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# Habitat and host associations of *Craterellus tubaeformis* in northwestern Oregon

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***Abstract:*** Knowledge of the habitat and host associations of *Craterellus tubaeformis* (winter chanterelle) is the key to understanding the ecological characteristics needed for its conservation. In this study, a survey of forest types in northwestern Oregon for mycorrhizal associates is performed and the hypotheses that stand age and the volume of well-decayed, coarse, woody debris (CWD) are significant to the standing crop biomass and the probability of *C. tubaeformis* occurrence are tested. Host associations were identified with polymerase chain reaction (PCR) amplification and restriction fragment-length polymorphism (RFLP) typing. Habitat associations were tested by measurements on 64 plots in the Coast and Cascade Ranges of northwestern Oregon. Data analysis found that stand age and well-decayed, coarse, woody debris were related significantly to the probability of *C. tubaeformis* occurrence but not to standing crop biomass. Results indicated the volume of well-decayed CWD is particularly important to the probability of *C. tubaeformis* occurrence in stands less than 100 yr of age. Well-decayed CWD was the substratum for 88% of *C. tubaeformis* sporocarps across all stands, despite the fact that ground area coverage of CWD ranged only from 3 to 26%. Slope, elevation and aspect were not related to the probability of *C. tubaeformis* occurrence or standing crop biomass. The occurrence of *C. tubaeformis* in northwestern Oregon is highly correlated to the presence of western hemlock (*Tsuga heterophylla*), and their mycorrhizal association was confirmed. *Craterellus tubaeformis* also can form mycorrhizae with Douglas-fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) but is encountered only rarely in stands without a hemlock component. In northwestern Oregon, the presence of *Hydnum* spp. in a stand is a good indicator of the presence of *C. tubaeformis*. Differences in genetic sequences between *C. tubaeformis* populations in western North America, eastern North America and Europe suggest the likelihood of several distinct species.

***Key words:*** *Cantharellus*, hemlock, *infundibuliformis, neotubaeformis, Tsuga*, winter chanterelle

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## INTRODUCTION

*Craterellus tubaeformis* (Fries) Quélet (Basidiomycota, Cantharellales, Cantharellaceae) is a small to medium-size mycorrhizal forest mushroom common in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973) of the Pacific Northwestern United States. Synonyms include *Cantharellus tubaeformis* Fr. and *Cantharellus infundibuliformis* Fr. (Petersen 1979, Dahlman et al 2000). It was listed for management under the Northwest Forest Plan Record of Decision (ROD) (U.S.D.A. et al 1994) based on evidence that it required late-seral stands with an abundance of well-decayed (class 4 and 5; Fogel et al 1973, Sollins 1982) coarse, woody debris (CWD), and also because of anticipated harvest pressure (W. Denison pers comm). In this study, a survey of forest types in northwestern Oregon for mycorrhizal associates is performed, and the hypotheses that stand age and the volume of well-decayed, coarse, woody debris are significant to the standing crop biomass of *C. tubaeformis* and the probability of its occurrence are tested.

*Host associations.*—*Craterellus tubaeformis* is known to be mycorrhizal (Kårén et al 1997, Jonsson et al 2000, M. Trappe et al 2000) but its host associations have not been thoroughly explored by molecular analysis. Suppositions about *C. tubaeformis* associates have been based on stand composition and in Europe have included European beech (*Fagus sylvatica*; Peyronel 1922, Kalmár 1950, Becker 1956, Gorova 1980, Tyler 1985, Hansen and Knudsen 1997, Persson 1997, Jonsson et al 2000), Norway spruce (*Picea abies*; Romell 1938, Becker 1956, Kraft 1978, Gorova 1980, Wästerlund and Ingelög 1981, Hansen and Knudsen 1997, Kårén et al 1997, Bandrud and Timmermann 1998, Högberg et al 1999, Jonsson et al 2000), Scotch pine (*Pinus sylvestris*; Kreisel 1957, Wästerlund and Ingelög 1981, Agerer 1985, Högberg et al 1999), Sitka spruce (Alexander and Watling 1987), and white fir (*Abies alba*) and oaks (*Quercus* spp; Becker 1956). In West Virginia *C. tubaeformis* has been reported in

stands of monoculture red spruce (*Picea rubens*; Bills et al 1986) and in Mississippi with pines (*Pinus* spp; T. Feibelman pers comm). In the Pacific Northwestern United States and western Canada, western hemlock and mountain hemlock (*Tsuga mertensiana*) have been suspected mycorrhizal symbionts (Kropp 1981, Kropp and J. Trappe 1982). J. Trappe (1962) and Molina et al (1992) speculated that *C. tubaeformis* might have a broad host range.

Considering that *C. tubaeformis* often is encountered and is well known, surprisingly little has been published on its ecology, trophic status or habitat requirements. The objectives of the research were to identify *C. tubaeformis*' mycorrhizal associates in northwestern Oregon, quantify its substratum preferences and determine whether stand age and the volume of class 4 and 5 CWD influence the occurrence and standing crop biomass productivity of *C. tubaeformis*. The hypotheses tested were that stand age and the volume of well-decayed, coarse, woody debris were significant to the standing crop biomass of *C. tubaeformis* and to the probability of its occurrence.

## MATERIALS AND METHODS

*Host associations.*—Root samples were collected from beneath *C. tubaeformis* basidiomata in the Oregon Coast and Cascade Ranges. Twenty-three of the source stands were of the *Tsuga heterophylla* type and 19 were of the *Picea sitchensis* type as described by Franklin and Dyrness (1973), although two of the former lacked western hemlock. All were closed canopy. Approximately 1 L of soil was excavated from beneath *C. tubaeformis* colonies at sites with high fruiting densities. Soil collections were washed with an elutriator (Eberhart et al 1996) to produce clean, intact root systems. Subsamples (~100 mL) of the tips of root systems were assayed for mycorrhizae with a stereo microscope. Mycorrhizae from each subsample were sorted by morphotype, briefly described and vouchered in CTAB buffer (Gardes and Bruns 1996).

