Short title: Emergence of ascocarps

Emergence of morel (*Morchella*) and pixie cup (*Geopyxis carbonaria*) ascocarps in response to the intensity of forest floor combustion during a wildfire

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Abstract: We studied the density of ascocarps (mushrooms) of morels (*Morchella*) and pixie cups (*Geopyxis carbonaria*) as a function of postfire duff (forest floor organic layer) depth in the first 4 y after a wildfire. The great majority of ascocarps of both species appeared in the first summer (2004) after an Aug 2003 fire in predominantly pine-spruce montane stands in Kootenay National Park, British Columbia. The spatial distribution of the ascocarps of both species was strongly biased toward (i) microsites with thin postfire duff and (ii) proximity to standing burned tree trunks. The bases of ascocarps of both species invariably were found just below the surface of the mineral soil. A field experiment in nearby intact forest showed that complete or partial duff removal in the absence of damage to the roots or crown did not lead to ascocarps of either species. We conclude that for both fungal species an unusually large abundance of ascocarps simultaneously requires damage to the associated trees and major duff reduction.

Key words: duff, fruiting, fungi, mushroom, organic layer, smoldering combustion

INTRODUCTION

The ascocarps of *Morchella* species comprise one of the most important non-timber forest products currently exploited in North America with 225 metric tons traded annually in North America (Bunyard et al. 1994, Duchesne et al. 2001, Pilz and Molina 2002, Wurtz et al. 2005). Cultivation of *Morchella* remains costly due to limited production of sclerotia; in consequence the industry has continued to rely on wild ascocarps, especially those arising after disturbances (Barnes and Wilson 1998, Obst et al. 2000, Winder and Keefer 2008).

Note that the taxonomy of *Morchella* is clearly in flux. In particular Pilz et al. (2004), relying on molecular evidence, recommended that *M. elata* (Fries) be split into three species, although the formal designation of these new species was not included and this suggestion still has not been widely adopted. In what follows we will refer to the pyrophilic species we studied as *Morchella*, although we have little doubt it is the same species simultaneously studied (in the same region, after the same fire) and deemed *M. elata* by Winder and Keefer (2008). It was certainly not the gray morel (*M. tomentosa*) as defined by Kuo (2008).)

How much do we know about morel fruiting ecology? The genus has both saprotrophic and mycorrhizal phases in the life cycle (Buscot 1989). The mycorrhizal phase occurs in spring when sclerotia (storage organs) produce mycelia that colonize root hairs (Buscot 1992, Miller et al. 1994, Wipf et al. 1997). Some authors have noted affinities between *Morchella* ascocarp abundance and specific tree species (Duchesne and Weber 1993, Dahlstrom et al. 2000, Mihail et al. 2007). As an alternate developmental path the sclerotia may produce ascocarps. Some have argued that ascocarp production

requires damage to the host plant or a severing of the connection to the host (i.e. a sharp reduction in nutrient supply). Miller's (2005a, b) in vitro ascocarp cultivation method called for killing the inoculated seedling host; Volk and Leonard (1989) argued that sclerotia are formed as the nutrient supply is used up. In the field there is a well known association between *Morchella* ascocarp production and forest disturbances, such as fire, insect outbreaks, logging and wind storms, especially in the first summer after the disturbance (e.g. Pilz et al. 2004). Miller et al. (1994) speculated that immediately after a disturbance mycelia form sclerotia that in turn fruit the next spring; in subsequent summers there is little fruiting simply because this ephemeral "sclerotium bank" has been exhausted.

An alternative argument is that ascocarp production requires removal of the overlying duff (forest floor organic layer) (Baar and Kuyper 1993, Pilz et al. 2004). *Morchella* sclerotia are formed just below the mineral-humus contact zone where they are protected from fire (Miller 2005a, Pilz et al. 2007). Organic layers in intact boreal and cordilleran forest floors are typically much deeper than the length of any ascocarp (Greene et al. 2007), and thus, given the placement of sclerotia, duff removal is necessary for exposure of the ascocarps. Of course it also might be that soil heating, a consequence of duff removal, is an important cue.

We hypothesize that both of these effects, serious damage to the tree (or perhaps only to the roots) as well as removal of the duff, are prerequisites for dense ascocarp production by this *Morchella* specie*s*. Either factor alone ought to lead to only a small increase relative to the normal "background" production in undisturbed forest. Furthermore this hypothesis can account for another phenomenon noted qualitatively by

both McFarlane et al. (2005) and Wurtz et al. (2005): After fire morel ascocarps tend to be clustered near standing burned trunks and large surface roots. While one could argue that this merely reflects the pre-fire mycorrhizal association, the near-tree microsites are precisely where duff consumption by smoldering combustion is greatest (Greene et al. 2007). In addition to looking at the effect of disturbance, duff consumption and distance to nearest standing burned trunk, we also examined whether *Morchella* ascocarps are preferentially found near certain tree species, presumably due to pre-fire mycorrhizal associations.

