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Productivity and diversity of morel mushrooms in healthy, burned, and insect-damaged forests of northeastern Oregon

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Abstract

Large commercial crops of morels are harvested annually from montane coniferous forests of the northwestern United States. Although some morels fruit annually in nondisturbed forests, others fruit copiously in areas experiencing fire, insect infestations, tree mortality, and soil disturbance. Many forest managers currently use thinning and prescribed fire to re-create forest conditions that existed before the advent of wide-scale fire suppression, thus opportunities exist to promote morel crops while achieving fire control and timber production goals. However, our limited understanding of morel productivity, diversity, and ecology hinders such synergistic management. We used morphological, genetic, and ecological data to identify and characterize five putative species found at our study sites. Three of these putative species fruited only on burned soils the first spring season following a wildfire. The other two putative species fruited in nonburned forests, in islands of nonburned soils in burned forests, or the second year following fire on burned soils. Unbiased landscape-level estimates of genus-level morel productivity (not partitioned by putative species) ranged from 80 to 4350 morels per hectare and from 0.550 to 9.080 kg per ha. Productivity followed the general trend of wildfire-burned forests > insect-damaged forests > healthy forests. We discuss the implications of our results for forest management.

Keywords: *Morchella*; Mushrooms; Fire; Species diversity; Genetics; Disturbance; Nontimber forest products

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1. Introduction

Morels (*Morchella* species) are highly prized, commercially harvested, wild edible mushrooms. In 1992, approximately 590 metric tonnes of morels were harvested in Oregon, Washington, and Idaho, providing harvesters with $ 5.2 million of income (Schlosser and Blatner, 1995). Managers of national forests must address whether the harvest of commercial forest products is sustainable (Cubbage et al., 1993; US House of Representatives Bill 2466, 2000); consequently, both foresters and harvesters share an interest in how morel crops are affected by management regimes, natural disturbances, and large-scale commercial mushroom harvesting (Amaranthus and Pilz, 1996; Molina et al., 1997).

Morels often fruit prolifically after fire, tree mortality, or ground disturbance (von Krombholz, 1834; Sturgis, 1905; Moser, 1949; Ramsbottom, 1953; Apfelbaum et al., 1984; Arora, 1986; Duchesne and Weber, 1993; Thompson, 1994; Weber, 1995a; Parks and Schmitt, 1997). Morel harvesters note all three factors in their annual search for good collecting locations (Boom, 1995; Low, 1995; Frampton, 1996). In montane forests east of the Cascade Range in the Pacific Northwest, decades of fire suppression have allowed development of dense, fire-prone stands (Kaufmann, 1990; Agee, 1993; Langston, 1995; DeBano et al., 1998). Periodic insect epidemics also have caused extensive tree mortality (Hessburg et al., 1994; Lehmkuhl et al., 1994). US federal forest managers plan to increase forest thinning and introduce more frequent prescribed fires to reduce the likelihood of catastrophic wildfires and insect infestations, but these management choices have associated biological, environmental, economic, and social consequences (Borchers and Perry, 1990; Jaindl and Quigley, 1996). A better understanding of how natural or human-induced disturbances influence morel crops will allow managers to intentionally provide opportunities for morel harvesting as they implement revised forest management strategies.

Index Fungorum (Kirk et al., 2003) lists over 190 names for species, and subspecific taxa in the genus *Morchella*. General agreement exists that at least two major groups can be clearly distinguished: those whose ribs darken to gray or black with age (''black morels'', *Elata* clade) and those whose ribs are cream to tan at maturity (''yellow'', ''blond'' or ''common'' morels, *Esculenta* clade) (Jacquetant, 1984; Weber, 1995a,b; O'Donnell et al., 2003). O'Donnell et al. (2003) estimate there are 28 putative phylogenetically distinct species globally; 24 of them appear to be endemic to a specific continent. Thirteen putative species in the *Esculenta* clade (yellow morels) and nine in the *Elata* clade (black morels) are known endemics in North America, the apparent center of diversity for the genus. Most have not been formally named.

Species diversity in the genus *Morchella* is mirrored by complex life cycles, several modes of nutrition, and a variety of ecological interactions with forest habitats (Ower, 1982; Volk and Leonard, 1990; Volk, 1991; Buscot, 1992a; Weber et al., 1996). Morel mycelia can produce dense masses of modified hyphae (pseudosclerotia) (Volk and Leonard, 1990) that are thought to supply stored nutrients for fruiting in response to disturbance (Buscot, 1993a; Miller et al., 1994). Morels have long been considered saprobes (Ower, 1982), although recent evidence indicates that some might be facultatively mycorrhizal (Buscot and Kottke, 1990; Buscot, 1992b, 1993b; Harbin and Volk, 1999; Dahlstrom et al., 2000).

Forming a comprehensive understanding of the role of morels in forest ecosystems will require a better understanding of their diversity and autecology, and field trials of management practices are needed to determine how silviculture, fire management, and logging systems affect their occurrence and abundance (Pilz et al., 1996; Weber et al., 1996). Managers wishing to ascertain the sustainability of morel harvesting often inquire whether picking affects subsequent fruiting. The weight or number of morels per unit area per year can be used to evaluate harvest sustainability or to assess efforts to enhance morel crops, but to date we know of no unbiased, landscape-level estimates of morel productivity. Estimating production of edible mushrooms also entails unique sampling challenges (Amaranthus and Pilz, 1996; Pilz and Molina, 2002), hence monitoring methods require testing.

Given the complexity and interrelatedness of these issues, we chose a multidisciplinary approach to study how morel productivity relates to forest management activities and disturbance events. We then narrowed the range of scientific questions and information

requested by cooperating foresters to a set of feasible research objectives for this project.

1.1. Objectives

1. Evaluate the efficiency, practicality, and adequacy of chosen methods for sampling morel productivity and diversity.
2. Document and compare 2 years of morel productivity in healthy (not recently disturbed), burned, and insect-damaged montane forest habitats of northeastern Oregon.
3. Test for potential short-term harvest impacts by comparing morel production in pick and no-pick sample plots.
4. Describe the putative species we find by using morphology, ecology, and molecular genetics.
5. Discuss management implications.

2. Methods

2.1. Field sampling

Table 1, "Acronyms and putative species", contains abbreviations we use throughout the remainder of the paper. We selected replicate sites, research stands, and strip plot locations in spring 1995 before morels started fruiting and without prior knowledge of morel occurrence. Three research stands with different habitat conditions were selected on each of three replicate sites for a total of nine research stands (Table 2). The habitat conditions were (1) relatively healthy forest stands with low recent tree mortality, (2) stands burned by moderate-intensity (10–50% of the dominant trees killed) wildfires in the late summer 1994, and (3) stands with extensive tree mortality from insect infestations during the previous 5 years. The three replicate sites are located on lands administered by the Malheur and Wallowa-Whitman National Forests. Both national forests are located in northeastern Oregon, but the Malheur site was 45 km distant from the two Wallowa-Whitman sites, which were 6 km apart. All the research stands were in the *Abies grandis* zone (Franklin and Dyrness, 1973) and consisted of mixtures of grand fir (*A. grandis* (Douglas) Lindley), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), lodgepole pine (*Pinus contorta* Loudon), western larch (*Larix occidentalis* Nutt.), and ponderosa pine (*Pinus ponderosa* P.&C. Lawson). Within each replicate site, the three research stands were located less than 2 km apart, often less than 100 m. Differences in elevation, original vegetation, and cardinal direction that the slope faced were kept to a minimum. For morel sampling, we systematically located 10 parallel strip plots (elongated rectangles, 2 m × 100 m) in each research stand. Narrow strip plots

Table 1
Acronyms and putative species

General acronyms	
PS	Putative species
RS	Research stand (numbered as in Table 2)
ANOVA	Analysis of variance
FS Rd.	U.S. Department of Agriculture, Forest Service road number
Voucher acronyms	
OSC	Oregon State College (herbarium at Oregon State University, Corvallis, OR)
MCC	M. Carol Carter's number for specimens (collected on and off strip plots in the research stands) used in molecular analyses
NSW	Nancy Smith Weber collection numbers (collected, or viewed in a fresh state, by NSW)
KEF	Kei E. Fujimura collection numbers
Molecular analysis acronyms	
DNA	Deoxyribonucleic acid
rDNA	Ribosomal deoxyribonucleic acid
rRNA	Ribosomal ribonucleic acid
bp	Base pair
ITS	Internal transcribed spacer
PCR	Polymerase chain reaction
RAPD	Random amplification of polymorphic DNA
RFLP	Restriction fragment-length polymorphism
CTAB	Cetyltrimethylammonium bromide
EDTA	Ethylenediaminetetraacetic acid
UPGMA	Unweighted pair group mean analysis
Putative species	**Vernacular names in use or suggested**
PS A	Natural black morel
PS B	Pink (burn) morel
PS C	Green (burn) morel
PS D	Gray (burn) morel
PS E	Mountain blond morel
PS A, PS B, and PS C	"Black" morel complex
PS B, PS C, and PS D	Morels fruiting the first year after Wildfire on burned soils
PS A and PS E	Morels fruiting on nonburned soils and nonburned islands within wildfires; PS A on all soil types the second year following fires; PS E not encountered second year