DNA was extracted as described by Gardes and Bruns (1993), except that the source material was not lyophilized. The PCR process and ingredients generally followed the protocols established by White et al (1990) and Gardes and Bruns (1993 and 1996). The ITS1F and ITS4 primers were used for PCR amplification of the ITS region of the *C. tubaeformis* nuclear rDNA. This region of the DNA is variable enough for useful application in species-level identifications among many fungi (White et al 1990, Erland et al 1994, Cullings and Vogler 1998). The PCR thermal cycling program parameters were an initial denaturation at 94 C for 30 s, then these temperature steps cycled 35 times: 93 C denaturing for 35 s, 55 C annealing for 53 s and 72 C extension for 30 s. Success of the PCR was checked by drawing 5 μL samples of the amplified product through a 2.5% DNA grade agarose gel in an electrophoresis bath (Sambrook et al 1989, Gardes and Bruns 1996).

The RFLP process followed the methods of Gardes and Bruns (1996). The enzymes used were HinF, AluI, DpnII and HaeIII (New England Biolabs), described in McClelland et al (1994). After incubation at 37 C for 3 h the samples were drawn through a 1%/2% RFLP-grade agarose gel in an electrophoresis bath (Sambrook et al 1989, Gardes and Bruns 1996). The restriction fragment patterns were compared with those generated from *C. tubaeformis* basidiomata to determine whether the fungal component of the mycorrhizae was *C. tubaeformis*.

If the mycorrhizal symbiont on a root tip was identified as *C. tubaeformis*, the DNA extract from that root tip would again be subjected to the same RFLP process, except that PCR primers 28C and 28KJ (Cullings 1992) were used. These primers amplify a part of the 28S LSU rDNA gene useful in the identification of most Pacific Northwest conifers, allowing positive identification of the host-tree species.

*Habitat associations.*—The habitat association study was designed for multiple linear and logistic regression analysis, with stand age (years) and class 4 and 5 CWD volume ($m^3$ $m^{-2}$) as explanatory variables. Thirty-two stands in the Oregon Coast Ranges and 32 in the northwestern Oregon Cascade Range (44°01′–45°04′N, 122°05′–123°46′W) were selected for survey plots (TABLE I). Sites were selected to represent a range of combinations of both stand age and CWD in an effort to disentangle the two variables and minimize correlation between them. Thus, site selection balanced the stand characteristics of early- and late-seral stages with above- and below-mean volumes of class 4 and 5 CWD.

Line intercept sampling (van Wagner 1968, Harmon and Sexton 1996) was used to quantify CWD volume of each decay class per unit area, measured in cubic meters of CWD per square meter of forest floor ($m^3$ $m^{-2}$). A 200 m sampling transect was established in each stand, and each piece of CWD crossed by the transect was inventoried by diameter and decay class (Fogel et al 1973, Sollins 1982): In class 1 CWD, the bark and small twigs are intact and wood texture is firm; in class 2 CWD the bark is intact but small twigs are gone, wood texture is firm; in class 3 CWD the bark is sloughing off and the sapwood is softening; in class 4 CWD the bark is gone, the sapwood and heartwood are soft and breaking into cubes, the wood color is darkening brown and small seedlings may be sprouting from it; and in class 5 CWD the wood texture is soft and settling into the soil, often becoming powdery and usually with a robust community of seedlings and saplings growing from it. Transects were either one 200 m line, two perpendicular 100 m lines, or an equilateral triangle with 67 m sides, depending on the geographic constraints of the stand. The formula used to calculate CWD volume ($V$) is

$$V = \pi^2 \sum (d^2/8L)$$

where d is the diameter (m) of each piece of CWD intersected by the transect and $L$ is the transect length (200 m). The volume of each decay class of CWD was recorded for each strip plot. For analysis, decay classes 1–3 were grouped together as were decay classes 4 and 5.

TABLE I. Summary of stand characteristics[1]

| Means and value ranges | Early seral, Low 4 & 5 CWD | Early seral, High 4 & 5 CWD | Late seral, Low 4 & 5 CWD | Late seral, High 4 & 5 CWD | All stands combined |
|---|---|---|---|---|---|
| Age, y | 44 (30–97) | 47 (30–96) | 307 (136–500) | 466 (128–650) | 200 (30–650) |
| Volume of class 4 and 5 CWD, $m^3\ m^{-2}$ | 0.023 (0.005–0.070) | 0.090 (0.077–0.141) | 0.037 (0.016–0.064) | 0.180 (0.071–0.348) | 0.070 (0.005–0.348) |
| Volume of class 1 to 3 CWD, $m^3\ m^{-2}$ | 0.064 (0.001–0.029) | 0.008 (0.001–0.040) | 0.014 (0.001–0.121) | 0.019 (0.001–0.108) | 0.107 (0.002–0.121) |
| Elevation, m | 440 (215–630) | 588 (228–969) | 598 (200–1000) | 666 (468–1000) | 579 (215–1000) |
| Slope, % | 15 (0–45) | 17 (0–35) | 23 (5–65) | 25 (3–50) | 21 (0–65) |
| Standing crop biomass, g | 0.5 (0.0–4.6) | 1.2 (0.0–5.2) | 0.9 (0.0–3.1) | 4.2 (0.03–11.2) | 1.4 (0.0–11.2) |
| With *C. tubaeformis* | 6 of 16 | 9 of 13 | 14 of 19 | 9 of 9 | 38 of 57 |

[1] n = 57 (64 stands minus 7 without western hemlock).

