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Mushroom crops in relation to weather in the southwestern Yukon

C.J. Krebs, Patrick Carrier, S. Boutin, R. Boonstra, and Elizabeth Hofer

Abstract: Epigeous mushroom production in the boreal forest ecosystem varies dramatically from year to year. We tested the hypothesis that the aboveground production of epigeous mushrooms in the Kluane region, Yukon, could be predicted by summer rainfall. There is a single crop in this part of the boreal zone with maximum production during the first 2 weeks of August. We measured standing crops from 1993 to 2007 at 13 areas along 210 km of the Alaska Highway and Haines Road in the southwestern Yukon. Aboveground mushroom crops averaged 24 kg/ha wet weight but varied from 0.0 to 117 kg/ha over the 15 years of study, with a coefficient of variation among years of 143%. Epigeous mushroom production could be predicted from June rainfall of the current year and May rainfall of the year previous with $R^2 = 0.85$. Part of the lack of a perfect fit to rainfall was due to the constraint that years of high mushroom crops could not be followed by another high year, no matter what the rainfall pattern. We were not able to identify the species of mushrooms in this study but we confirm from natural history observations that mushrooms are a critical food for several of the small mammal species in the Yukon boreal forest.

Key words: epigeous mushrooms, biomass prediction, boreal forest, Kluane Lake, Yukon, rainfall.

Résumé : La production de champignons épigés des écosystèmes de la forêt boréale varie fortement d'une année à l'autre. Les auteurs ont vérifié l'hypothèse à savoir que la production, au-dessus du sol, des champignons épigés dans la région de Kluane au Yukon, pourrait être prédite à l'aide de la précipitation estivale. Dans cette partie de la forêt boréale, il y a une seule poussée avec un maximum de production au cours des deux premières semaines d'août. Ils ont mesuré la ressource produite annuellement de 1993 à 2007 sur 13 sites étalés sur 210 km de l'autoroute de l'Alaska et de la route Haines, dans le sud-ouest du Yukon. La productivité épigée en champignons atteint une moyenne de 24 kg/ha en poids frais, mais a varié de 0,0 à 117 kg/ha au cours des 15 années de l'étude, avec un coefficient de variation au cours des années de 143 %. On peut prédire la production des champignons épigés à partir de la précipitation en juin de l'année en cours et celle de mai de l'année précédente avec $R^2 = 0,85$. On constate que les années de fortes productions de champignons ne peuvent pas être suivies par une autre année de forte production, quel que soit le patron de précipitation; ceci constitue une contrainte qui empêche d'obtenir une corrélation parfaite. Les auteurs n'ont pas été en mesure d'identifier les espèces de champignons dans cette étude, mais les observations de naturaliste confirment que les champignons y constituent une nourriture critique pour plusieurs des petits mammifères qui vivent dans la forêt boréale du Yukon.

Mots-clés : champignons épigés, prédiction de la biomasse, forêt boréale, lac Kluane, Yukon, pluie.

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Introduction

Aboveground mushroom crops in the boreal forest are known to fluctuate dramatically from year to year, and these crops are used as food both by small mammals and the local people (Luoma et al. 2003; Yun and Hall 2004; Maser et al. 2008). Red squirrels (*Tamiasciurus hudsonicus*) use both epigeous and hypogeous mushrooms in summer when spruce cone crops fail and also eat them in winter (Currah et al. 2000; Vernes et al. 2004). Red-backed voles (*Clethrionomys rutilus*) also utilize mushrooms as an important food source (Dyke 1971). Years of high epigeous mushroom

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Table 1. Number of sites sampled, number of subsample plots, total number of subsamples over all sites, and dates of sampling from 1993 to 2007.

Year	No. of Sites	No. subsamples per site	Total N	Dates sampled
1993	4	80	320	14–22 August
1994	4	80	320	9–15 August
1995	4	80–86	332	8–18 August
1996	1	80	80	8 August
1997	2	80–86	166	3–11 August
1998	2	80–86	166	3–4 August
1999	3	30–86	196	2–9 August
2000	9	42–100	672	2–27 August
2001	10	50–100	940	9–25 August
2002	10	50–100	972	16–24 August
2003	11	50–150	1007	28 July – 18 August
2004	10	50–100	922	27 July – 22 August
2005	10	50–100	922	26 July – 14 August
2006	10	50–100	913	29 July – 20 August
2007	8	50–100	722	3–19 August

crops are typically synchronous over large areas of the southwestern Yukon, as they are in Norway (Mehus 1986), and climatic events are usually put forward to explain these large synchronous variations in production. We have explored the ability of summer climatic variables to predict berry crops in the southwestern Yukon[2], and in this paper we ask whether we can predict epigeous mushroom crops with local summer weather variables.