Table 2
Location of research stands

Research stand	Habitat condition	Replicate site	National forest	County	Locality	Latitude and longitude	U.S. geological survey, Willamette Meridian
RS 1	Healthy	1	Wallowa-Whitman	Union	Between Lookout and Little Fly Creeks, South of FS Rd. 5160-516	45.08°N, 188.49°W	SE 1/4 S36, T5S, R34E
RS 2	Insect	1	Wallowa-Whitman	Union	North of FS Rd. 5160 and south of Lookout Creek, just west of spur road 5160-516	45.09°N, 188.49°W	NE 1/4 S36, T5S, R34E
RS 3	Burn	1	Wallowa-Whitman	Union	Between Lookout and Little Fly Creeks, just north of FS Rd. 5160-176	45.08°N, 188.50°W	SW 1/4 S36, T5S, R34E
RS 4	Burn	2	Wallowa-Whitman	Union	Along Sheep Creek, FS Rd. 5164 off FS Rd. 5160	45.04°N, 188.48°W	NE 1/4 S22, T6S, R35E
RS 5	Healthy	2	Wallowa-Whitman	Union	Along Sheep Creek, FS Rd. 5164 off FS Rd. 5160	45.04°N, 118.48°W	NE 1/4 S22, T6S, R35E
RS 6	Insect	2	Wallowa-Whitman	Union	Along Sheep Creek, FS Rd. 5164 off FS Rd. 5160	45.04°N, 188.47°W	SW 1/4 S14, T6S, R35E
RS 7	Insect	3	Malheur	Grant	NW of Austin junction, along FS Rd. 4557 off FS Rd. 20	44.68°N, 188.64°W	SE 1/4 S20, T10S, R34E
RS 8	Healthy (Burn, 1996)	3	Malheur	Grant	NW of Austin junction, along FS Rd. 4557 off FS Rd. 20	44.68°N, 118.64°W	SE 1/4 S20, T10S, R34E
RS 9	Burn	3	Malheur	Grant	NW of Austin junction, along FS Rd. 4557 off FS Rd. 20	44.07°N, 188.63°W	NW 1/4 S21, T10S, R34E

permitted field personnel to search for inconspicuous morels from opposite perspectives without trampling soil within the plots. Ten strip plots per stand gave us a measure of variability among plots, thus indicating how uniformly morels are distributed within a stand, and providing cooperating managers with confidence intervals on productivity estimates for each stand.

In the springs of 1995 and 1996, plots were visited weekly from the first appearance of morels until several weeks after the last ones were observed. Morels were collected or measured when first found; that is, no minimum size criterion was used. To examine whether harvesting influenced fruiting, the 10 strip plots in each research stand were randomly assigned pick or no-pick sampling methods. On the five pick plots in each stand, the morels were cut cleanly from their bases as close to the soil as possible, weighed as a single collection, and counted. On the other five plots, the width and height of each morel's head were measured and they were marked with colored toothpicks so they would not be sampled again.

From the morels collected within each strip plot, a representative subset was selected that included specimens of all the obvious morphological groups and a range of sizes. Each such specimen was weighed fresh, the height and width of the head were measured, and the morel was sliced in half. One-half of each morel was frozen for genetic analysis; the other half was dried for corresponding morphological examination. Commercially available food dryers with warm airflow were used to dry specimens quickly, thus avoiding degradation. The halves that were dried also were weighed before and after drying. These measurements allowed us to determine moisture content and correlate fresh and dry weights with dimensions of the heads so that the weight of morels on the no-pick plots could be estimated. Ephemeral features thought to be taxonomically important were noted before each specimen was processed.

During 1995, we realized that our weekly sampling interval did not allow time for morels to mature (Weber, 1995b). We therefore collected mature specimens near the strip plots in 1996 by using methods described in Weber et al. (1997); these specimens were used solely for genetic and morphological analysis. A wildfire in the summer of 1996 burned our insect-damaged stand on

the Malheur National Forest (RS 8) after we finished sampling that spring. We revisited this newly burned stand in spring 1997 to collect additional specimens for morphological and genetic analyses.

2.2. Productivity analyses

The productivity values we report are sums of all the morels found on any given strip plot regardless of putative species. Count and fresh-weight productivity were analyzed by using a split-plot (sampling method), repeated measures (year) ANOVA with sites as replicates and habitat conditions as treatments. Counts and fresh weights (estimated on no-pick strip plots) were summed for each season (year) across the five pick and five no-pick strip plots within each research stand. Dry weight ANOVAs yielded results that were virtually identical to those for fresh weight, so are not reported. To estimate morel weights on the no-pick strip plots, we regressed an easily calculated correlate of head volume (head width^2 $\times$ head height) with fresh and dry weights. We log-transformed both the independent and dependent variables to stabilize their variance and create linear relations. The count distribution was normalized with a $\log(\text{count} + 1)$ transformation before conducting the ANOVA because the range of values was greater than an order of magnitude, and some values were less than 10 (Sabin and Stafford, 1990).

2.3. Molecular analyses

Specimens obtained from the field collections were stored at −80 °C. Approximately, 0.3 g of each analyzed sporocarp was ground in liquid nitrogen and extracted by a CTAB extraction protocol, then quantified and evaluated for DNA quality (Carter et al., 1996). Degraded specimens were not examined and degraded, low-molecular weight DNA was excluded from the analysis.

Several random primers were surveyed for their usefulness in RAPD-PCR studies of *Morchella* species. Primer S3 (CAGAGGTCCC, Operon, Westburg BV, The Netherlands) was selected to screen the unknown *Morchella* specimens for species groupings because it consistently gave strong, discriminating amplicon banding patterns. Each 25 μl reaction contained 19 μl of sterile distilled water, 1 μl formamide, 1.0 μl primer at 15 pmol per μl, one Ready-To-Go™ RAPD analysis bead (Pharmacia, Piscataway, NJ) and 5 μl of sample DNA (2 ng/μl). Amplification for RAPD was conducted in an MJ Research (Watertown, MA) Hot Bonnet thermocycler. After a 30-s melt at 94 °C, an amplification temperature regime of 94 °C for 5 s, 38 °C for 30 s, and 72 °C for 2 min was followed for 40 cycles. The PCR concluded with a 4 min extension at 72 °C. A control tube containing no added DNA was included in each amplification run. Amplification products and molecular weight markers were electrophoresed through 1.8% agarose gels, each 14 cm long, for a standard period as determined by track dye position. Gels were stained in ethidium bromide, photographed, and photocopied. Lanes of individual samples were cut out from photocopies and sorted into similar groups, using lines extended from molecular weight marker bands for alignment. If necessary, samples were run again side by side to confirm placement within groups.

A subset of RAPD-PCR products from DNA samples prepared from specimens collected in 1995, 1996, and 1997 was rerun together on the same gel to score for presence and absence of amplicon bands within a size range of 200–2500 bp. Weak or diffuse bands, were not scored or scored as absent. Data were analyzed by using MEGA2 software (Kumar et al., 2000) for amino acid analysis. The amino acid setting was used to enter the data as ''p'' and ''a'' (present and absent) with no gaps and to give equal weight to both states. The p distance setting was used to derive the distance matrix (Puterka et al., 1993; Kumar et al., 2000). Dendrograms were generated from the distance values by UPGMA (Sneath and Sokal, 1973) by using MEGA Tree Builder (Kumar et al., 2000). Five hundred bootstrap trials were used to determine confidence values of branch nodes.

Representatives from each of the groups of putative species identified by RAPD-PCR were used for ITS amplicon analysis. ITS regions were amplified in 25 μl reaction volumes with primers ITS1-F and ITS4 (Gardes and Bruns, 1996). After a 1 min melt at 94 °C, an amplification temperature regime of 94 °C for 25 s, 55 °C for 55 s, and 72 °C for 2 min was followed for 35 cycles. The PCR concluded with a 10 min extension at 72 °C. Portions of each amplified product were digested with various 4-base-cutter restriction enzymes (Gardes and Bruns, 1996).

Table 3
Log(morel count + 1) ANOVA values

Source	d.f.	*F*-value	*P*-value
Habitat condition	2	5.7550	0.0177
Sample method	1	0.9498	0.3490
Sample method × habitat condition	2	1.0593	0.3770
Year	1	24.4279	0.0003
Year × habitat condition	2	0.6660	0.5317
Sample method × year	1	1.0192	0.3326
Sample method × year × habitat condition	2	0.0512	0.9503

Restricted and unrestricted ITS amplicons from different samples were electrophoresed in 3% agarose containing Gel Star (Cambrex, E. Rutherford, NJ, USA) DNA stain. Gel photographs were computer scanned, and ITS amplicon fragment lengths were estimated by the molecular weight calibration program of SigmaGel™ 1995 (Jandel Scientific Software, San Rafael, CA, USA).

2.4. Morphological analysis

Field data sheets were developed for crews to record significant features of the fresh specimens. The characters included habit; size; color of ribs, pits, and stalk; and texture of ribs and stalk. Character states known to us at the start of the study were listed. For the specimens collected offsite, standard techniques were used (Smith et al., 1981; Weber et al., 1997). Microscopic features were described from dried sporocarps following standard methods (Smith et al., 1981). Ascospores were mounted in water and held for less than 30 min before measuring them.

All dried specimens were examined for potential usefulness in morphological descriptions, and a useful subset was selected for detailed examination. The material genetically analyzed in Figs. 2–4 included some additional specimens not examined for morphological traits.

3. Results

3.1. Productivity results

Only PS A, PS B, and PS C (see Section 3.2) were found in our strip plots. During our 2 years of sampling, morels fruited in 87 of our 90 strip plots (96.7%). Mean moisture content ((fresh weight − dry weight)/fresh weight) was 0.887 (S.E. = 0.002).

Table 4
Fresh weight (kg per ha) ANOVA values

Source	d.f.	*F*-value	*P*-value
Habitat condition	2	3.2448	0.1109
Year	1	0.14024	0.2811
Year × habitat condition	2	1.0155	0.4170

Values derived from only the picked strip plots where morels were actually weighed.

Tables 3 and 4 present ANOVA values. Productivity levels among habitat conditions exhibited the order wildfire > insect > healthy for both counts ($P < 0.0177$) and fresh weight ($P < 0.1109$). A least-squared-means test for counts ($\alpha = 0.05$) showed that more morels fruited in wildfire habitats than in healthy habitat conditions, but no other individual contrasts were significant. Counts were also higher in 1995 than in 1996 ($P < 0.0003$), but weights did not differ significantly between years ($P < 0.281$). Fig. 1 shows how values for habitat conditions varied by year.