We simultaneously examine the circumboreal discomycete pixie cups (*Geopyxis carbonaria* [Alb. & Schwein]), which, although a species of no economic importance, has ascocarps that typically are found with *Morchella*, especially in recently burned areas. We did this simply because it was so common in the same post-fire stands as this *Morchella* species. The co-occurrence of *Morchella* and *G. carbonaria* is common in western North America with pixie cups invariably the more abundant (Obst and Brown 2000, Wurtz et al. 2005). Indeed Obst and Brown (2000) thought that *G. carbonaria*, fruiting somewhat earlier than *Morchella*, could serve as a guide for morel harvesters to those areas that subsequently would become dense with the more valuable *Morchella*. Little is known about *G. carbonaria* beyond the agreement that it is primarily saprotrophic, although capable of being mycorrhizal (Vrålstad et al. 1998). Egger and Paden (1986) found it to be moderately pathogenic due to associations with damaged hosts but believed that the formation of a Hartig net was evidence of potential mutualistic association. As with *Morchella* species, Vrålstad et al. (1998) argued that the species required damage to the host for prolific fruiting.

MATERIALS AND METHODS

We examined the abundance of *Morchella* morels and *G. carbonaria* ascocarps 2004–2007 after an Aug 2003 fire in Kootenay National Park, British Columbia. Before the burn our study area in the Rocky Mountains consisted of montane stands dominated by roughly equal proportions of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry) with some subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) at approximately 1200 m. The long drought in summer 2003 promoted the greatest area burned in the park since the 1920s; all fires were started by lightning and extinguished by rain. We worked in the largest of these burns, the 18 000 ha Tokumm-Verendrye fire, which was active Jul 31–Sep 10.

Ascocarp densities were measured once in late May to late June each year along 16 transects 1 m wide. Transects were chosen with a single criterion: They all began in partially killed stands then passed across a relatively sharp edge into extensive (> 1 ha) areas with 100% mortality of trees. Four of the 16 transects were 50 m long (due to the presence of a rock face) and the other 12 were 100 m long. Thus the total area examined each year was 1400 m^2. The transects were divided across four sites on the valley floor and spaced parallel approximately 15 m apart at each site. Each transect began in partially burned timber (averaging 25% tree mortality), extending into the burn at a right angle to the fire edge. The fire edge was defined as the point where we first encountered 100% tree mortality. At the base of every ascocarp within the transect we measured duff depth as well as distance to the nearest tree having a diameter at breast height (DBH) greater than 10 cm. Also duff depth and distance to nearest tree were recorded every 0.5 m along the central axis of the transect. These latter measurements will be referred to as the uniform points. For the closest tree to every uniform point or ascocarp we measured the DBH and species identity.

To experimentally relate duff depth to ascocarp formation in undisturbed forest, we used four sets of randomly positioned plots (each 1 × 4 m) for three treatments in an intact forest at Kootenay National Park in May 2005 about 30 km southwest of the burn. The site was similar in tree species composition (dominance of Engelmann spruce and lodgepole pine), elevation, distance to river and slope angle to the 2003 fire transects. In the first treatment all duff was removed; in the second treatment all but 1–2 cm duff was removed; and in the third (control) the duff was left intact. The root systems of the trees were not

affected by duff removal. The plots were re-examined in late May 2005, 2006 and 2007 for ascocarp formation.

Kolmogorov-Smirnov tests were used to determine the relationship between ascocarp clustering and distance to nearest trunk or to duff depth. Correlation of log-transformed values was used to measure associations of ascocarps with tree species.

RESULTS

Ascocarp densities were much higher in the first year after fire than in subsequent years (TABLE I), with summer 2004 accounting for 98% of *Morchella* and 95% of *G. carbonaria*. Density decreased sharply in 2005 but did not continue to decline over the next 2 y; indeed more ascocarps were found in 2007 than in 2006 ($P < 0.001$; chi-square test; TABLE I).

Ascocarp density for both species was much higher in the burn than in the adjacent partially burned stands where each transect began; only 1.2% and 3.8% of the *Morchella* and *G. carbonaria* respectively were found in the forest edge (25% tree mortality) even though these stands comprised 10% of transects. While charring of twig tips certainly indicated that some modest duff smoldering occurred in the partially burned edge stands, the mean duff depth was much lower in the more intense part of the burn (mean = 2.7 cm; standard deviation = 3.8) than at the partially burned edge (mean = 5.7 cm; standard deviation = 4.9). Far from any edge similar (but unburned) stands averaged 8 cm duff depth (standard deviation = 5.1). In what follows we will exclude the partially burned portions of transects; instead all values will refer only to transect portions within the severely burned (i.e. 100% tree mortality) area.

Within the burn ascocarps of both species were clustered near trees. The mean distance to the nearest tree was 0.76 m for *Morchella* and 1.08 m for *G. carbonaria* but

1.37 m for the uniform points. This relative clustering around trunks was highly

significant (FIG. 1; K-S tests comparing the ascocarps to the uniform points; $D_{max} = 0.37$

and 0.52 for *Morchella* and *G. carbonaria* respectively; $P < 0.001$ for both).