Seral stage (early or late) was used to categorize stands in the study-site selection process and was determined by stand structure and the age of the predominant cohort. Stand age (of the dominant cohort) necessarily was used as the nominal variable in data analysis. Stand ages were 30–650 yr and were determined either by documented stand histories or by increment boring. If the bole radius of a sampled tree was greater than the 45 cm length of the increment borer, the age was extrapolated from the rings at the pith end of the core. The oldest "early-seral" stand was a 97 yr old stand predominated by even-age western hemlock. The youngest "late-seral" stand had a 128 yr old predominant cohort of Douglas-fir and western hemlock, with occasional larger trees and a mixed species midstory.

One strip plot 70 m long and 10 m wide was established in each selected stand to create a uniform area for linear regression analysis of productivity data. Strip plots were placed by means of a constrained randomized bearing that avoided influential factors such as streams, roads, cliffs or deep wind-throw. Each strip plot was surveyed for the presence of *C. tubaeformis* every 3–4 wk from Sep 1999 to Apr 2000 and once during Feb–Mar 2001. The occurrence and standing crop biomass of *C. tubaeformis* were recorded at each visit, along with substratum data for all collections.

The mean level of class 4 and 5 CWD differed between the Coast and Cascade ranges: In the Coast Range it was 0.034 $m^3\ m^{-2}$, and in the Cascade range it was 0.060 $m^3\ m^{-2}$. In the Coast Range 16 stands were below the mean and 16 stands above, and in the Cascade Range 14 stands were below the mean and 18 stands above. In each of the two ranges 16 stands were late-seral and 16 were early-seral. The mean age of late-seral stands was 358 yr (128–650), and of early-seral stands 46 yr (30–97). This mix of stands with varying combinations of seral stages and volumes of class 4 and 5 CWD was designed to enable separation of their explanatory effects. Although data on the volume of class 1–3 CWD, elevation, slope and aspect were collected at each site, balanced replication of these variables was not a goal in site selection. All sites were located below 1000 m elevation to facilitate winter accessibility.

All *C. tubaeformis* basidiomata within strip-plot boundaries were collected at each survey iteration. Surveying consisted of looking at every square meter in a strip plot for *C. tubaeformis*. *Craterellus tubaeformis* normally occurs in colonies, a colony being defined as a group of basidiomata sharing the same immediate substratum. Each colony on a plot was treated as a separate collection. When a *C. tubaeformis* colony was observed, its substratum was recorded (CWD by decay class, needle litter, mineral soil, etc.), along with distance from, and decay class of the nearest CWD. Collections were mapped, dried, weighed, vouchered and accessioned in the Oregon State University herbarium (OSC). Fresh weights of 74 voucher colonies that were collected on days without precipitation and could be weighed within 3 h were recorded to determine mean water content.

The standing crop productivity of *C. tubaeformis* was measured in mean grams of biomass, calculated by dividing the total dry biomass of *C. tubaeformis* collected within each strip plot by the number of times that each plot was surveyed (usually six times, minimum four times, 398 total site

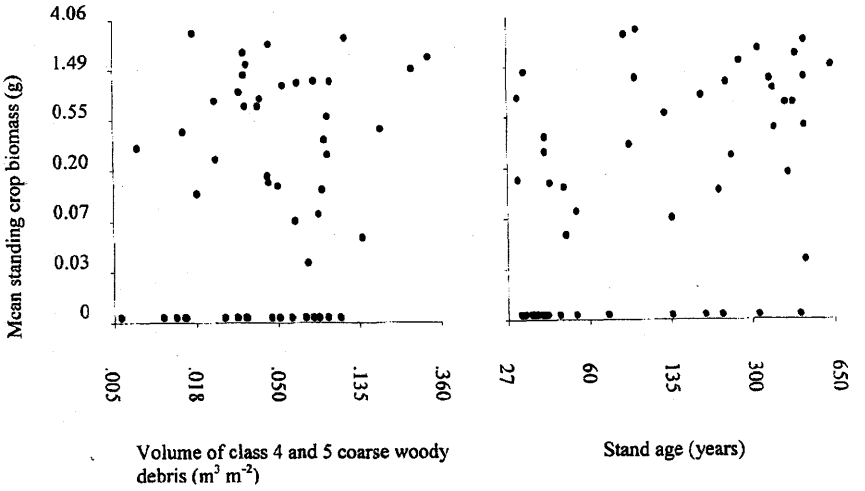


FIG. 1. Relationships between mean standing crop biomass productivity, stand age and volume of class 4 and 5 coarse, woody debris, including plots with no *Craterellus tubaeformis* occurrence.

visits). Some stands were inaccessible because of snow in Jan and Feb 2000; these sampling dates for all plots were removed from analysis. Stepwise multiple linear regression was used to test significance of stand age, volume of class 4 and 5 CWD, volume of class 1–3 CWD, elevation and slope on *C. tubaeformis* standing crop biomass productivity. Pearson's correlation analysis was used to test for relationships between explanatory variables. All explanatory variables were transformed logarithmically to normalize residuals. ANOVA was used to analyze the (categorical) aspect data (north, south, east and west facing).

During this study, only one *C. tubaeformis* basidiocarp was recorded among the seven stands lacking western hemlock. To test the significance of this observation, 18 additional stands without western hemlock (Douglas-fir monoculture) were surveyed for the presence of *C. tubaeformis*; it was found in only one of them. The likelihood of *C. tubaeformis* occurrence in a stand with western hemlock was significantly higher than in one without western hemlock (Fisher's Exact Test, $P = 0.012$, $n = 82$). All seven stands in the original design lacking western hemlock accordingly were excluded from data analysis. All of the excluded stands were in the Coast Ranges and had below-mean levels of class 4 and 5 CWD; four were late-seral stands and three were early seral.