The sampling method (pick versus no-pick plots) exhibited no significant difference for counts ($P < 0.349$). In the weight ANOVA, however, there was an inexplicable significant ($P < 0.0061$) interaction between sample method and year, even though we had derived fairly tight ($R^2 \approx 0.80$) correspondence between fresh morel weight and our rectangular correlate of cap volume. Because we were unable to explain this interaction, we excluded the pick versus no-pick comparison from the weight ANOVA and based the analysis only on the weighed morels in the five picked strip plots in each research stand.

Table 5 presents the means and 90% confidence intervals of count and weight productivity for each stand in each year. Count estimates are derived from all 10-strip plots (both pick and no-pick) in each stand, but weight estimates are only from the 5-strip plots in each stand where morels were picked and weighed. The confidence intervals in this table are derived from variation among the strip plots within each stand, not from the ANOVAs in Tables 3 and 4 where values from individual strip plots within a stand were

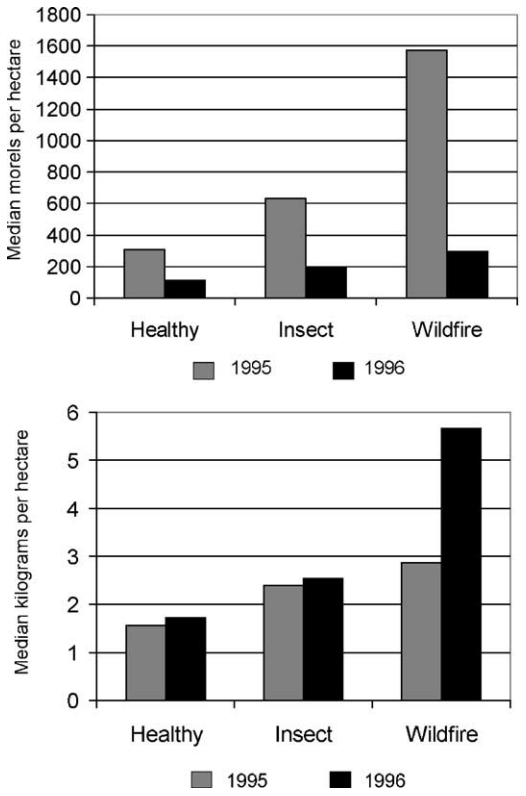

Fig. 1. Morel productivity per hectare per year by habitat condition. Counts are back-transformed from the log transformation used in the ANOVA, hence are median, not mean values.

summed before comparing treatments. This table is presented to illustrate the large variability of productivity estimates that would be derived from sampling any one given stand.

3.2. Molecular results

Two-hundred-and-fifty-one specimens from collections made during the 2-year study period were analyzed by RAPD-PCR by using the S3 RAPD primer. The amplicons from this primer produced a DNA fingerprint for each specimen after separation by electrophoresis. The fingerprints were sorted into groups based on shared bands and absence of bands. Sorting produced five classes (Fig. 2), which we call PS A, PS B, PS C, PS D, and PS E (Table 1). Although many of the specimens have unique fingerprints, the overall fingerprint pattern of members of each putative species is similar, and pattern differences among putative species are apparent. The samples were scored for presence and absence of amplicons at 45 band positions and analyzed by UPGMA. The resultant dendrogram is shown in Fig. 3. The tree shows that PS A, PS B, and PS C cluster independently. Each of these putative species forms its own relatively tight clade with bootstrap confidence levels of clades PS A, PS B, and PS C at 97, 100, and 98%, respectively. PS D and PS E, each represented by only one specimen, both cluster loosely with PS B with low confidence levels.

To further investigate their genetic distinctiveness, samples from each putative species were characterized for sequence variability within the ITS region of rDNA by PCR and RFLP. Representatives of PS A, PS B, and PS C produced ITS amplicons of approximately 750 bp, although the PS C ITS is slightly smaller than PS A and PS B. Representatives from PS D and PS E produced ITS fragments of approximately 950 bp (Fig. 4).

Table 5
Mean productivity (sporocarp counts and fresh weight per ha per year) and 90% confidence intervals for each research stand during each fruiting season

Replicate site	Habitat condition	Morels/ha, 1995	kg/ha, 1995	Morels/ha, 1996	kg/ha, 1996
1	Healthy	565 (±324)	1.358 (±1.025)	215 (±95)	1.596 (±0.969)
	Insect	1030 (±326)	3.301 (±1.350)	320 (±169)	3.640 (±2.342)
	Wildfire	2950 (±600)	4.158 (±1.819)	450 (±309)	9.080 (±7.136)
2	Healthy	205 (±148)	1.852 (±2.562)	105 (±111)	2.100 (±2.219)
	Insect	700 (±305)	3.027 (±2.460)	80 (±66)	0.550 (±0.601)
	Wildfire	4350 (±2342)	3.800 (±2.608)	290 (±119)	2.230 (±1.323)
3	Healthy	305 (±208)	1.467 (±0.888)	120 (±86)	1.490 (±1.540)
	Insect	385 (±147)	0.863 (±.732)	285 (±174)	3.420 (±4.547)
	Wildfire	315 (±202)	0.650 (±0.470)	325 (±199)	5.710 (±5.523)

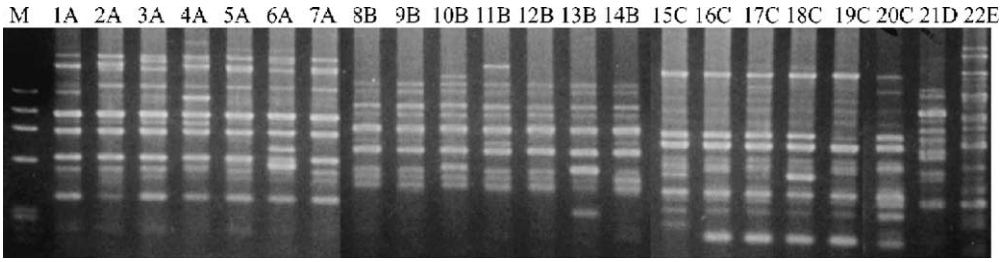

Fig. 2. Morel specimens of PS A through PS E as defined by electrophoretic analysis of amplicons produced by RAPD-PCR. This is a rearranged series of lanes from a single gel. Lane M shows molecular weight size marker bands of 1353, 1078, 872, 603, 310, and 280 bp (lowest). Lane, putative species, and specimen identification (respectively) are as follows. 1A: MCC 10-96; 2A: MCC 22-97; 3A: MCC 28-97; 4A: MCC 29-97; 5A: MCC 30-97; 6A: MCC 31-97; 7A: MCC 32-97; 8B: 14-97; 9B: 16-97; 10B: MCC 19-97; 11B: MCC 20-97; 12B: MCC 23-97; 13B: MCC 27-97; 14B: MCC 103-95; 15C: MCC 15-97; 16C: MCC 17-97; 17C: MCC 18-97; 18C: MCC 21-97; 19C: MCC 24-97; 20C: MCC 136-95; 21D: MCC 106-95; 22E: MCC 8-95. [Collection data for these specimens are included in the corresponding "Material examined" sections of Sections 3.5–3.9].

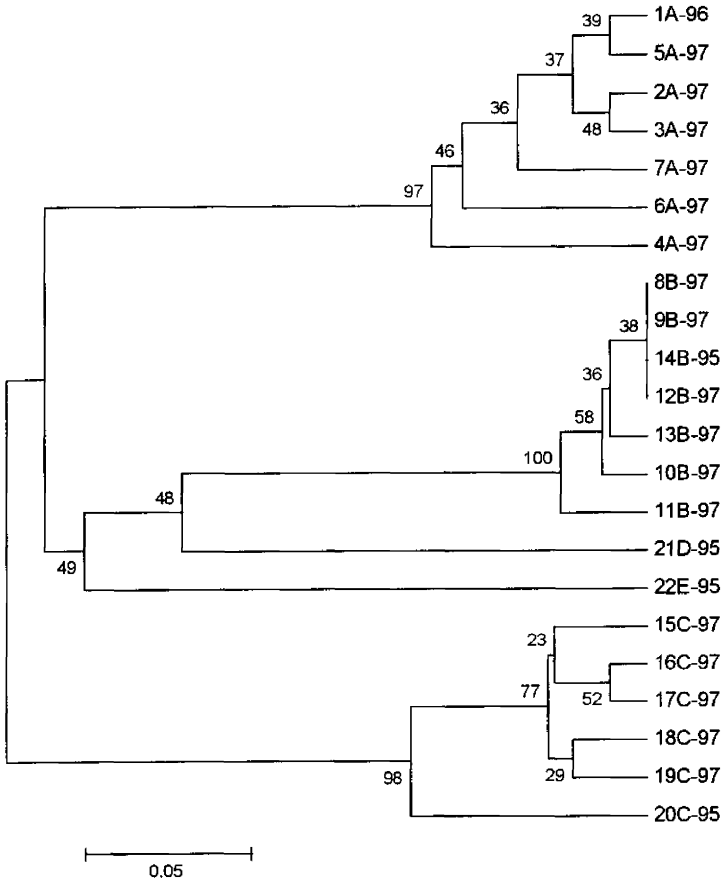

Fig. 3. Dendrogram constructed by UPGMA showing the relationships within and among our putative species, derived from scoring as present or absent the amplicon band positions shown in Fig. 2. The dendrogram specimen labels (far right) designate lane numbers (from Fig. 2), putative species, and year of collection. Bootstrap confidence values (500 trials) as percentages are shown at each interior branch.