Of the trees sampled along transects 41.5% were Engelmann spruce, 41.5% were

lodgepole pine and 17% were subalpine fir. The mean basal area per area for these > 100

y old stands was around 30 m^2/ha. Neither fungal species showed a significant

relationship between ascocarp density and the presence of a particular tree species ($P \gg$

0.05 for all three tree species); we illustrated the log-transformed correlation with

Engelmann spruce as an example (FIG. 2).

Ascocarps of both species were restricted essentially to the thinnest part of the

forest floor (FIG. 3). A majority of the ascocarps of *Morchella* (95%) and *G. carbonaria*

(97%) were found on residual duff less than 3 cm deep, despite the fact that these shallow

organic layers comprised only 67% of the transects (FIG. 3; K-S tests comparing

ascocarps to uniform points; for *Morchella*, $D_{max} = 0.69$, $P \ll 0.001$; and for *G.*

cabonaria, $D_{max} = 0.6753$, $P \ll 0.001$). Note that these D_{max} values are far higher and

therefore the *P* values far lower than in the preceding analysis using distance to nearest

trunk. A relative measure of preference is the ratio of the percentage of ascocarps to

uniform points in the first duff depth class. For *Morchella* this ratio was by far the highest

in the 0–1 cm depth category, while for *G. carbonaria* the ratio was highest in the 1–3 cm

depth category. In short both species were most abundant on a relative basis in the very

thinnest duff classes.

Examination of the *Morchella* ascocarps revealed that each had its base in the

gray podzolic mineral soil within 1 cm of the mineral. A more cursory examination of a

subsample of *G. carbonaria* ascocarps revealed that their bases also were located within 1 cm of the mineral surface.

Of the exposed ascocarps no *Morchella* ascocarp was found extending through a duff depth exceeding 5 cm despite the fact that about half the ascocarps were taller than this. Likewise no *G. carbonaria* was found emerging through duff greater than 4 cm, even though some ascocarps were (rarely) longer than this. Removal of several meters squared of adjacent thick, charred duff along one part of transect revealed no ascocarps of either species. The experimental removal of duff in the nearby intact pine-spruce forest in 2005 led to no ascocarp formation in any of the treatments in either 2006 or 2007.

DISCUSSION

As generalized by Buscot (1989), Vrålstad et al. (1998), Obst and Brown (2000) and Pilz et al. (2007) ascocarp production of pyrophilic *Morchella* species is maximized in the summer after a major disturbance. Our results were more dramatic than reported by Pilz et al. (2004) and Winder and Keefer (2008) with 95–97% of all ascocarps arising in the first post-fire summer. By contrast our *Morchella* densities for the second through fourth post-fire summers were more similar to other studies, averaging $0.01/m^2$ (two orders of magnitude lower than our first post-fire summer). For example Pilz et al. (2004) in Oregon reported a mean morel density of about $0.03/m^2$ in the second post-fire summer.

The ascocarps of both fungal species showed no tendency to associate with any particular burned tree species. Some authors have noted affinities between *Morchella* ascocarp abundance and specific tree species, although such studies invariably are large scale and might be telling us more about correlative responses of vascular plants and fungi to the same elevation and moisture gradients (Duchesne and Weber 1993, Mihail et

al. 2007). Conversely it might be that whatever discernable association may exist between plant species and ascocarp abundance is overwhelmed by the effect of residual duff depth. Post-fire duff depth in turn was unrelated to tree species identity in these mixed stands. Our mean densities for both species were the highest yet recorded in the literature. Pooling the reports of Obst and Brown (2000), Pilz et al. (2004) and Winder and Keefer (2008) for the first post-fire summer only, these authors averaged 0.1 morels per m^2, an order of magnitude lower than what we observed (only Winder and Keefer [2008] with 0.8 morels per ha for the same 2003 Kootenay fire we studied approached our value). The reason is undoubtedly that we focused on a severely burned section of the fire with 100% tree mortality and on average intense duff consumption. The cited authors were making fire-wide ascocarp production estimates and thus deliberately included areas that were lightly burned. Indeed the tree mortality in the burned stands studied by Pilz et al. (2004) was only 10–50%. Wurtz et al. (2005) in Alaska reported even lower values for *Morchella*.

Post-fire duff depth strongly controls the first post-fire summer abundance of both species. All morel ascocarp bases were within the first centimeter of the mineral soil layer. There was no physical impediment either above or below this stratum; in particular ascocarp bases were never found within residual duff. It remains unclear whether *Morchella* ascocarps arise directly from near-surface sclerotia or, as speculated by Pilz et al. (2007), from coalescing hyphae arising above deeper sclerotia.