Nineteen of the plots produced no *C. tubaeformis* and were excluded from the productivity analysis because their presence in the model violated the assumption of constant variance and consequently had disproportionate influence on regressions. The information provided by these nonproducing plots was captured by logistic regression analysis, described below. Relationships between mean standing crop biomass, stand age and volume of class 4 and 5 coarse, woody debris (including nonproducing plots) are depicted in FIG. 1. All data analyses were performed using SAS version 6.12 (SAS Institute 1996).

Logistic regression was used to analyze the probability of *C. tubaeformis* occurrence. Logistic regression is robust to null data points (Allison 1999; e.g., if *C. tubaeformis* is found just once at a stand then it does not matter whether that stand is accessible for future survey iterations, and conversely if *C. tubaeformis* is absent in five successful survey iterations it is unlikely to be present on the occasion that the stand was inaccessible). Presence/absence data for the logistic regression was not restricted to the confines of the productivity strip plots, though only rarely was *C. tubaeformis* recorded in a stand but not on the strip plot. If *C. tubaeformis* was recorded in a stand at any time during data collection, the stand was scored as "*C. tubaeformis* present"; plots that never produced *C. tubaeformis* on any survey were scored "*C. tubaeformis* absent". Logistic regression provides the odds of *C. tubaeformis* occurrence in mixed Douglas-fir/western hemlock stands in northwestern Oregon. Odds are converted to probability by the formula

$$\text{Probability} = \text{Odds}/1 + \text{Odds}$$

The probability is a value between zero and one, which can be interpreted as the percent chance of *C. tubaeformis* occurrence in a stand given its age and volume of class 4 and 5 CWD. Again, logarithmic transformation was required on all explanatory variables to normalize residuals.

*Hydnum* spp. seemed to be an effective indicator for *C. tubaeformis*. In addition to the 57 stands used for biomass data collection, data were collected at another 65 stands of similar composition. Thirty five of these had *C. tubaeformis* and western hemlock; 30 (by coincidence) had no *C. tubaeformis* and no western hemlock. Maximum-likelihood analysis was used to check relationships between the occurrence of *C. tubaeformis* and *Hydnum* spp. in the 122 stands over three fruiting seasons (Oct–Apr 1999–2001). Only one datapoint was permitted for any given site, even if *C. tubaeformis* and *Hydnum* spp. repeatedly were observed together.

## RESULTS

*Host associations.*—*Craterellus tubaeformis* was documented by field observation in 69 of 92 mixed west-

ern hemlock/Douglas-fir stands (the 57 stands in this study plus the 35 aforementioned other stands), even when the western hemlock component was minimal. All *C. tubaeformis* host rootlets analyzed from these stands were of western hemlock; none were Douglas-fir. These results initially seemed to indicate that in the Pacific Northwest, *C. tubaeformis* might be mycorrhizal with western hemlock but not with Douglas-fir. However, *C. tubaeformis* has been reported in Douglas-fir/*Libocedrus decurrens* (incense cedar) stands in southern Oregon entirely lacking western hemlock (D. Luoma pers comm). Intensive surveys of 25 monoculture Douglas-fir stands (the seven stands discarded from the original 64 stands, plus the 18 additional monoculture Douglas-fir stands mentioned earlier) in northwestern Oregon revealed populations of *C. tubaeformis* in only two of them, and its mycorrhizal association with Douglas-fir was confirmed by RFLP analysis. The overall odds of locating *C. tubaeformis* in a stand with western hemlock were 6.25 times greater than in a stand without western hemlock ($\chi^2$, $P = 0.017$). Association of *C. tubaeformis* with Douglas-fir when western hemlock is available has yet to be demonstrated.

On the Oregon coast Sitka spruce usually is interspersed with western hemlock, but some pure Sitka spruce stands occur in exposed coastal locations (Franklin and Dyrness 1973, Roche and Haddock 1987). Nineteen Sitka spruce stands located between Florence and Lincoln City on the Oregon coast were surveyed for the presence of *C. tubaeformis* during Jan and Feb 2001. Seven of these had no western hemlock component and lacked *C. tubaeformis*. The other 12 stands were mixed western hemlock/Sitka spruce, and *C. tubaeformis* was documented in eight of them. *C. tubaeformis* mycorrhizae were confirmed by RFLP on several Sitka spruce roots at one site, an approximately 50 m diam pocket of pure spruce in an otherwise mixed spruce/hemlock stand at Carter Lake, south of Florence on the Oregon coast.

*Productivity of* C. tubaeformis.—The strip plots were 87% effective at representing the presence of *C. tubaeformis* (in only 12 of 92 site visits where *C. tubaeformis* was located somewhere in the stand was it not represented on the strip plot). Among the 38 stands that produced *C. tubaeformis,* the average mean biomass was 2.29 g (0.03–11.23 g) per 700 $m^2$ plot. The best fit stepwise multiple regression model (adjusted $R^2 = 0.213$) included the volume of less decayed (class 1–3) CWD ($P = 0.052$), elevation ($P = 0.0194$, an inverse relationship), and the volume of well decayed (class 4 and 5) CWD ($P = 0.109$). When the volume of less decayed CWD was regressed individually against the standing crop biomass of *C. tubaeformis* it remained marginally significant ($P = 0.065$) but the adjusted $R^2$ was only 0.07, indicating that this characteristic does not explain much of the observed effect.

The volume of class 4 and 5 CWD on a plot was only marginally suggestive of a relationship to *C. tubaeformis* standing crop biomass productivity ($P = 0.109$). Eleven of the 12 stands with the highest levels of class 4 and 5 CWD had *C. tubaeformis* populations, but five of those 11 stands had standing crop biomass levels below the mean. Five of the 12 stands with the lowest levels of class 4 and 5 CWD produced *C. tubaeformis,* but only one of them was above the mean biomass.