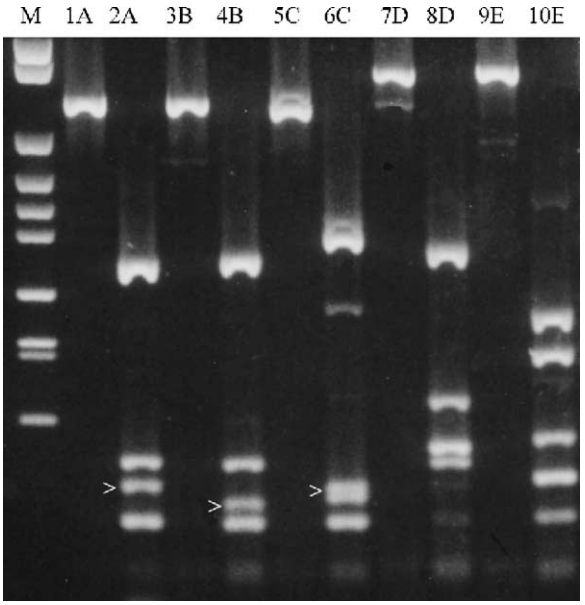

Fig. 4. Morel putative species as defined by RFLP-ITS. Putative species A, B, and C each produced an ITS fragment of approximately 750 bp each (lanes 1A, 3B and 5C, respectively), whereas putative species D and E produced ITS fragments of approximately 950 bp each (lanes 7D and 9E). *Hae* III digests resolved all our putative species into distinctive fragment-length polymorphisms (lanes 2A, 4B, 6C, 8D, and 10E, respectively). The small fragments indicated by the arrowheads in lanes 2A, 4B, and 6C, distinguish among A, B, and C putative species. In lane M, the molecular weight marker, the topmost band is 1030 bp, and the lowermost band is 154 bp.

The ITS amplicons of putative species representatives were subjected to single restriction digests with seven, 4-base cutter enzymes (*Alu* I, *Hae* III, *Mae* I, *Nla* III, *Rsa* I, *Sau*3A I, *Taq* I). Samples from PS A, PS B, and PS C gave similar restriction patterns and fragment sizes for 6 of the 7 enzyme digests, while PS D and PS E each produced distinctive RFLPs for all enzymes. Only *Hae* III digests produced banding patterns that allowed differentiation of all putative species by small fragment-length polymorphisms (Fig. 4, lanes 2A, 4B, 6C, 8D, and 10E).

In summary, although RAPD analyses shows all our putative species as genetically distinct, ITS analysis shows that PS A, PS B, and PS C have the greatest genetic similarity. Also, while PS D and PS E have similarly sized (uncut) ITS amplicons, their RFLP patterns are dissimilar.

Table 6
Sporocarp tally for each putative morel species for each habitat type each year[a]

Putative species	1995			1996		
	Healthy	Insect	Wildfire	Healthy	Insect	Wildfire
A	31	34	6	28	36	34
B	0	0	17	0	0	0
C	0	0	9	0	0	0
D	0	0	4	0	0	0
E	1	0	0	0	0	0

[a] Only specimens from our research sites, that were analyzed and identified by RAPD-PCR, are included in this tally. Specimens for genetic analysis were not chosen randomly, rather we selected morels from each picked-strip plot collection that represented the range of observed morphological characters so that rare types would not be missed. Specimens of PS D and PS E were obtained from the additional collections outside the strip plots but within the Research Stand.

Specimens identified as these distinct putative species by molecular analyses were tallied in relation to habitat conditions (healthy, insect, and wildfire) and year of collection (Table 6). Although not intentionally weighted toward a particular putative species, this tally is not based on unbiased sampling. Most of the specimens were selected from the additional collections made for morphological and genetic analysis, and specimens from the strip plots were nonrandomly selected to represent macroscopic morphological variation. PS A dominated in healthy and insect habitat conditions. Wildfire habitats had the greatest diversity of morel taxa in 1995 (the first spring after the fires), with PS B dominating. In 1996, diversity in wildfire habitats was lost, and PS A became the dominant morel in wildfire as well as in healthy and insect habitats. PS D was rare; we only found it in the wildfire habitat in 1995. Our study design envisioned only 1995 and 1996 collections; however, a new wildfire in summer 1996 burned the insect-damaged stand on the Malheur National Forest (RS 8). This created the opportunity to compare morel taxa in the same stand before and after a fire. In spring 1997, we made one more collection of morels from this stand for genetic analysis. Of 17 specimens collected, there were 6 PS As, 6 PS Bs, and 5 PS Cs. In contrast, collections from the previous 2 years had yielded only PS As from this stand.

3.3. Morphological results

Problems with keeping the genetic samples frozen in transit, poor or no amplification of DNA from some samples, and immaturity of most voucher specimens, greatly reduced the number of specimens that could be compared genetically and morphologically. We did, however, use molecular methods to confirm the putative species identity of all the specimens examined in detail for the morphological descriptions.

We had not anticipated the existence of two nearly indistinguishable black burn morels (PS B and PS C) and our crews were inadequately trained to record subtle macroscopic differences in sporocarp form, structure, and color. Much of the following descriptive information is drawn from better documented collections of mature specimens found near the strip plots or gathered elsewhere in Oregon. The molecular genetic profiles of morels collected elsewhere matched those of the specimens from our research stands.

Nomenclature for members of the genus *Morchella* is in a state of flux as traditional methods of systematics incorporate molecular data. Because no consensus yet exists on species concepts and appropriate scientific names for these morels, we have assigned common names to the putative species we recognize. Many of these names are frequently used in the Pacific Northwest, and others we suggest. For instance, we suggest the terms ''pink'' and ''green'' morels for PS B and PS C, respectively, because no common names currently distinguish them. The usefulness of this color distinction is tentative and requires further investigation. Similarly, ''black stocking morel'' is a term that could be applied to our PS D because we suspect that two species of ''gray'' morels exist in western North America, and the presence or absence of a black stem on young specimens differentiates them macroscopically.

PS D (the gray morel) and PS E (the mountain blond morel) are relatively easy to distinguish from each other, and from PS A, PS B, and PS C (the black morel complex), by using combinations of morphological and ecological features presented in the key. PS B (the pink morel) and PS C (the green morel) are very distinct at the molecular level, but the fruiting bodies are similar enough macroscopically that our crews did not note any consistent distinguishing features. In fact, except for their fruiting substrate, PS B and PS C were difficult to distinguish from PS A (the natural black morel).

No effort was made to include other putative species suspected to occur in eastern Oregon in our key or descriptions because they were not encountered in our study and are found in different vegetation associations (such as riparian areas). Dimensions such as typical head size are not included in our preliminary key or the descriptions of each putative species because most of the specimens examined were immature. Color descriptions were made in daylight or using natural light spectra, so the key should be used in the comparable lighting. We did not correlate our putative species with the putative phylogenetic species of O'Donnell et al. (2003) because the study methods and objectives differed. Specimens used for both morphological and genetic analyses are cited in the ''Material examined'' section of each description. Cited collections will be accessioned to the OSC fungal herbarium. See Table 1 for acronyms used to cite specimens.

3.4. Field key to the putative species identified in our study

1a. Surface of stalk in young specimens distinctly velvety, dark brown to black, becoming paler in age as the velvety layer is stretched apart (use a hand lens to look for dark tufts of hyphae in old specimens) ... PS D (gray morels *pro parte*).

1b. Surface of stalk entirely off-white, ivory, tan, dull pink or dull purple at all ages, never with tufts of pigmented hyphae ... 2.

2a. Ribs separating pits on the head becoming paler (ivory to nearly white) than the lining of the pits with age, by maturity (mature spores present) off-white sometimes with amber stains or bruises; pits gray when very young, becoming tan, golden, or straw yellow at maturity ... PS E (mountain blond morel).

2b. Ribs separating pits on the head becoming darker (gray to black) than the lining of the pits at an early age, by maturity dark gray to dark blackish brown or black; pit color variable, consistently either paler than the mature ribs, or, if similar in color, some shade of dark gray to grayish brown ... (black morels) 3.

3a. Young pits dull grayish tan to steely gray becoming grayish tan or pale tan by maturity . . . PS A (natural black morel).
3b. Young pits either: (1) cream-colored to dusky pink or pinkish tan, or (2) tinted with dull grayish olive green; in either instance traces of the pink or olive tones typically persist in mature fruiting bodies and are evident in mature specimens . . . 4.
4a. Young pits and ridges cream-colored to tinted with dusky rose or pale salmon; ribs darkening by maturity to black; mature pits rosy tan to pinkish brown . . . PS B (pink morel).
4b. Young pits and ridges gray to olive gray; ribs darkening by maturity to black; mature pits olive gray to olive brown . . . PS C (green morel).

3.5. PS A

3.5.1. Vernacular names

Natural (black) morel, black morel, conicas, angusticeps.

3.5.2. Description

Head: in profile broadly rounded, conic to irregularly ellipsoid when young, often broadening especially near the stalk as it matures. *Ribs*: minutely and inconspicuously velvety when young, becoming dry and glabrous age; when young shades of dull grayish tan, steely gray, or dark brownish gray becoming black by maturity; edges typically remaining intact and sterile. *Pits*: when young dull grayish tan to steely gray, in age grayish tan or light brown. *Stalk*: when young ivory to light tan or washed with dusky rose, in age varying to tan or rosy tan; surface smooth at first, appearing granulose in age; ornamentation never brown to black. *Ascospores*: (23–) 26−33 × 15−16(–18) μm.

3.5.3. Ecology

This common morel fruits on nonburned soils, litter, and duff including nonburned islands in burned areas or on burned soils but then apparently no sooner than the second spring after an intense wildfire.