There are two hypotheses for the fact that the great majority of post-fire morels are produced in the summer of the year after the fire. First, as speculated by Pilz et al. (2007), subsequent post-fire metabolism of charred organic material in the nearby (< 1 m

distant) thick, charred duff could lead to rapid metabolism by hyphae, emanating from sclerotia after the fire, which then coalesce into ascocarp primordia. An alternative argument is that the nutrient supply for ascocarps is derived almost entirely from pre-existing sclerotia. As Buscot (1989) points out with regard to *M. rotunda* the first hypothesis is problematic because fruiting comes at the expense of pre-existing mycelial structures, and the Kootenay 2003 burn, like most cordilleran (and high latitude) fires a late summer event, permits only a narrow temporal window for rapid metabolism. At best the hyphae could metabolize necromass during the 6 cold wk (say, mid-August to late September) before the ground froze; this could be augmented by the few weeks of thawed ground before ascocarp emergence in late spring. Metabolism certainly could occur under the snow but only at an exceedingly slow rate. It seems far simpler to imagine that the post-fire ascocarps were fueled essentially by the sclerotial reserves.

One wonders what duff depth-determined cues might govern whether an ascocarp is produced. It is possible that the sclerotia (or the hyphae derived from the sclerotium) respond to cues that can be decisive only when there is no or little residual duff present (e.g. mean near-surface soil temperature or the magnitude of diurnal changes in near-surface soil temperature). It is also possible that the heat generated by smoldering that extends to a depth near the mineral surface accentuates the cue. It seems likely that major duff removal must occur for a major crop of ascocarps. Boreal and cordilleran duff depths in intact, mature stands average 15 cm with 94% of substrate greater than 6 cm thick (Greene et al. 2007). Meanwhile few *Morchella* and no *G. carbonaria* ascocarps are taller than this. Given that every ascocarp base we examined was (roughly) at the mineral-duff

interface, it follows that major duff removal by some means (fire, skid paths created by harvesting machinery, windthrow, etc.) is a prerequisite for a large flush of ascocarps.

At first glance our results arguing for the importance of deep duff combustion after intense fire seem to be at odds with two recent studies that concluded that *Morchella* ascocarp density in western forests would be greatest on intermediately burned sites. Interviews with morel harvesters indicated that moderately burned microsites (defined as areas locally covered with reddened conifer needles) were the best for production of the closely related gray morel (*M. esculenta*), according to Wurtz et al. (2005). Red needles indicate incomplete combustion of leaves in the canopy and thus less extreme intensity at the flaming front within the crown. Ultimately the pickers interviewed by Wurtz et al. (2005) suggested that intermediate fire intensities are optimal for morel production. This is of course different from our conclusion. However we point out that (i) there is no quantification of the effect, (ii) red needles may be more visible against mineral soil than against the porous thick residual duff (i.e. they may sift down through the latter), (iii) trees with red needles are as dead as those with ashed needles and (iv) there is no strong correlation between the intensity of smoldering combustion of the forest floor and the severity (percent mortality of trees) within the canopy except at the extreme values (say, 10% vs. 100% tree mortality), partly because the former process can operate for weeks after the aerial portion of the fire has been extinguished by rain (Miyanishi 2001; Greene et al. 2005, 2007). Likewise Winder and Keefer (2008) argued that the greatest post-fire *Morchella* ascocarp numbers were found in intermediate duff depth categories. But they made no correction for depth class abundance (as we could here because we had the uniform point measurements)**.**

The tendency for *Morchella* ascocarps to lie near post-fire standing trees has been discussed qualitatively (McFarlane et al. 2005, Wurtz et al. 2005); the present study offers the first quantitative evidence for the pattern. However we think that the spatial pattern is primarily a result of the correlation of smoldering combustion intensity with distance to trunk, which is such a general feature of cordilleran and boreal fires (Greene et al. 2007). Certainly, as we saw, the probability of the null hypothesis being rejected was much lower for distance to nearest trunk than for duff depth when comparing either predictor with ascocarp abundance via a Kolmogorov-Smirnov test.

These results support our initial hypothesis that a high local density of morel ascocarps requires both a removal of duff and severe damage to the nearby trees. Whether the importance of the latter factor is due to a sudden reduction in nutrition for the mycelia or the change in surface soil temperature or both is not at all clear. The evidence for the coupling is as follows.

First, our experimental removal of duff in the intact forest (a stand outwardly similar to the areas where we had transects in the burn) did not lead to any *Morchella* or *G. carbonaria* ascocarp development. Much of the local root system and of course the above-ground parts of the trees were not damaged in any way. If the response to total and partial duff removal had been as strong as in the first post-fire summer, our sampling intensity should have provided us with about 50 *Morchella* and 350 *G. carbonaria* ascocarps.

Second, as we saw, a deep layer of post-fire duff did not engender ascocarps despite 100% tree mortality. By contrast well combusted duff did sponsor a high density of ascocarps. This differentiation in depth and ascocarp abundance occurred laterally at

the scale of about 1 m (Greene et al. 2007), far lower than the presumed spatial extent of hyphal networks.

Third, at the edge of the fire the stands with a few burned trees and a modestly combusted forest floor had ascocarp densities 10 times (*Morchella*) or 2.5 times (*G. carbonaria*) lower than in the adjacent burn. That is a modest amount of duff removal and of damage to overtopping trees led to a correspondingly modest amount of ascocarp production. Indeed these edge areas supported morel densities much more typical of the literature than what we found within the most intensely burned forest.