Stand age was not significantly correlated to *C. tubaeformis* standing crop productivity (Pearson's correlation analysis, $P = 0.292$). Eighteen of the 20 oldest stands produced *C. tubaeformis,* but biomass for 12 of those was below the mean. Four of the eight highest-producing stands were less than 100 yr old, and two of the most productive stands were respectively 30 and 48 yr old (mean biomass 7.16 and 7.75 g).

Slope was not significantly correlated to *C. tubaeformis* productivity (Pearson's correlation analysis, $P = 0.585$), but it was closely correlated with stand age (Pearson's correlation analysis, $P = 0.004$). The mean slope across all stands with western hemlock was 21%. Ten of the 17 stands with slopes less than the mean were under 100 yr old, and 15 of the 21 stands with slope greater than the mean were more than 200 yr old, suggesting that in the stands under study, the older trees occur on steeper slopes.

No single aspect had *C. tubaeformis* productivity significantly different from the mean. In all cases sample sizes were small for effective statistical analysis. Twelve stands were south-facing and had a mean biomass productivity of 1.45 g. Fourteen stands had north-facing aspects and mean biomass productivity of 2.61 g. Eight stands faced west with a mean biomass of 2.78 g, and four stands faced east with a mean biomass of 1.86 g.

*Probability of* C. tubaeformis *occurrence.*—The best logistic regression model (adjusted $R^2 = 0.44$; Nagelkerke 1991) contained only the explanatory terms of stand age and volume of class 4 and 5 CWD. TABLE II shows the estimates for the intercept term and explanatory variables with their associated 95% confidence limits and *P* values. Elevation and the amount of class 1 to 3 CWD were not significant to the occurrence of *C. tubaeformis.* Slope initially seemed significant ($P = 0.0445$) but again was highly correlated with stand age ($P = 0.021$). Though late-seral stands with above-mean class 4 and 5 CWD levels generally

TABLE II. Logistic regression model estimates for the likelihood of *Craterellus tubaeformis* occurrence based on stand age and volumes of class 4 and 5 coarse woody debris, with associated confidence limits and *P*-values ($\alpha = 0.95$, n = 57)

| $\beta_0$ (intercept) | Confidence | $\beta_1$ ln (age) | Confidence | $\beta_2$ ln (CWD) | Confidence |
|---|---|---|---|---|---|
| −0.3376 | −4.044 to 3.369<br>$P = 0.8583$ | 0.9382 | 0.246 to 1.63<br>$P = 0.0079$ | 1.0293 | 0.191 to 1.868<br>$P = 0.0161$ |

had slightly more class 4 and 5 CWD than the early-seral stands with above-mean class 4 and 5 CWD levels, correlation between stand age and class 4 and 5 CWD volume was not significant even after stands without western hemlock were removed (Pearson's correlation analysis, $P = 0.133$). The interaction term of stand age and class 4 and 5 CWD volume also was not significant ($P = 0.549$). The resulting model for the effect of stand age and volume of class 4 and 5 CWD on the odds of the presence of *C. tubaeformis* in stands with western hemlock is

$$\text{Odds} = {}_e[-0.3376 + 0.9382(\ln \text{Age}) + 1.0293(\ln \text{Volume of class 4 and 5 CWD})]$$

FIGURE 2 graphs the probability (calculated from the odds) of *C. tubaeformis* occurrence with stand ages of 30 and 650 yr and 95% confidence limits against the range of class 4 and 5 CWD volumes encountered in the field. The model is extrapolative, and the high *P* value and wide confidence limits at the intercept suggest diminished certainty in stands with very little class 4 and 5 CWD. This reflects the distribution of stand ages and class 4 and 5 CWD volumes measured in the field; the model consequently is most confident in those stand age and class 4 and 5 CWD volume combinations likely to be encountered (e.g., the confidence limits are widest in older stands with less class 4 and 5 CWD volume and in younger stands with more class 4 and 5 CWD volume). For example, the model predicts a 55.5% chance of locating *C. tubaeformis* in a 650 yr old stand with 0.005 $m^3\ m^{-2}$ of class 4 and 5 CWD; however no late-seral stands had such low volumes of class 4 and 5 CWD and *C. tubaeformis* was never located in a stand with less than 0.009 $m^3\ m^{-2}$ of class 4 and 5 CWD.

The mean volume of class 4 and 5 CWD in early-seral stands was 0.040 $m^3\ m^{-2}$ (0.005–0.141) and in late-seral stands was 0.055 $m^3\ m^{-2}$ (0.016–0.348). The stand with the lowest level of class 4 and 5 CWD recorded in this study (0.005 $m^3\ m^{-2}$) was 53 yr old with almost no decayed wood greater than 10 cm diam; the class 4 and 5 CWD groundcover was composed of smaller twigs and few if any well-decayed stumps were present. The highest level of class 4 and 5 CWD recorded in this study (0.348 $m^3\ m^{-2}$) was a 500 yr old stand with many large class 4 and 5 fallen boles, well decayed stumps, and abundant class 4 and 5 CWD aggregate in the organic soil horizon.

