By incorporating summaries of this habitat information into geographic information system (GIS) databases, we will be able to select appropriate habitat strata for application of remotely sensed canopy data. This approach will allow us to more accurately estimate mushroom productivity and crop values at watershed, landscape, or regional scales.

CONCLUSIONS

The research outlined in this paper seeks to build on our current understanding of the influence of forest management on mushroom productivity (Pilz and Molina 2002). By elucidating the processes that influence edible mushroom productivity, we will better understand the relative importance of site conditions and silvicultural choices for sustaining or enhancing the production of this valued forest resource. Regardless of forest management goals for any given landowner, the model we propose should enable foresters to evaluate a range of management options for those that best meet their objectives. Additionally, this approach should prove feasible across a broad range of forest types and scales of analysis. Although useful as an instrument for ecosystem research, the model we propose to develop is specifically intended as a practical management tool and will be developed with ease of application as a primary goal. As managers struggle with the complexity of applying theories of ecosystem management, sustaining the production of multiple resources, and preserving or restoring forest health, tools such as these hold promise for enhancing the ability of our forests to meet our needs and those of generations to come.

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This proposed research project would not be possible without decades of research that have quantified forest ecosystem processes and the integration of that research into a process-based quantitative carbon allocation model designed for use by practicing foresters. Web sites that discuss the 3PG model and some of its applications include the following:

- Landsberg Consulting (Download 3PG program in Excel format) <http://www.landsberg.com.au/>
- Physiological Principles for Predicting Growth from Satellites <http://www.ffp.csiro.au/nfm/mdp/pgs/pgshome.htm>
- 3PG in SW Oregon <http://www.ffp.csiro.au/nfm/mdp/bevr/home1.html>
- 3PG in New Zealand http://www.ffp.csiro.au/nfm/mdp/nz/nz_fram.htm

LITERATURE CITED

- Alexander, S.J.; Pilz, D.; Weber, U.S. et al. 2002. Mushrooms, trees, and money: value estimates of commercial mushrooms and timber in the Pacific Northwest. *Environmental Management* 30: 129-141.
- Bergius, N.; Danell, E. 2000. The Swedish matsutake (*Tricholoma nauseosum* syn. *T. matsutake*): distribution, abundance, and ecology. *Scandinavian Journal of Forest Research*. 15: 318-325.

- Coops, N.C.; Waring, R.H.; Landsberg, J.J. 1998. Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite derived estimates of canopy photosynthetic capacity. *Forest Ecology and Management*. 104: 113-127.
- Danell, E. 1994. Formation and growth of the ectomycorrhiza of *Cantharellus cibarius*. *Mycorrhiza*. 5: 89-97.
- Danell, E. 1999. *Cantharellus*. In: Cairney, J.W.G.; Chambers, S.M., eds. Ectomycorrhizal fungi: key genera in profile. Springer-Verlag. Berlin: 253-267. Chapter 10.
- Egli, S.; Ayer, F.; Chatelain, F. 1990. Der Einfluss des Pilzsammelns auf die Pilzflora. *Mycologia Helvetica*. 3: 417-428.
- Hall, I.; Buchanan, P.K.; Yun, W.; Cole, A.L.J. 1998. Edible and poisonous mushrooms: an introduction. Christchurch, NZ: New Zealand Institute for Crop and Food Research Limited. 189 p.
- Landsberg, J.J.; Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation use efficiency, carbon balance and partitioning. *Forest Ecology and Management*. 95: 209-228.
- Miller, S.A.; Rittenburg, J.H.; Peterson, F.P.; Grothaus, G.D. 1988. Application of rapid, field usable immunoassays for the diagnosis and monitoring of fungal pathogens in plants. In: Brighton Crop Protection Conference, Pests and Diseases. Surrey, UK: British Crop Protection Council: 795-803.
- Norvell, L. 1995. Loving the chanterelle to death? The ten-year Oregon chanterelle project. *McIlvainea*. 12: 6-25.
- Neuner-Plattner, I.; Grabher, T.; Hall, I.R. [et al.]. 1999. A comparison of immunological assays for the identification of *Tuber* spp. and other edible EM fungi. *Mycological Research*. 103(4): 403-412.
- Perry, D.A. 1994. Forest ecosystems. London: John Hopkins Press, Ltd. 649 p.
- Pilz, D.; Molina, R. 1998. A proposal for regional monitoring of edible forest mushrooms. *Mushroom, The Journal of Wild Mushrooming*. 16(3): 19-23.
- Pilz, D.; Brodie, F.D.; Alexander, S.; Molina, R. 1998. Relative value of chanterelles and timber as commercial forest products. In: Liegel, L.H., comp. The biological, socioeconomic, and managerial aspects of chanterelle mushroom harvesting: the Olympic Peninsula, Washington State, U.S.A. *Ambio, A Journal of the Human Environment*. Stockholm, Sweden: Royal Swedish Academy of Sciences. Special Report Number 9: 14-15.
- Pilz, D.; Smith, J.; Amaranthus, M.P. [et al.]. 1999. Mushrooms and timber: managing commercial harvesting in the Oregon Cascades. *Journal of Forestry*. 97(3): 4-11.
- Pilz, D.; Molina, R. 2002. Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: issues, management, and monitoring for sustainability. *Forest Ecology and Management*. 155: 3-16.
- Pothier, D.; Margolis, H.A.; Waring, R.H. 1989. Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. *Canadian Journal of Forest Research*. 19: 432-439.
- Yajima, I.; Yanai, T.; Nakamura, M. [et al.]. 1981. Volatile flavor compounds of matsutake-*Tricholoma matsutake* (Ito et Imai) Sing. *Agricultural and Biological Chemistry*. 45(2): 373-377.