Fourth, as Pilz et al. (2004) showed, insect disturbances (tree death without any effect on duff depth) led to *Morchella* densities only about twofold greater than the "background" morel density; densities of these morels, they showed, were far higher after fire.

We suggest a simple experiment to test our hypothesis that high morel ascocarp density requires both removal of the duff layer as well as serious damage to trees. In an intact forest in the late summer one could establish plots with varying degrees of duff removed with a rake. For each intensity of duff reduction plots then would be either trenched around their perimeter (thus ending the photosynthate supply to the within-plot roots) or left undisturbed. Finally, in some of these plots trees would be harvested.

Turning to the ecological significance of the immediate response of these two fungal species to fire, there is one novel generalization we can make. For very different reasons these ascocarps are found on the same microsites preferred by tree germinants and pioneer mosses such as *Polytrichum* (Greene et al. 2007). The moss spores and the germinants (the latter necessarily small because they are derived from the small seeds that

typify high latitude and high altitude forests) cannot successfully establish on porous (rapidly drying), deep duff. By contrast, within less than 1 m distance there might be thick duff layers where there are abundant asexual stems deriving from (primarily) shade-tolerant shrubs and perennial herbs (Schimmel and Granstrom 1996, Greene et al. 2007). The asexual response is precluded on the well combusted microsites because the subaerial perennating organs are killed by the heat (Schimmel and Granstrom 1996). Thus at the scale of 1 m one sees very different responses among these taxa, the contrast arbitrated by the intensity of the smoldering combustion.

ACKNOWLEDGMENTS

LITERATURE CITED

Baar J, Kuyper TW. 1993. Litter removal in forests and effect on mycorrhizal fungi. In: Pegler DN, Boddy L, Ing B, Kirk PM, eds. Fungi of Europe: investigation, recording and conservation. Kew: Royal Botanic Gardens. p 275–286.

Barnes S, Wilson A. 1998. Cropping of the French black morel: a preliminary investigation. Australia: Rural Industries Research and Development Corp. 98/44. 14 p.

Bunyard BA, Nicholson MS, Royse DJ. 1994. A systematic assessment of *Morchella* using RFLP analysis of the 28S ribosomal RNA gene. Mycologia 86(6):762–772.

Buscot F. 1989. Field observations on growth and development of *Morchella rotunda* and *Mitrophora semilibera* in relation to forest soil temperature. Can J Bot 67(2):589–593.

———. 1992. Synthesis of two types of association between *Morchella esculenta* and *Picea abies* under controlled culture conditions. J Plant Physiol 141:12–17.

Dahlstrom JL, Smith JE, Weber NS. 2000. Mycorrhiza-like interaction by *Morchella* with species of the Pinaceae in pure culture synthesis. Mycorrhiza 9:279–285.

Duchesne LC, Weber MG. 1993. High incidence of the edible morel *Morchella conica* in a Jack Pine, *Pinus banksiana,* forest following prescribed burning. Can Field-Nat 107(1):114–116.

———, Zasada JC, Davidson-Hunt I. 2001. Ecological and biological considerations for sustainable management of non-timber forest products in northern forests. In: Davidson-Hunt I, Duchesne LC, Zasada JC, eds. Forest communities in the third millennium: linking research, business and policy toward a sustainable non-timber forest product sector. St Paul, Minnesota: USDA Forest Service p 102–109.

Egger KN, Paden JW. 1986. Biotrophic associations between lodgepole pine seedlings and postfire ascomycetes (Pezizales) in monoxenic culture. Can J Bot 64(11):2719–2725.

Greene DF, Macdonald SE, Cumming S, Swift L. 2005. Seedbed variation from the interior through the edge of a large wildfire in Alberta. Can J For Res 35(7):1640–1647.

———, ———, Haeussler S, Domenicano S, Noël J, Jayen K, Charron I, Gauthier S, Hunt S, Gielau ET, Bergeron Y, Swift L. 2007. The reduction of organic layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can J For Res 37(6):1012–1023.

Kuo M. 2008. *Morchella tomentosa*, a new species from western North America, and notes on *M. rufobrunnea*. Mycotaxon 105:441–446.

McFarlane EM, Pilz D, Weber NS. 2005. High-elevation gray morels and other *Morchella* species harvested as non-timber forest products in Idaho and Montana. Mycologist 19:62–68.

Mihail JD, Bruhn JN, Bonello P. 2007. Spatial and temporal patterns of morel fruiting. Mycol Res 111(3):339–346.

Miller SC. 2005a. Cultivation of *Morchella*. US Patent No. 6 907 691 B2.

———. 2005b. Cultivation of *Morchella*. US Patent No. 6 951 074 B2.

Miller SL, Torres P, McClean TM. 1994. Persistence of basidiospores and sclerotia of ectomycorrhizal fungi and *Morchella* in soil. Mycologia 86(1):89–95.