FIGURE 3 shows the probability of *C. tubaeformis* occurrence with the highest and lowest levels of class 4 and 5 CWD encountered in this work (0.005 and 0.348 $m^3\ m^{-2}$), along a gradient of stand ages. Again the model extrapolates, and it is noteworthy that in this study the late-seral stand with the least amount of class 4 and 5 CWD was 374 yr old and had 0.016 $m^3\ m^{-2}$ of class 4 and 5 CWD. The early-seral stand

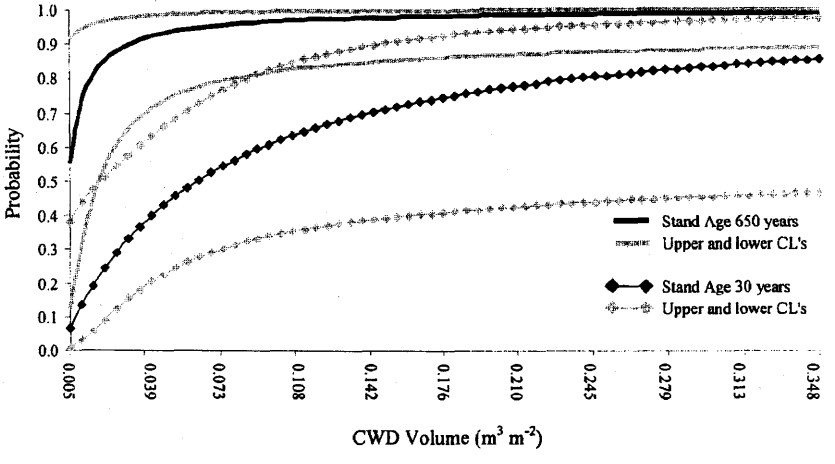


FIG. 2. Probability of *Craterellus tubaeformis* occurrence with stand ages of 30 and 650 yr plotted against a gradient of class 4 and 5 coarse, woody debris volumes, with 95% confidence limits.

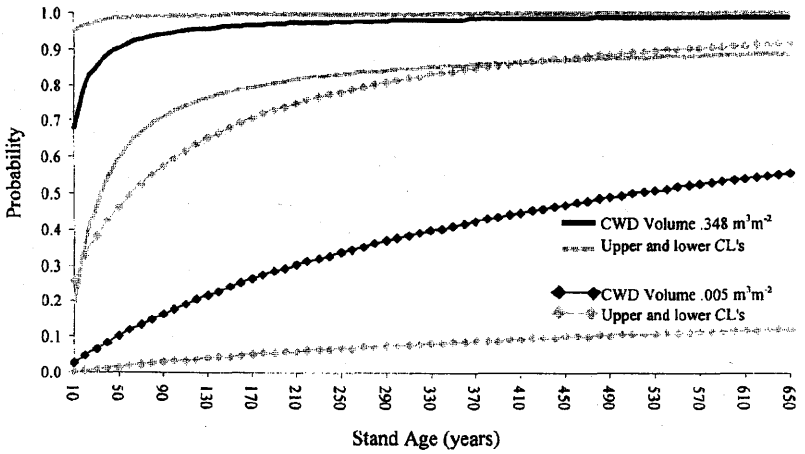


FIG. 3. Probability of *Craterellus tubaeformis* occurrence with class 4 and 5 coarse, woody debris volumes of 0.005 and 0.348 $m^3$ $m^{-2}$ plotted against a gradient of stand age, with 95% confidence limits.

with the greatest amount of class 4 and 5 CWD conversely was 48 yr old and had 0.141 $m^3$ $m^{-2}$ of class 4 and 5 CWD. Thus, some of the combinations of variables depicted in the graph are unlikely to be encountered in the field.

*Substrata of* C. tubaeformis.—Eighty-eight percent of the biomass of *C. tubaeformis* colonies in northwestern Oregon was produced on or near class 4 and 5 CWD (within 10 cm) despite the fact that ground area coverage of class 4 and 5 CWD ranged only from 3 to 26%. *Craterellus tubaeformis* frequently occurs on the accumulated slough immediately adjacent to larger pieces of CWD in northwestern Oregon, and buried chunks of class 4 and 5 CWD aggregated under moss or needle litter also were encountered often as substratum. It usually was impossible to determine the species of tree from which the more decayed CWD originated. Only one colony was clearly associated with class 3 CWD and none with class 1 or 2 CWD.

Stumps were not uncommon as *C. tubaeformis* substratum (4.4% of documented *C. tubaeformis* biomass). Stumps were categorized differently from other types of CWD substratum because the sapwood and heartwood were often decay class 4 or 5 while the bark would remain at decay class 3. *Craterellus tubaeformis* fruited from the soft wood at the top of stumps as well as from the outside of the class 3 bark, sometimes more than a meter above ground.

Mossy areas and needle-covered ground with no detectable subterranean class 4 and 5 CWD were less common as substrata (3.25% and 3.0% of total biomass, respectively). Most basidiomata on these substrata were collected in older stands with lower levels of class 4 and 5 CWD. Another substratum occasionally encountered (0.35% of biomass) was the bark of living trees. This substratum was observed twice, in both cases at the base of old-growth Douglas-fir trees (less than 20 cm above ground) in mesic stands. On these trees, the bark underneath the basidiomata was permeated with active fine roots.

Hydnum *species as an indicator.*—The presence of *Hydnum* spp. proved to be a positive indicator for the presence of *C. tubaeformis* in stands with western hemlock during the fruiting season. The likelihood of finding *C. tubaeformis* in the presence of *Hydnum* spp. was 90% ($P = 0.0001$) and in the absence of *Hydnum* spp. 42% ($P = 0.269$). The probability of finding *Hydnum* spp. in the presence of *C. tubaeformis* was 74% ($P = 0.0001$) and in the absence of *C. tubaeformis* 70% ($P = 0.0005$). Mycorrhizae from *Hydnum* spp. were identified positively by RFLP in this study and often were found in the same root samples as *C. tubaeformis* mycorrhizae.