3.5.4. Material studied

RS 1 (off strip plots), 1995.05.25, MCC 61-95; *RS* 2 (off strip plots), 1995.05.24, MCC 82-95; *RS* 3 (strip plot 3), 1995.05.20, MCC 10-96; (strip plot 3), 1995.06.07, MCC 13-95; *RS* 4 (strip plot 7), 1995.06.14, MCC 48-95; *RS* 5 (off strip plots), 1995.05.15, MCC 109-95; *RS* 6 (off strip plots), 1995.05.16, MCC 124-95; *RS* 7 (strip plot 6), 1995.05.17, MCC 7-95; *RS* 8 (off strip plots), 1995.05.17, MCC 133-95; *RS* 9 (off strip plots) 1997.05.28, NSW 8029/MCC 29-97, NSW 8031/MCC 31-97, NSW 8032/MCC 32-97; (strip plot 3), 1995.05.30, MCC 58-97; (strip plot 7), 1997.05.28, NSW 8028/MCC 28-97, NSW 8030/MCC 30-97; Oregon, Union Co., Wallowa-Whitman National Forest NW of La Grande along FS 21 (Spring Creek Rd.), 1996.05.29, NSW 7746, NSW 7749A, 7749B.

3.6. PS B

3.6.1. Vernacular names

Lumped with those referred to as angusticeps, conicas, burn, fire, or black morels; pink morel might be an appropriate name.

3.6.2. Description

Head: at first elongate conic with rounded conic apex, sometimes expanding to broadly conic in age. *Ribs*: not conspicuously velvety when young, becoming dry and glabrous in age; when young cream-colored to pale shell pink, typically black well before maturity; edges typically remaining intact, sometimes with a fertile strip down the center. *Pits*: when young cream-colored to dusky pink or pinkish tan becoming pinkish tan to light pinkish brown at maturity. *Stalk*: white or nearly so at all ages, smooth at first becoming slightly granulose in age, ornamentation never brown to black. *Ascospores*: 21−24 μm × 13−16 μm.

3.6.3. Ecology

Fruiting of both PS B and PS C in our plots were restricted to burned plots, presumably burned soils, the first spring/summer after a fall fire and were not found the second year after a fire.

3.6.4. Material studied

RS 3 (strip plot 9), 1995.05.24, MCC 54x-95; (strip plot 2), 1995.06.07, MCC 41-95; *RS* 4 (off strip plots), 1995.05.15, MCC 103-95; (strip plot 8), 1995.05.31, MCC 4x-95; *RS* 8 after the 1996 Summit fire (strip plot 1), 1997.05.28, NSW 8014/MCC

14-97; (strip plot 3), 1995.06.12, MCC 38-95, 1997.05.28, NSW 8016/MCC 16-97, NSW 8023/MCC 23-97, NSW 8027/MCC 27-97; (strip plot 6), 1997.05.28, NSW 8019/MCC 19-97; (strip plot 8), 1997.05.28, NSW 8020/MCC 20-97; *RS* 9 (strip plot 3), 1995.06.12, MCC 38-95; Oregon, Harney Country, Malheur National Forest, Kidd Flat, 1998.06.07, KEF 74.

3.7. PS C

3.7.1. Vernacular names

Lumped with those referred to as angusticeps, conicas, burn, fire, or black morels; green morel might be an appropriate name.

3.7.2. Description

Head: at first elongate conic with rounded conic apex, sometimes expanding to broadly conic in age. *Ribs*: not conspicuously velvety when young, becoming dry and glabrous in age; when young gray, becoming black well before maturity; edges typically remaining intact, sometimes with a fertile strip down the center. *Pits*: when young dark gray to dark olive gray, in age olive gray to olive brownish gray. *Stalk*: white or nearly so at all ages, smooth at first becoming slightly granulose in age, ornamentation never brown to black. *Ascospores*: $20-24\,\mu m \times 13-16\,\mu m$.

3.7.3. Ecology

Fruiting of both PS B and PS C in our plots were restricted to burned plots, presumably burned soils, the first spring/summer after a fall fire and were not found the second year after a fire.

3.7.4. Material studied

RS 3 (strip plot 9), 1995.05.24, MCC 54y-95; *RS* 4 (strip plot 8), 1995.05.31, MCC 4y-95; *RS* 8 after the 1996 Summit fire (off strip plots), 1997.05.28, NSW 8024/MCC 24-97; (strip plot 2), 1997.05.28, NSW 8015/MCC 15-97; (strip plot 4), 1997.05.28, NSW 8017/MCC 17-97; (strip plot 5), 1997.05.28 NSW 8018/MCC 18-97; (strip plot 10), 1997.05.28, NSW 8021/MCC 21-97; *RS* 9 (off strip plots), 1995.05.30, MCC 139-95; (strip plot 10), 1995.06.12, MCC 9-95; Oregon, Harney County, Malheur National Forest, Kidd flat, 1998.06.17, KEF 49.

3.8. PS D

3.8.1. Vernacular names

Gray, fire, or burn morels; black stocking morel.

3.8.2. Description

Head: when young elongate-ovoid to nearly columnar expanding variously in age. *Ribs*: when young conspicuously velvety/hairy, the hairs collapsing with age; when young silvery gray to charcoal gray, gray to black at maturity where intact; edges extremely fragile, soon cracking and breaking away to expose the white to ivory underlying tissue, lacking fertile tissue. *Pits*: when young deep gray to nearly black, in age varying from gray to grayish tan. *Stalk*: charcoal gray to nearly black when young becoming pale gray to grayish tan at maturity; when young densely velvety from projecting hyphae, in age velvety layer stretched apart leaving tufts of brown hyphal tips on an ivory, off-white, or pale tan background. *Ascospores*: $19-25\,\mu m \times 13-16\,\mu m$.

3.8.3. Ecology

PS D was found only in one burned research stand, presumably on burned soil. We have seen it fruit in abundance elsewhere the year after a wildfire.

3.8.4. Material studied

RS 4 (off strip plots), 1995.06.22, MCC 104-95, 105-95, 106-95, 107-95; Oregon, Lane Co., Willamette National Forest, north side of Bunchgrass Ridge, site of Warner Creek fire of autumn 1991, 1992.07.10, NSW 6850, NSW 6864; Oregon, Lane Co., Willamette National Forest, North of Waldo Lake, site of Moolack fire of August–September 1996, 1977.07.08, NSW 8061, NSW 8064.

3.9. PS E

3.9.1. Vernacular names

Blond morel, mountain blond, esculenta (misapplied in scientific sense).

3.9.2. Description

Head: columnar to narrowly obtusely conic when young, variously expanding with maturity but typically remaining relatively narrow in relation to height. *Ribs*: when young essentially glabrous, in age becom-

ing dry and waxy; when young pale grayish tan, in age ivory to pale tan and then often with rusty ochre stains in age; edges typically remaining intact and sterile. *Pits*: when young light smoky gray, in age near straw yellow or the color of a manila folder. *Stalk*: ivory to cream-colored, sometimes with rust-colored or amber discolorations; glabrous. *Ascospores*: 23–26(−28) μm × 14.3–16(−18) μm.

3.9.3. Ecology

To date, we have positively documented PS E only from nonburned soils in living forests or in nonburned areas within the fire perimeter.

3.9.4. Material studied

RS 8 (off strip plots), 1995.06.12, MCC 8-95; 1996.05.31, NSW 7753; Oregon, Union County, Wallowa-Whitman National Forest, NW of La Grande along FS 21 (Spring Creek Rd.), 1996.05.29, NSW 7747, NSW 7748.

4. Discussion

- *Objective 1*. Evaluate the efficiency, practicality, and adequacy of chosen methods for sampling morel productivity and diversity.

  Drying specimens the same evening they were collected yielded useful voucher specimens for morphological analysis, but freezing and maintaining frozen tissues in good condition during transit proved more difficult than we anticipated. Dried specimens are now commonly used for genetic analysis, but early in development of a research plan, participating specialists in molecular genetics should be consulted about their preferred methods of collection and preservation. Where fresh material is desired, the mushroom can be sliced open with a clean knife, a piece of the inside of the mushroom excised, and the fresh material placed into a small, capped, plastic vial of CTAB (Table 1) solution (a detergent commonly used in genetic extractions). Specimens for genetic or taxonomic analysis should have thorough documentation of their habitat and fruiting substrate, they should be accompanied by descriptions of fresh characters in all stages of development (including old specimens with mature spores), color descriptions should be determined in daylight or daylight spectra, and they should be deposited in herbaria for future reference (Weber et al., 1997; Crous and Cother, 2003). In collections containing multiple specimens, those specimens also sampled for genetic analysis should be clearly labeled. Anticipating that some species can be very difficult to distinguish macroscopically, such as our PS A, PS B, and PS C, we encourage future researchers to thoroughly train their crews in sporocarp features and to take meticulous notes.

  Narrow strip plots worked well for detecting inconspicuous morels, avoiding soil compaction, and keeping track of already-surveyed areas as the crews searched. With the exception of not obtaining mature specimens, weekly visits captured most of the fruiting on the plots. Most of the morels grew large enough for commercial harvesting within a week. If we had used longer intervals, more morels might have been picked by unauthorized harvesters or consumed by microarthropods. However, our lack of a minimum size criterion for picking likely increased variation in recorded weights because some strip plots (on some visits) had large numbers of very small morels. The large confidence intervals on estimates of productivity for individual stands (Table 5) suggest that managers who wish determine the productivity of a given stand will either have to accept uncertain estimates of productivity, install more than the 10-strip plots that we used, or measure productivity by counting or collecting all the morels. A manuscript is in preparation that compares the statistical efficacy of the strip plots used in this study with plots of differing sizes and shapes used in other studies.