Miyanishi K. 2001. Duff consumption. In: Johnson EA, Miyanishi K, eds. Forest fires: behavior and ecological effects. San Diego: Academic Press. p 437–475.

Obst J, Brown W. 2000. Feasibility of a morel mushroom harvest in the Northwest Territories. Arctic Ecology and Development (AED) Consulting, Deton'cho Corp. and government of Northwest Territories.

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. For Ecol Manage 155:3–16.

———, McLain R, Alexander S, Villarreal-Ruiz L, Berch S, Wurtz TL, Parks CG, McFarlane E, Baker B, Molina R, Smith JE. 2007. Ecology and management of morels harvested from the forests of western North America. USDA Forest Service, Pacific Northwest Research Station, Gen. Tech. Report PNW-GTR-710.

———, Weber NS, Carter MC, Parks CG, Molina R. 2004. Productivity and diversity of morel mushrooms in healthy, burned and insect-damaged forests of northeastern Oregon. For Ecol Manage 198(1–3):367–386.

Schimmel J, Granström A. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77(5):1436–1450.

Volk TJ, Leonard TJ. 1989. Physiological and environmental studies of sclerotium formation and maturation in isolates of *Morchella crassipes*. Appl Environ Microbiol 55(12):3095–3100.

Vrålstad T, Holst-Jensen A, Schumacher T. 1998. The postfire discomycete *Geopyxis carbonaria* (Ascomycota) is a biotrophic root associate with Norway spruce (*Picea abies*) in nature. Mol Ecol 7(5):609–616.

Winder RS, Keefer ME. 2008. Ecology of the 2004 morel harvest in the Rocky Mountain Forest District of British Columbia. Botany 86(10):1152–1167.

Wipf D, Koschinsky S, Clowez P, Munch JC, Botton B, Buscot F. 1997. Recent advances in ecology and systematics of morels. Cryptogamie: Mycol 18(2):95–109.

Wurtz TL, Wiita AL, Weber NS, Pilz D. 2005. Harvesting morels after wildfire in Alaska. USDA Forest Service, Pacific Northwest Research Station, Research Note PNW-RN546.