## DISCUSSION

*Habitat associations.*—Both stand age and the volume of class 4 and 5 CWD are significant to the probability of *C. tubaeformis* occurrence in stands with western hemlock (TABLE II). In older stands, probability of occurrence is quite high even with minimal class 4 and 5 CWD volumes. It also is evident that *C. tubaeformis* can thrive in younger stands. The volume of class 4 and 5 CWD is particularly significant to the probability of *C. tubaeformis* occurrence in stands less than 100 yr old, as probability increases rapidly with increasing class 4 and 5 CWD volume in this age range. Younger stands with a great abundance of class 4 and 5 CWD are more likely to have *C. tubaeformis* than older stands with a paucity of class 4 and 5 CWD.

The marginal significance of the volume of class 1–3 CWD to *C. tubaeformis* standing crop productivity ($P = 0.52$) seems contrary to the findings of the logistic regression. It is likely an artifact of the removal of stands that produced no *C. tubaeformis* biomass from linear regression analysis, and the weakness of the connection is indicated by its low adjusted $R^2$ value (0.07). Less than 1% of *C. tubaeformis* field collections were associated with class 1–3 CWD. Another interesting observation is that the volume of class 1–3 CWD was not significantly correlated with the volume of class 4 and 5 CWD (Pearson's correlation analysis, $P = 0.513$). One might expect such a relationship because the input of fresh, woody debris represents the next cohort of decayed woody debris. A possible explanation is that CWD persists in decay classes 4 and 5 much longer than in classes 1–3 (Maser et al 1989). This could result in the levels of class 1 through 3 CWD being more variable at any given sampling iteration because of seasonal effects and recent weather events.

The inverse relationship between elevation and *C. tubaeformis* productivity was unexpected but is unsurprising. Although the *C. tubaeformis* fruiting season begins earlier at higher elevations, the lower elevations are less subject to frost and hence tended to have higher basidiomata productivity over the course of a season.

Given the significance of stand age and class 4 and 5 CWD volume for the probability of *C. tubaeformis* occurrence, it might seem somewhat counterintuitive that these factors are not significant to standing crop biomass productivity. In several cases, only one small area in a young stand might produce *C. tubaeformis* but in tremendous quantities. For example, the class 5 CWD slough surrounding one large stump might produce hundreds of basidiomata in a stand with little other class 4 and 5 CWD. This scenario often was encountered in younger stands; older stands usually had a greater diversity of class 4 and 5 CWD forms. Fully one-third of the stands did not produce any *C. tubaeformis* basidiomata, and removing them from the linear regression certainly affected the significance of the results, but the influence of these nonproductive stands was more appropriately evaluated with logistic regression.

The presence of western hemlock and the volume of class 4 and 5 CWD clearly were demonstrated to be important factors in the probability of *C. tubaeformis* occurrence. Western hemlock commonly uses larger pieces of class 4 and 5 CWD as seedbed (Minore 1972), and its roots and mycorrhizae permeate the CWD (Kropp and Trappe 1982, Maser and Trappe 1984). Does the close association of *C. tubaeformis* with class 4 and 5 CWD in the Pacific Northwest result from its frequent association with western hemlock? The roots of western hemlock also permeate mineral and organic soil away from CWD, yet *C. tubaeformis* is not nearly as prevalent in those areas in northwestern Oregon. Likewise, stands with abundant class 4 and 5 CWD but no hemlock are unlikely to have *C. tubaeformis*. This suggests that an interaction between the presence of western hemlock and the volume of class 4 and 5 CWD affects the probability of *C. tubaeformis* occurrence.

Some mycorrhizal fungi produce lignase, cellulase or peroxidase enzymes (Trojanowski et al 1984, Griffiths and Caldwell 1992, Durall et al 1994, Bending and Read 1995, 1997). The saprobic capability of *C. tubaeformis* is unknown, but it seems a likely adaptation to its ecological niche in northwestern Oregon. Kropp and Trappe (1982) hypothesized that, because western hemlock usually regenerates on class 4 and 5 CWD in the understory, western hemlock mycorrhizal associates would have to compete with the extant fungal community. The ability to extract energy from CWD could provide a competitive advantage for *C. tubaeformis* in such adverse circumstances. The C : N ratio in Douglas-fir and western hemlock CWD is 200:1–500:1 (Graham and Cromack 1982, Sollins et al 1987), and most plants can access nitrogen only when the C : N ratio falls below about 25:1 (Russell 1988, Maser et al 1989). Fungi that have saprobic capabilities can extract nitrogen from substrata with C : N ratios as high as 1800:1 (Maser et al 1989). This could explain some of the ability of both *C. tubaeformis* and western hemlock to gain a foothold in the competitive understory of established forests. More research is needed on the saprobic capabilities of *C. tubaeformis*.

Coarse, woody debris provides a stable source of moisture throughout seasonal variations, thereby helping to support mycorrhizae during dry periods (Amaranthus et al 1989, Maser et al 1989, Amaranthus et al 1994). Boddy (1983) showed that water can comprise more than half of the mass of class 4 and 5 CWD. Most mushrooms have high water content; Pilz et al (1998) reported that the mean moisture content of *Cantharellus formosus* (Pacific golden chanterelle) was 89% (57%–98%, n = 80 basidiomata) but indicated that the specimens with high water content likely were "past their prime" or collected on rainy days and might have been influenced by hydroscopy (D. Pilz pers comm). The mean water content of *C. tubaeformis* is slightly higher at 93.4% but much less variable (90.0%–94.1%, n = 74 colonies), though in this study only fresh specimens collected on days without precipitation were analyzed for water content. Coarse, woody debris would offer the reservoir of water necessary for substantial *C. tu-*

*baeformis* basidiomata production (a typical *C. tubaeformis* colony of approximately 3 g dry weight would contain more than 45 g of water); however, substantial precipitation characterizes the *C. tubaeformis* fruiting season and soils often are saturated. The water content of class 4 and 5 CWD during the drier parts of the year may facilitate the acquisition and storage of nutrients needed for basidiome formation, but it is unclear how this would affect *C. tubaeformis* differently from any other fungal species.