  Some of the strip plots in wildfire-habitat stands crossed a mosaic of burned and nonburned areas; better correlations between putative species and wildfire habitat conditions would have been obtained by ensuring the strip plots encompassed only burned areas or nonburned areas. We discontinued our sampling on most sites after about 5 weeks, when fruiting seemed to have ceased. Subsequent discussions with harvesters suggested that our PS D, the ‘‘gray’’ morels typically fruit later in summer (given adequate moisture). All our specimens of PS D were immature, an indication that we likely missed its peak fruiting season. The strip plots (over both years) yielded a total of 1465

picked specimens that were examined by our crews for unusual morphotypes. Nevertheless, PS D and PS E were only found outside the strip plots during walk-through surveys of the research stands, thus indicating the efficacy of this approach for detecting diversity.

Our results show that several morel species can be identified by two fingerprinting methods: RAPD fingerprinting with primer CAGAGGTCCC and ITS amplicon analysis with RFLPs produced by *Hae* III digest. RAPD-PCR, a fingerprinting method with relatively high resolution, is useful for delimiting both strains and species in fungi (Weising et al., 1995). RAPD fingerprinting produces distinctive species patterns, but high-quality DNA is required and precise protocols must be followed for comparative RAPD studies. ITS amplicon analysis is less demanding because high-quality DNA is not required, dried specimens can be used, and the high copy ribosomal DNA targets generally produce strong amplification results.

Several other investigators have proposed that species delineation in morels might be possible through characterization of ITS amplicons (O'Donnell et al., 1993, 1997; Mitchell et al., 1995; Buscot et al., 1996; Wipf et al., 1996, 1999). Wipf et al. (1996, 1999) sequenced ITS amplicons from representative black and yellow morel species and showed that, although the embedded 5.8S rRNA genes were highly conserved among the species, both ITS1 and ITS2 regions in the ITS amplicon were extremely divergent, a condition that is somewhat unusual within a genus (Gardes and Bruns, 1996). Wipf et al. (1996, 1999) found that a group of black morels reported as *M. angusticeps*, *M. conica*, *M. costata*, and *M. elata* had ITS amplicon fragments of approximately 750 bp, yellow morels reported as *M. esculenta*, *M. vulgaris*, and a strain of *M. crassipes* had amplicons of approximately 1150 bp, and specimens identified as *M. spongiola*, *M. hortensis*, and two strains of *M. crassipes* had amplicons of approximately 1230 bp. A double digest by using *Eco* RI and *Rsa* I resolved interspecific differences among some of the yellow morels but did not resolve interspecific differences within the black morel group (Wipf et al., 1999). Similarly, we found *Rsa* I digestion did not resolve the "blacks" (PS A, PS B, and PS C) but did resolve PS D and PS E. *Hae* III separated representatives of all of the putative species among samples collected in this study, but without confirmation by RAPDs or other molecular analyses, identification of unknown morels by RFLP might be equivocal.

- *Objective 2*. Document and compare 2 years of morel productivity in burned, insect-damaged, and relatively healthy montane forest habitats of northeastern Oregon.

Because PS D and PS E were not found on the strip plots, they did not contribute to the productivity data. Interpretation of our productivity analysis is complicated by the fact that three putative species (PS B, PS C, and some PS A) fruited the first year following fire in our wildfire-habitat stands, whereas only PS A fruited in nonburned stands or the second year following fire in wildfire stands. Additionally, although sites were intended as relatively uniform replicates of habitat conditions, productivity varied considerably among them. For instance, the wildfire-habitat stand on the Malheur National Forest produced far fewer burn morels in 1995 than did the other two wildfire stands (Table 5). Although the only statistically significant difference in productivity among the habitat conditions was for the number of morels (wildfire-burned > healthy), both morel counts and weights followed the anticipated trend of wildfire-burned > insect-damaged > healthy habitat conditions.

Puzzling differences exist between the patterns of count and weight productivity though (Fig. 1). The number of morels was significantly higher in 1995 than in 1996, but the same did not hold true for estimates of weight. Burn morels (PS B and PS C) tend to be smaller than "naturals" (PS A), so this might account for some of the difference in the wildfire habitat stands. If morel growth rates and the timing of site visits differed during the 2 years we sampled, the lack of a minimum size criterion also might have contributed to this disparity (Fig. 1).

The productivity values we report are considerably smaller than values recently reported from two wildfire sites in Canada (Duchesne and Weber, 1993; Obst and Brown, 2000), but those researchers

examined areas of known high productivity, and neither paper described a probabilistic (unbiased) approach to select plot locations. By contrast, our productivity values are unbiased stand- and landscape-level estimates rather than potential maximums. The fact that we likely missed late-season flushes of PS D in the wildfire stands in 1995 also might partially explain our lower productivity estimates.

The 88.7% moisture content of our morels fell on the low end of the previously reported range of 89.5–91.2% (Crisan and Sands, 1978; Ferndock, 1984). Our study was located in a relatively dry region, however, and humidity was low on many of the days that the crews visited the sites.

- *Objective 3*. Test for potential short-term harvest impacts by comparing morel production in pick and no-pick sample plots.

  The lack of significant differences in morel counts between pick and no-pick plots is not surprising, because other studies have suggested picking per se does not affect subsequent fruiting of chanterelles (Egli et al., 1990; Norvell, 1995) or matsutake (Eberhart et al., 1999; Pilz, unpublished data). We assume that the systematic differences between the two sampling seasons in our weight estimates for morels on the no-pick plots (as evidenced by the inexplicable interaction term in our original ANOVA) were the result of inconsistently applied procedures. Using regression equations to estimate weight on nonpicked plots likely remains an effective method if correctly applied (Pilz et al., 1998, 1999).
- *Objective 4*. Describe the putative species we find by using morphology, ecology, and molecular genetics.

  PS A, the natural black morel, corresponds to what has been referred to as *M. elata* sensu lato (Smith et al., 1981; Weber, 1995a). It appears to be widespread, common, and routinely harvested in the Pacific Northwest. Black morels, that we believe were this species, fruited prolifically in nonburned but insect-killed, grand fir stands on the Lakeview Ranger District of the Fremont National Forest, Oregon in 1994 (Weber et al., 1996). The second spring after our wildfire stands burned, this was the most abundant morel on our plots.

The existence of two (PS B and PS C) putative species of early season black ''burn'' morels first came to light in the genetic analysis; the field notes were of little use in characterizing them as distinct from PS A. Further study of these putative species, involving detailed notes on the fresh specimens and genetic analysis, is needed to see what morphological features correlate with the molecular differences. Specimens of PS A, PS B, and PS C all ''key out'' to the *Morchella elata* (complex), *M. conica*, or *M. angusticeps*, depending on the reference used.

Although not found on our strip plots, PS D (the gray morel) was found late in the fruiting season, the first year following fire, on burned soils. PS D is a good match morphologically for what McKnight (1987) called the ''burnsite morel'' or *Morchella atrotomentosa* (Moser) Bride. Because Moser (1949) described *M. esculenta* var. *atrotomentosa* as a ''*nov. var. ad.*[*sic*] *int.*'' or ''temporary new variety'', not as an unqualified new variety, it is not considered to have been published in accordance with the standards for scientific names of plants and fungi (Greuter et al., 2000). Thus neither that name nor combinations based on that name are available for use. By current interpretations, this morel would not be considered closely related to *M. esculenta*. The common name of ''gray'' morel is widely used for this species in the Pacific Northwest; however, in eastern North America, young specimens of what is called *M. esculenta* sensu lato also are called ''gray'' morels as is at least one more western postfire morel not encountered in this project.

PS E (mountain blond morel). Specimens belonging in PS E more closely resemble *Morchella esculenta* sensu lato than other species illustrated in most field guides. In parts of Oregon they are often lumped together as ''esculentas''. However, a close comparison of specimens belonging in PS E and most descriptions of *M. esculenta* from Europe or elsewhere in North America reveal numerous differences. Further clarification of species limits and nomenclature for morels is needed before we will feel comfortable applying an existing scientific name or a new one to PS E. Unlike members of the complex centered on *M. esculenta*, in PS E, the head is relatively narrow rather than

oval or rounded, especially in young specimens, and the primary ribs are strongly vertical and relatively straight producing elongated pits rather than the rounded to somewhat irregular pits generally attributed to *M. esculenta*. Furthermore, PS E seems to be characteristic of conifer forests including either lodgepole or ponderosa pine, whereas the complex centered on *M. esculenta* is commonly associated with hardwoods sometimes mixed with conifers. Both PS E and a morel that fits the classical concept of *M. esculenta* occur in eastern Oregon, but only PS E occurred in our research stands. Although this species was collected in a wildfire-habitat stand, we suspect it was fruiting on an unburned island within the perimeter of the burn; all other collections of this putative species we have seen were from unburned forests or unburned substrates within the perimeter of a fire.

- *Objective 5*. Discuss management implications.
  - *Productivity and commercial value*

    Based on informal discussions with harvesters and buyers PS A is the most consistently collected morel in nondisturbed coniferous forests of northeastern Oregon where it is one of the first morels to fruit during spring. PS B and PS C are commercially collected because they are so abundant following fires, but they are comparatively fragile and less suited for long-distance transport while fresh, thus are often dried. Specimens of PS D and PS E are firm and less likely to crumble during collection, processing, and shipping, making them especially well suited for the fresh market. The robust, meaty, and abundant grays (PS D) are considered a valuable mushroom crop in high-elevation and northern forests. Ash often adheres to fire morels (PS B, PS C, and PS D in our study), therefore they tend to be dirtier than morels that fruit in nonburned habitats (such as PS A and PS E).