LEGENDS

FIG. 1. The relative density of morels (*Morchella*), pixie cups (*G. carbonaria*) and uniform points as a function of distance to the nearest tree. Uniform points occur every 0.5 m along the central axis of the transect. The partially burned edge is excluded.
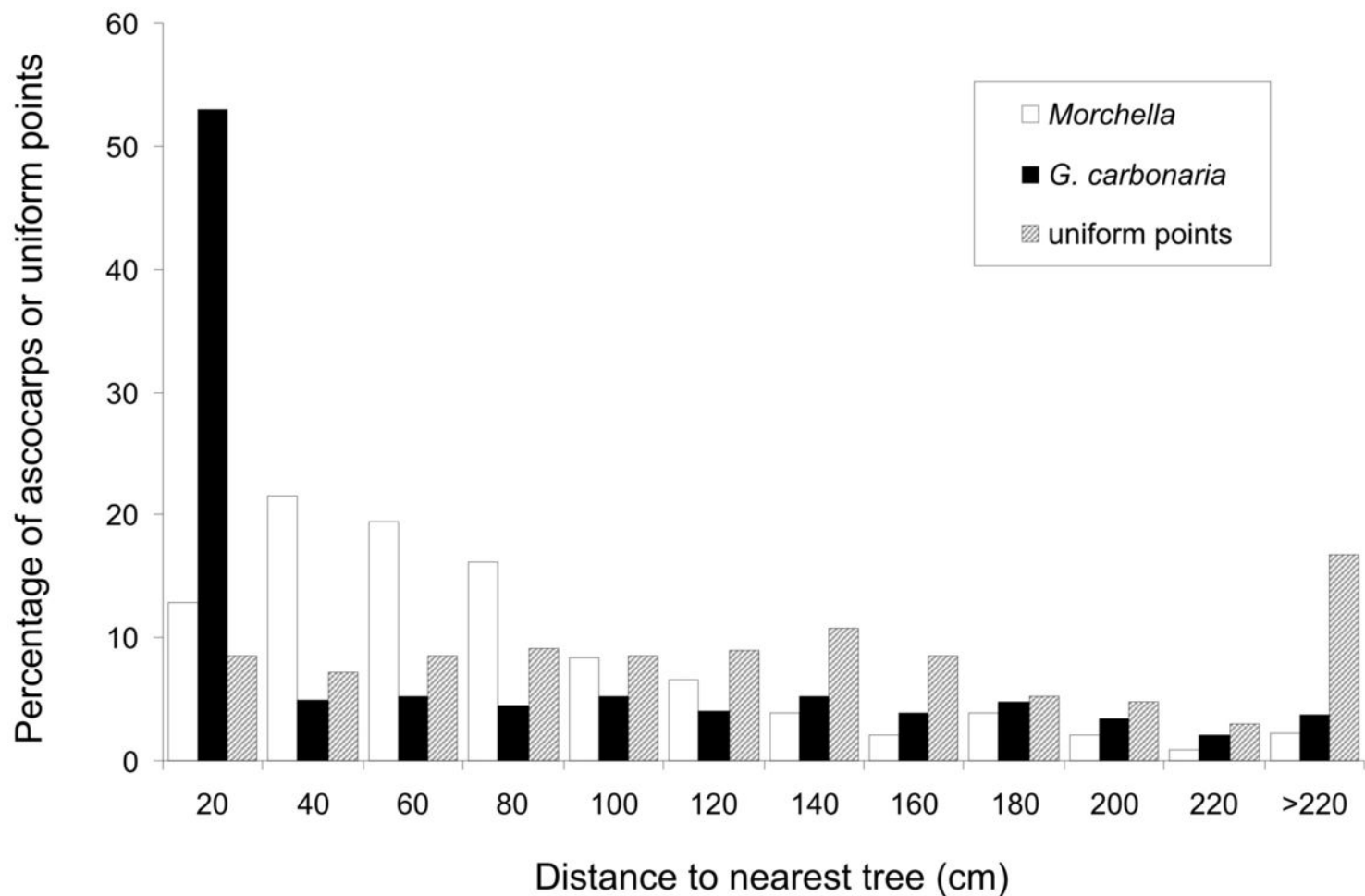
FIG. 2. Ascocarp density of both fungal species in 10 m long segments in relation to Engelmann spruce density. The partially burned edge is excluded.
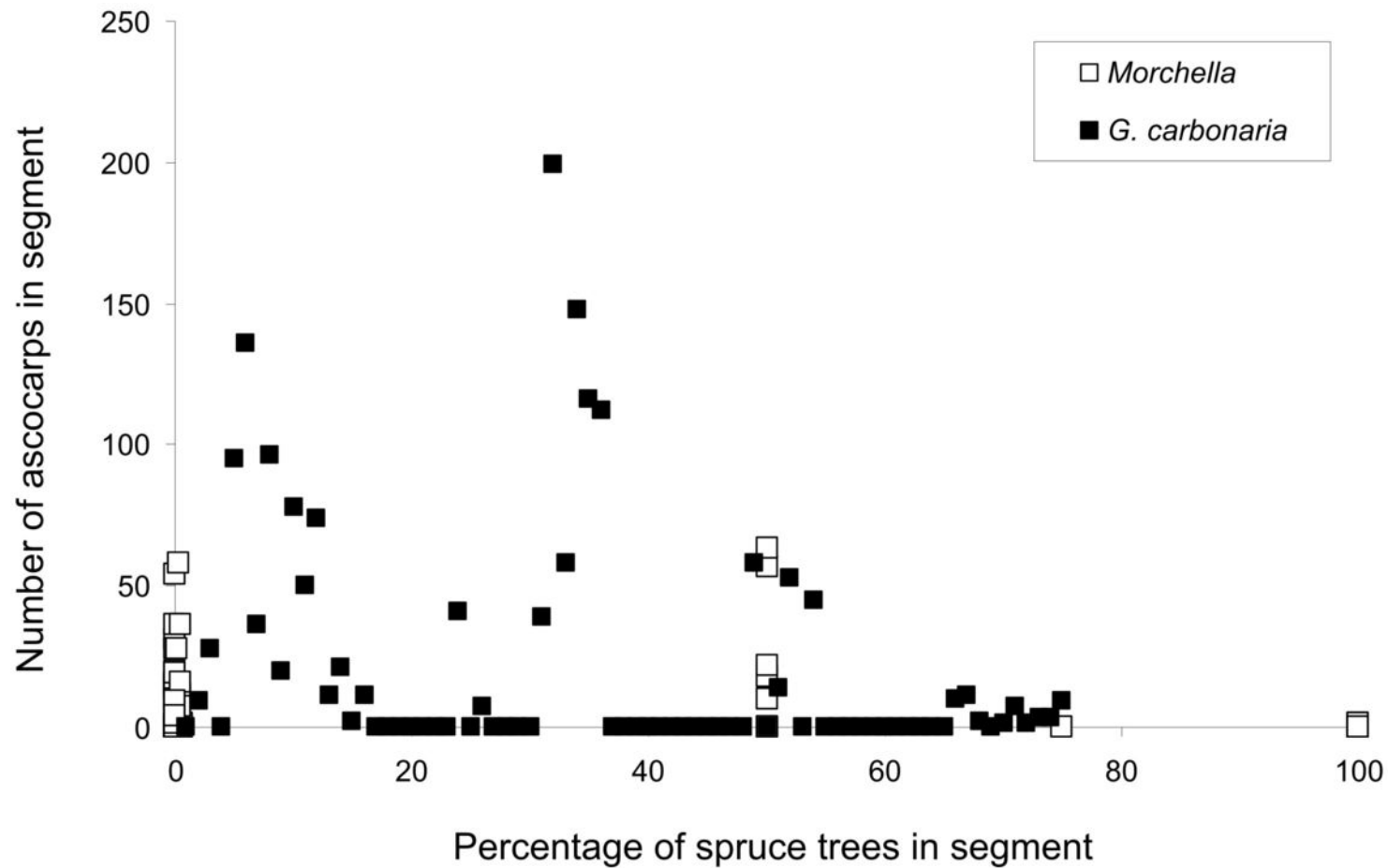
FIG. 3. The percentage of morels (*Morchella*), pixie cups (*G. carbonaria*) and uniform points as a function of duff depth. The partially burned edge is excluded.