In Europe the habitat association of *C. tubaeformis* with class 4 and 5 CWD is not nearly as prominent (Persson 1997; G. Gulden and E. Danell pers comm). There it associates with both deciduous and coniferous trees, and generally less CWD is available. Tyler (1985) and Persson (1997) note that *C. tubaeformis* in Swedish beech forests is found in areas with more acidic soils. Alexander and Watling (1987) report that their collections in Sitka spruce plantations in Scotland were "mostly on mineral soil." In the Appalachian Mountains of the southeastern United States *C. tubaeformis* is found in moss and leaf litter along streams (R. Petersen pers comm). Peck (1887) recognized a *Cantharellus infundibuliformis* var. *subcinereus* and noted it "occurs especially among Sphagnum in marshes" in New York. More research is needed to quantify the habitat preferences of *C. tubaeformis* in different settings and to determine whether these differences are congruent with genetic patterns.

*Host associations.—Craterellus tubaeformis* occurs only infrequently in Douglas-fir stands lacking western hemlock in northwestern Oregon. It can form mycorrhizae with Douglas-fir but might do so only in the absence of western hemlock. Most pure Douglas-fir stands in western Oregon are plantations that replaced native mixed Douglas-fir/western hemlock, and these Douglas-fir may be colonized by relict *C. tubaeformis* mycorrhizae from the previous stand. In contrast, *C. tubaeformis* forms mycorrhizae with Sitka spruce but this has been observed only when western hemlock is present; during a concerted search *C. tubaeformis* was not observed in pure Sitka spruce stands. Pure Sitka spruce stands are usually natural in origin and may never have had a western hemlock component. It is possible that in the Sitka spruce/western hemlock stands the hemlock provides a launching point for colonization of spruce by *C. tubaeformis*. The sample size of pure Sitka spruce stands is small, however, and more research on *C. tubaeformis* in the spruce forests of the Pacific Northwest coast is needed.

The apparent differences in host association might be a result of *C. tubaeformis* being a broad-spectrum mycorrhizal fungus that responds to regional differences in available hosts; on the other hand regional variants of *C. tubaeformis* might have evolved to fill specific niches (congruent with Harley and Smith's [1983] concept of "ecological specificity"). Bills et al (1986) report *C. tubaeformis* with monoculture red spruce in eastern North America but not in mixed hardwood stands (*Acer, Betula, Fagus, Fraxinus, Ilex, Prunus, Quercus* and *Sorbus* spp), suggesting host specificity or at least preference. However, many of these hardwood genera are the same ones reported as mycorrhizal associates of *C. tubaeformis* in Europe; clearly more data are needed. Alexander and Watling (1987) reported *C. tubaeformis* in monoculture Sitka spruce plantations in Scotland. They speculated that, because Sitka spruce was introduced to these stands by seed rather than by transplants, the mycorrhizal flora (including *C. tubaeformis*) might have migrated from native relict *Betula* or *Pinus* stands. This would tend to suggest broader host compatibility. Kårén et al (1997) identified *C. tubaeformis* mycorrhizae in Sweden but their study was conducted in *Pinus sylvestris* and *Picea abies* stands, species not naturally found in western Oregon.

The likelihood of finding *C. tubaeformis* is more than twice as great when *Hydnum* spp. is present (90% versus 42%) in stands with western hemlock. The presence of *C. tubaeformis* is not as effective an indicator for *Hydnum* spp. (74% with *C. tubaeformis* versus 70% without). Their fruiting seasons are concurrent, but field observations suggest that *Hydnum* spp. are more common in pure Douglas-fir and Sitka spruce stands than *C. tubaeformis,* and thus may have more potential habitat in northwestern Oregon. Because *C. tubaeformis* seems to have a more limited range of habitats, one would expect the indicator relationship to be the reverse of that observed.

*Genetic variation within* C. tubaeformis.—Feibelman et al (1994) found differences in the length of the ITS region between specimens identified as *C. tubaeformis* from Mississippi and Germany and specimens identified as *C. infundibuliformis* from California. They also noted a smaller difference in ITS region size between the two *C. tubaeformis* specimens. Kårén et al (1997) reported different RFLP fragment sizes produced by *C. tubaeformis* in Sweden from those produced by Oregon specimens (Trappe et al 2000). Phylogenetic analyses by Dahlman et al (2000) indicated the variant of *C. tubaeformis* in eastern North America seems more closely related to the European variant than to the Pacific Northwestern variant. Published descriptions (Fries 1821, 1838, Corner 1966, Donk 1969, Petersen 1979) report no striking morphological differences between *C. tubaeformis* collec-

tions from these geographic regions beyond what might be expected from intraspecific variability. If the geographic variants of *C. tubaeformis* are genetically isolated to the extent that they have evolved different host compatibility matrices (as discussed by Petersen and Hughes [1999], "requisite in this process is a hiatus in gene exchange ... allow(ing) each group to accumulate genetic differences."), they probably would qualify as distinctly different species with their own epithets (Mayr 1970, Carson 1985, Brasier 1997). Sequencing of herbaria specimens from around the globe suggests this is the case for *C. tubaeformis* (Trappe unpubl data). Preliminary phylogenetic analyses group together specimens from eastern Russia, Europe and eastern North America, distinct from western North American specimens. Pilz et al (2003) used the name *Craterellus neotubaeformis* nom. prov., and it is likely that a comprehensive phylogenetic analysis of the *C. tubaeformis* complex will result in a formal name change for the western North American variant. The region of geo-genetic divide in North America remains an intriguing question that will be answered only by further sampling and analysis.

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