    Alexander et al. (2002) used our landscape-level estimates of morel productivity to conduct an economic analysis that compared the relative value of timber and morels (jointly produced in the same stand in perpetuity). Under a typical timber management scenario incorporating periodic thinning and prescribed fire, the timber was worth 20–110 times more than the morels.
  - *Trophic modes and reproduction*

    Our results suggest that it is not possible to make management recommendations for the genus *Morchella* as a whole, but that managers must consider groups of morel species with similar trophic modes and conditions that trigger fruiting. A better understanding of how morels obtain and store nutrients, and what factors trigger their fruiting, is needed to design management regimes that sustain or enhance morel crops. Although Ower (1982) first demonstrated that morels could complete their life cycle in pure culture as saprobes, Dahlstrom et al. (2000) showed that mycelia of two of our putative species (PS A and PS E) are capable of forming mycorrhizal associations with four species in the Pinaceae in pure culture synthesis experiments. Hobbie et al. (2001) reported that sporocarps of the mountain blond had nitrogen/carbon isotope profiles suggesting they were at least facultatively mycorrhizal and thus in agreement with Dahlstrom et al. (2000). However, sporocarps of the natural black morel had profiles characteristic of saprobic fungi in contrast to Dahlstrom's results. These results are based on just a few specimens and isolates, and no comparable studies have been made on morels that fruit on burned substrates.

    At least one postfire mycorrhizal cup-fungus, *Geopyxis carbonaria* (Alb. et Schwein.: Fr.) Sacc., has a complex life cycle, is mycorrhizal on deep roots of members of the Pinaceae, and only fruits when the trees die (Vrålstad et al., 1998). A topic that is ripe for further research is whether *G. carbonaria* and burn-species of *Morchella* have both evolved similar adaptations to periodic forest fires and how such adaptations might confer competitive reproductive advantage.

    Only after 2 weeks do full-grown morels begin releasing mature spores, but then they do so in prodigious quantities (Ower, 1982; Weber, 1995b). Nevertheless, the role of spore dispersal in morel reproduction remains an open question. We do not know, for instance, whether spores released by either burn or non-

burn morels preferentially germinate in burned mineral soil or in the forest floor litter layers of adjacent nonburned stands. Morel spores have thin walls and, under laboratory conditions, germinate readily given adequate moisture; hence long persistence in the soil or atmosphere is questionable. Trials of artificial spore dissemination for enhancing morel crops would be difficult to replicate if the spores of more than one putative species were admixed.

- *Management activities and disturbance*

The large percentage of our strip plots with at least some morels (96.7%) suggests that the spatial distribution of morels might be more uniform than that of obligately ectomycorrhizal mushrooms such as American matsutake (*Tricholoma magnivelare* (Peck) Redhead) or chanterelles (*Cantharellus* species). By comparison, American matsutake only fruited in 41 of 54 (75.9%) 100 m^2 plots during 5 years of sampling (Pilz et al., 1999); and chanterelles only fruited in 39 of 55 (70.9%) 800 m^2 plots during 2 years of sampling (Pilz et al., 1998). If true, selection of trees to be left during stand thinning might be more important for retaining colonies of other edible ectomycorrhizal species than *Morchella*.

Morels are commonly observed to fruit where soil is disturbed or compacted. Harvesters will follow the paths of logging equipment to search for concentrations of morels, and sometimes morels fruit in the footprints of previous harvesters. Even if soil compaction actually stimulates morel fruiting, little is known about cumulative impacts of repeated soil disturbance on morel crops. Because extensive soil compaction is detrimental to tree growth and soil disruption can accentuate erosion, intentionally deriving enhanced morel crops from these disturbances would be a costly resource tradeoff.

Given that burn and nonburn morel species do not seem to fruit at the same time, trials should be conducted to determine if two crops of morels could be produced by staggering thinning and burning activities at least a year apart. The concept of sustainable mushroom production might need modification in the case of burn morels that are harvested after the episodic disturbance of wildfire. In much the same manner that sustainable timber harvesting is defined across landscapes and decades, ''sustainable burn morel crops'' might need to be defined on larger spatial and longer temporal scales than mushrooms that are harvested from the same location annually.

5. Future research

Teasing apart the black morel complex (PS A, PS B, and PS C) is a good example of how genetic, ecological, and morphological studies can compliment one another. The use of radiocarbon isotope ratios (Hobbie et al., 2002) to determine whether field-collected morels are the product of saprobic or mycorrhizal mycelia is a promising new technique. Better understanding of the autecology of each species could help managers tailor silvicultural practices to maintain morel populations and improve crops.

Our research examined natural disturbances. For greater applicability to forest management, activities such as timing and intensity of prescribed fires (Martin, 1990; Pyne et al., 1996), thinning methods, tree species selection, and soil disturbance, are good candidates for replicated field studies on triggering morel crops. To be meaningful, the research design must take into account the morel species likely to be encountered, their possible trophic modes, and when, where, and under what conditions they fruit.

Interdisciplinary research can be challenging, but we found such collaboration useful for interpreting our results. Careful attention should be paid to integrating study methods and analysis early in the planning phase. Forest management decisions and mushroom harvest regulations are almost always developed in the context of competing social, environmental, and economic values, especially on public lands, but we derived valuable ideas and information from our cooperation with forest managers and morel harvesters and buyers.

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References

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, 493 pp.

Alexander, S.J., Pilz, D., Weber, N.S., Brown, E., Rockwell, V., 2002. Value estimates of commercial mushrooms and timber in the Pacific Northwest. Environ. Manage. 30 (1), 129–141.

Amaranthus, M., Pilz, D., 1996. Productivity and sustainable harvest of wild mushrooms. In: Pilz, D., Molina, R. (Eds.), Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvests. USDA Forest Service General Technical Report PNW-371, pp. 42–61.

Apfelbaum, S.I., Haney, A., Dole, R.E., 1984. Ascocarp formation by *Morchella angusticeps* after wildfire. Mich. Bot. 23, 99–102.

Arora, D., 1986. Mushrooms Demystified: A Comprehensive Guide to the Fleshy Fungi. Ten Speed Press, Berkeley, CA, 959 pp.

Boom, M., 1995. Fungal Lust. East Bay Express, vol. 17, pp. 10–18.

Borchers, J.G., Perry, D.A., 1990. Effects of prescribed fire on soil organisms. In: Walsted, J.D., Radosevich, S.R., Sandberg, D.V. (Eds.), Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, OR, pp. 143–158.

Buscot, F., Kottke, I., 1990. The association of *Morchella rotunda* (Pers.) Boudier with roots of *Picea abies* (L.) Karst. New Phytol. 116, 425–430.

Buscot, F., 1992a. Mycorrhizal succession and morel biology. In: Read, D.J., Lewis, D.H., Fitter, A.H., Alexander, I.J. (Eds.), Mycorrhizas in Ecosystems. CAB International, Oxon, UK, pp. 220–224.

Buscot, F., 1992b. Strategies ecologiques et biologiques des morilles. Cryptog. Mycol. 13, 171–179.

Buscot, F., 1993a. Mycelial differentiation of *Morchella esculenta* in pure culture. Mycol. Res. 97, 136–140.

Buscot, F., 1993b. Synthesis of two types of association between *Morchella esculenta* and *Picea abies* under controlled culture conditions. J. Plant Physiol. 141, 12–17.

Buscot, F., Wipf, D., Di Battista, C., Munch, J.C., Botton, B., Martin, F., 1996. DNA polymorphism in morels. I. PCR/RFLP analysis of the ribosomal DNA spacers and microsatellite-primed PCR. Mycol. Res. 100, 63–71.

Carter, M.C.A., Robertson, J.L., Haack, R.A., Lawrence, R.K., Hayes, J.L., 1996. Genetic relatedness of North American populations of *Tomicus piniperda* (Coleoptera: Scolytidae). J. Econ. Entomol. 89 (6), 1345–1353.

Crisan, E.V., Sands, A., 1978. Nutritional value. In: Chang, S.T., Hayes, W.A. (Eds.), The Biology and Cultivation of Edible Mushrooms. Academic Press, New York, pp. 137–168.

Crous, P.W., Cother, E.J., 2003. The reality of a virtual laboratory: reference to personal herbaria and culture collections is bad science. Inoculum 54 (5), 2–3.

Cubbage, F.W., O'Laughlin, J., Bullock III, C.S., 1993. Forest Resource Policy. Wiley, New York, pp. 528–539.

Dahlstrom, J.L., Smith, J.E., Weber, N.S., 2000. Mycorrhiza-like interaction by *Morchella* with species of the Pinaceae in pure culture synthesis. Mycorrhiza 9, 279–285.

DeBano, L.F., Neary, D.G., Ffolliott, P.F., 1998. Fire's Effects on Ecosystems. Wiley, New York, 333 pp.

Duchesne, L.C., Weber, M.G., 1993. High incidence of the edible morel *Morchella conica* in a Jack pine, *Pinus banksiana*, forest following prescribed burning. Can. Field-Nat. 107, 114–116.

Eberhart, J.L., Luoma, D.L., Pilz, D., Amaranthus, M.P., Abbott, R., Segotta, D., Moore, A., 1999. Effects of harvest techniques on American matsutake (*Tricholoma magnivelare*) production. Abstract MP4.02. Abstract Book. In: Proceedings of the IX International Congress of Mycology, Sydney, Australia, p. 238.

Egli, S., Ayer, F., Chatelain, F., 1990. Der Einfluss des Pilzsammelns auf die Pilzflora. Mycol. Helv. 3, 417–428.

Ferndock, M., 1984. Morels deserve the best [Catalogue] M. Ferndock, Denison, Minnesota.

Frampton, J., 1996. Study Mushroom's Habits Before you Leave. Recreation Section, vol. 5. Baker City Herald, Baker City, OR.

Franklin, J.F., Dyrness, C.T., 1973. Natural Vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Portland, OR, pp. 193–200.

Gardes, M., Bruns, T.D., 1996. ITS-RFLP matching for identification of fungi. In: Clapp, J.P. (Ed.), Methods in Molecular

Biology, vol. 50. Humana Press Inc., Totowa, NJ, pp. 177–186.