FOOTNOTES

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Figure caption omitted; axis labels: Y-axis "Number of ascocarps in segment", X-axis "Percentage of spruce trees in segment". Legend: □ *Morchella*, ■ *G. carbonaria*
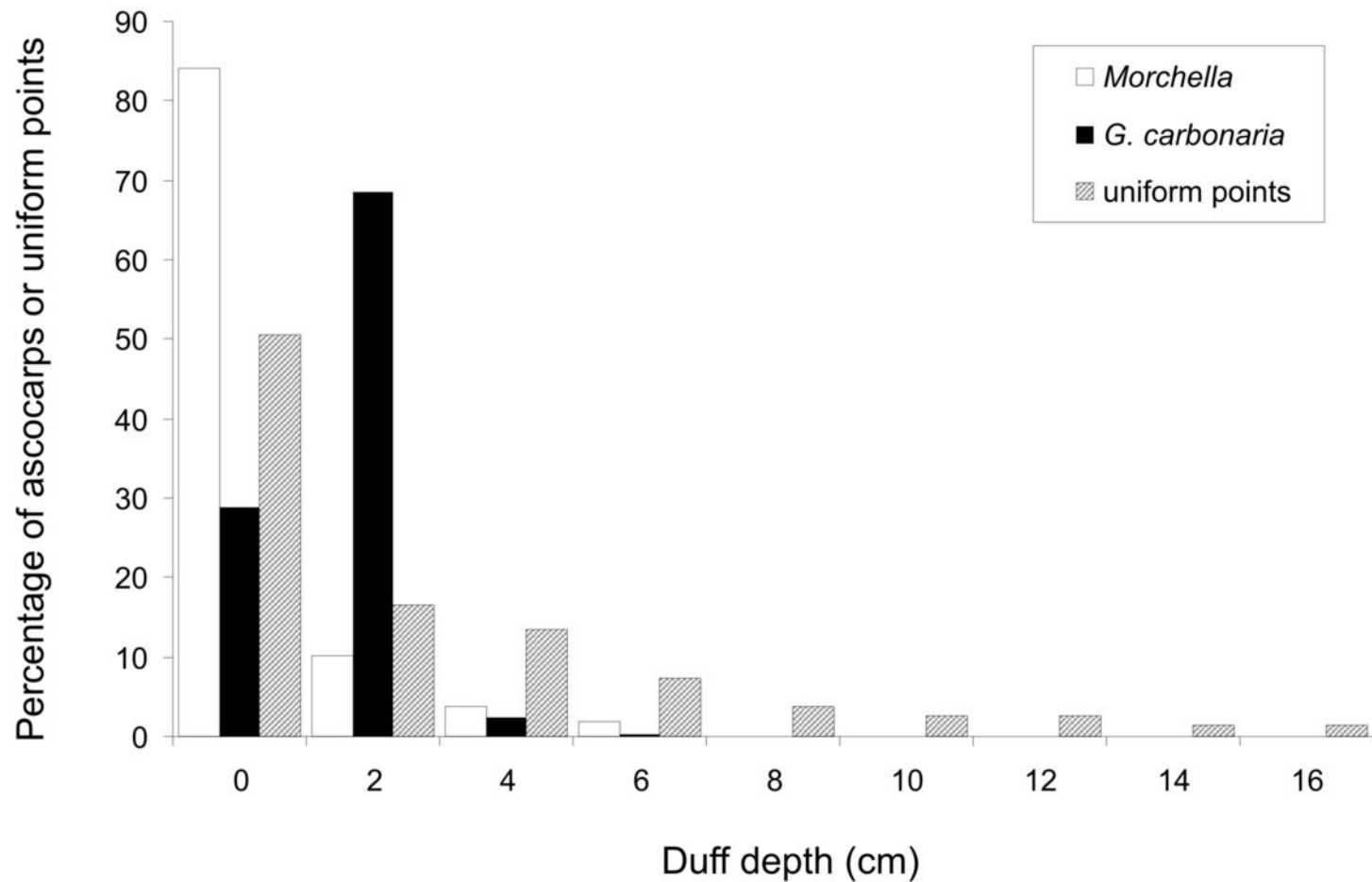
TABLE I. Ascocarp mean density ($\#/m^2$) by year on the same transects after a 2003 fire. The portion of the transects in the partially burned forest is excluded.

Year	Morchella	G. carbonaria
2004	1.49	10.6
2005	0.003	0.570
2006	0	0
2007	0.022	0.030