Greuter, W., McNeill, J., Barrie, E.R., Burdet, H.M., Demoulin, V., Filguerias, T.S., Nichelson, D.H., Silva, P.C., Skog, J.E., Trehane, P., Turland, N.J., Hawksworth, D.H., 2000. International Code of Botanical Nomenclature (St. Louis Code). *Regnum Vegetabile* 138.

Harbin, M., Volk, T.J., 1999. The relationship of *Morchella* with plant roots. Abstract. In: Proceedings of the XVI International Botanical Congress, St. Louis, Missouri, USA, p. 59.

Hessburg, P.F., Mitchell, R.G., Filip, G.M., 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. USDA Forest Service General Technical Report PNW-327, 72 pp.

Hobbie, E.A., Weber, N.S., Trappe, J.M., 2001. Mycorrhizal vs. saprotrophic status of fungi: the isotopic evidence. New Phytol. 150, 601–610.

Hobbie, E.A., Weber, N.S., Trappe, J.M., van Klinken, G.J., 2002. Using radiocarbon to determine the mycorrhizal status of fungi. New Phytol. 156, 129–136.

Jacquetant, E., 1984. Les morilles. Plantanida, Lausanne, Switzerland.

Jaindl, R.G., Quigley, T.M., 1996. Search for a Solution: Sustaining the Land, People, and Economy of the Blue Mountains. American Forests, Washington, DC.

Kaufmann, J.B., 1990. Ecological relationships of vegetation and fire in Pacific Northwest Forests. In: Walsted, J.D., Radosevich, S.R., Sandberg, D.V. (Eds.), Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, OR, pp. 39–51.

Kirk, P.M. (Coord.) 2003. www.indexfungorum.org.

Kumar, S., Tamura, K., Jakobsen, I., Nei, M., 2000. MEGA: Molecular, Evolutionary Genetics Analysis, version 2. www.megasoftware.net.

Langston, N., 1995. Forest Dreams, Forest Nightmares: The Paradox of Old Growth in the Inland West. Univ. Wash. Press, Seattle, Wash., 359 pp.

Lehmkuhl, J.F., Hessburg, P.F., Everett, R.L., Huff, M.H., Ottmar, R.D., 1994. Historical and current forest landscape of eastern Oregon and Washington. Part 1. Vegetation pattern and insect and disease hazards. USDA Forest Service General Technical Report PNW-328, 88 pp.

Low, J. 1995. Missouri's Magnificent Morels, vol. 56. Missouri conservationist, Jefferson City, MO, pp. 20–23.

Martin, R.E., 1990. Goals, methods, and elements of prescribed burning. In: Walsted, J.D., Radosevich, S.R., Sandberg, D.V. (Eds.), Natural and Prescribed Fire in Pacific Northwest Forests. Oregon State University Press, Corvallis, OR, pp. 55–66.

McKnight, K.H., 1987. A Field Guide to Mushrooms [of] North America. The Peterson Field Guide Series: 34. Houghton Mifflin Co., Boston, MA, 429 pp.

Miller, S.L., Torres, P., McClean, T.M., 1994. Persistence of basidiospores and sclerotia of ectomycorrhizal fungi and *Morchella* in soil. Mycologia 86, 89–95.

Mitchell, J.I., Roberts, P.J., Moss, S.T., 1995. Sequence or structure? A short review on the application of nucleic acid sequence information to fungal taxonomy. Mycologist 9, 67–75.

Molina, R., Vance, N., Weigand, J.F., Pilz, D., Amaranthus, M.P., 1997. Special forest products: integrating social, economic, and biological considerations into ecosystem management. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 315–336.

Moser, M., 1949. Über das Massenauftreten von Formen der Gattung *Morchella* auf Waldbrandflächen. Sydowia Ser. II 3, 174–195.

Norvell, L., 1995. Loving the chanterelle to death? The ten-year Oregon chanterelle project. McIlvainea 12, 6–25.

Obst, J., Brown, W., 2000. Feasibility of a morel mushroom harvest in the Northwest Territories. Artic Ecology and Development Consulting and Deton'cho Corporation, Yellowknife, NT, Canada, 49 pp.

O'Donnell, K., Weber, N.S., Haines, J.H., Mills, G.L., 1993. Molecular systematics and phylogenetics of Morchellaceae [Abstract]. Inoculum 44 (2), 51.

O'Donnell, K.O., Cigelnik, E., Weber, N.S., Trappe, J.M., 1997. Phylogenetic relationships among ascomycetous truffles and the true and false morels from 18S and 28S ribosomal DNA sequence analyses. Mycologia 89 (1), 48–65.

O'Donnell, K., Weber, N.S., Rehner, S., Mills, G., 2003. Phylogeny and biogeography of *Morchella*. In: Proceedings of the 22nd Fungal Genetics Conference, March 2003, Asilomar. Fungal Genet. Newsl. 50 (Suppl.) Abstract # 443. http://www.fgsc.net/asil2003/PopBioPosterAbstracts2003.htm.

Ower, R., 1982. Notes on the development of the morel ascocarp: *Morchella esculenta*. Mycologia 74, 142–144.

Parks, C.G., Schmitt, C.L., 1997. Wild edible mushrooms in the Blue Mountains: resource and issues. USDA Forest Service General Technical Report PNW-393, 22 pp.

Pilz, D., Molina, R., Amaranthus, M.P., Castellano, M., Weber, N.S., 1996. Forest fungi and ecosystem management. In: Pilz, D., Molina, R. (Eds.), Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvests. USDA Forest Service General Technical Report PNW-371, pp. 86–103.

Pilz, D., Molina, R., Liegel, L.H., 1998. Biological productivity of chanterelle mushrooms in and near the Olympic Peninsula Biosphere Reserve. In: Liegel, L.H. (Comp.), The Biological, Socioeconomic, and Managerial Aspects of Chanterelle Mushroom Harvesting: The Olympic Peninsula, Washington State, USA AMBIO Special Report No. 9, pp. 8–13.

Pilz, D., Smith, J., Amaranthus, M.P., Alexander, S., Molina, R., Luoma, D., 1999. Managing the commercial harvest of the American matsutake and timber in the southern Oregon Cascade Range. J. For. 97, 8–15.

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.

Puterka, G.J., Black, W.C., Steiner, W.M., Burton, R.L., 1993. Genetic variation and phylogenetic relationships among world wide collections of the Russian wheat aphid, *Diuraphis noxia*

(Mordvilko) inferred from allozyme and RAPD-PCR markers. Heredity 70, 604–618.

Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. Introduction to Wildland Fire, 2nd ed. Wiley, New York. 769 pp.

Ramsbottom, J., 1953. Mushrooms and Toadstools: A Study of the Activities of Fungi. Collins, London, 306 pp.

Sabin, T.E., Stafford, S.G., 1990. Assessing the need for transformation of response variables. Special Publ. 20. For. Res. Lab., College of Forestry, Oregon St. Univ., Corvallis, OR.

Schlosser, W.E., Blatner, K.A., 1995. The wild edible mushroom industry of Washington, Oregon and Idaho: a 1992 survey of processors. J. For. 93, 31–36.

Smith, A.H., Smith, H.V., Weber, N.S., 1981. How to Know the Non-gilled Mushrooms. Wm. C. Brown Co., Dubuque, IA, 324 pp.

Sneath, P.H.A., Sokal, R.R., 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. Freeman, San Francisco, CA, 573 pp.

Sturgis, W.C., 1905. Remarkable occurrence of *Morchella esculenta* (L.) Pers. J. Mycol. 11, 269.

Thompson, V.V., 1994. Morel: A Lifetime Pursuit. Missouri Mycological Society, Glencoe, MO, 36 pp.

US House of Representatives Bill 2466. 2000. Department of the Interior and Related Agencies Appropriations Act, 2000. Title III. General Provisions, Sec. 339. In: Proceedings of the 106th Congress.

Volk, T.J., 1991. Understanding the morel life cycle: key to cultivation. McIlvainea 10, 76–81.

Volk, T.J., Leonard, T.J., 1990. Cytology of the life-cycle of *Morchella*. Mycol. Res. 94, 399–406.

von Krombholz, J.V. Naturgetreue Abbildungen und Beschreibungen der essbaren, Schädlichen und Verdächtigen Schwämme 3, 1834, 1–36.

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, 609–616.

Weber, N.S., 1995a. Overview of research pertinent to morels or *Morchella* spp. as special forest products. In: Schnepf, C. (Comp., Ed.), Dancing With The Elephant. In: Proceedings of the Conference and Exposition of the Business and Science of Special Forest Products, University of Idaho Extension Service, Moscow, ID, pp. 129–133.

Weber, N.S., 1995b. A Morel Hunter's Companion: A Guide to the True and False Morels. Thunder Bay Press, Holt, MI, 209 pp.

Weber, N.S., Pilz, D., Carter, C., 1996. Morel life histories: beginning to address the unknowns with a case study in the Fremont National Forest near Lakeview, Oregon. In: Pilz, D., Molina, R. (Eds.), Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvests. USDA Forest Service General Technical Report PNW-371, pp. 62–68.

Weber, N.S., Trappe, J.M., Denison, W.C., 1997. Studies on western American Pezizales. Collecting and describing ascomata macroscopic features. Mycotaxon 61, 153–176.

Weising, K., Nybom, H., Wolff, K., Meyer, W., 1995. DNA Fingerprinting in Plants and Fungi. CRC Press, Boca Raton, FL, 322 pp.

Wipf, D., Bedell, J.-P., Munch, J.C., Botton, B., Buscot, F., 1996. Polymorphism in morels: isozyme electrophoretic analysis. Can. J. Microbiol. 42, 819–827.

Wipf, D., Fribourg, A., Munch, J.C., Botton, B., Buscot, F., 1999. Diversity of the internal transcribed spacer of rDNA in morels. Can. J. Microbiol. 45, 769–778.