We can find little quantitative data on mushroom production in the boreal forests of northern Canada. Carrier (2003) irrigated three 1.4 ha areas of the Kluane boreal forest during the growing season and found a large increase in epigeous mushroom production, suggesting that summer water supplies might be the limiting factor driving epigeous mushroom crops. We assume in this paper that rainfall and possibly temperature are the critical variables, as they are farther south (Wilkins and Harris 1946; Fogel 1976; Straatsma et al. 2001). The climate of the boreal forest is relatively severe with a short growing season and this simplifies measurements because a single mushroom crop is produced in late July and early August, in contrast to spring and autumn crops in more temperate areas. We explore in this paper a series of weather hypotheses involving both temperature and rainfall of the current and the previous summer as potential explanatory variables for the size of the aboveground mushroom crop. Our aim is to produce a quantitative hypothesis that can be tested with additional data in future studies.

Methods

Study area and experimental sites

We sampled a total of 13 areas near Kluane Lake in the southwestern Yukon along the Alaska Highway and the Haines Road, ranging from the Donjek River crossing north of Kluane Lake south to St. Elias Lake along the Haines Road south of Haines Junction, a transect of 210 km. Sites were on average 27 km apart (range 3 to 43 km). Three of the 13 sites were dropped because of experimental work on the site, and new sites were added to preserve the geographical spread, particularly after 1999 (Table 1). Most of these sites lie in open spruce forest within the Shakwak Trench system (61°01′N, 138°24′W), and all are in the rain shadow of the St. Elias Mountains. Mean annual precipitation at Haines Junction is ca. 308 mm (1945–2007), which includes an average annual snowfall of approximately 100 cm.

The tree community in the Kluane region of the boreal forest is dominated by white spruce (*Picea glauca* (Moench) Voss) interspersed with trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The shrub layer is composed of willow (*Salix* spp.), soapberry (*Shepherdia canadensis* (L.) Nutt.), and dwarf birch (*Betula glandulosa* Michx.), and the ground layers are composed of dwarf shrubs and herbaceous plants such as bearberries (*Arctostaphylos rubra* (Rehd. & Wils.) Fern. and *Arctostaphylos uva-ursi* (L.) Spreng. s.l.), crowberry (*Empetrum nigrum* L.), blueberry and (or) cranberry (*Vaccinium* spp.), toadflax (*Geocaulon lividum* (Richards) Fern.), arctic lupine (*Lupinus arcticus* S. Wats), and other forbs (Turkington et al. 2002).

We sampled only epigeous mushroom fruiting bodies. We do not have any data on the abundance of hypogeous fungi on our study sites. In the Kluane area there is a single season for the appearance of mushroom sporocarps, which varies from late July to mid-August. We sampled every year from 1993 to 2007 at the peak of appearance of sporocarps at the dates indicated in Table 1. Sites (36 ha each) were the unit of replication. At each study site a systematic subsample was taken usually of 80–100 circular plots of 3 m radius (area sampled 28.3 m^2) spaced 30 m apart. All aboveground sporocarps of all species were counted in each plot. We separated mushrooms by diameter into small (0–4 cm cap diameter), medium (4–8 cm), and large (>8 cm diameter). At each site we measured the diameters of a sample of

[2] C.J. Krebs, R. Boonstra, and K. Cowcill. Climatic determinants of berry crops in the boreal forest of the southwestern Yukon. Unpublished.

Fig. 1. Log–log regression of the cap area (cm^2) of Kluane region mushrooms to their wet biomass (*g*). The equation is log(wet weight) = –0.4617 + 1.200234 log(cap-area), $n = 155$, $R^2 = 0.95$. This equation provided the best fit when evaluated against alternatives by means of AIC_c. (Anderson 2008). This regression differs slightly from that given in Carrier (2003), which was based on fewer data.

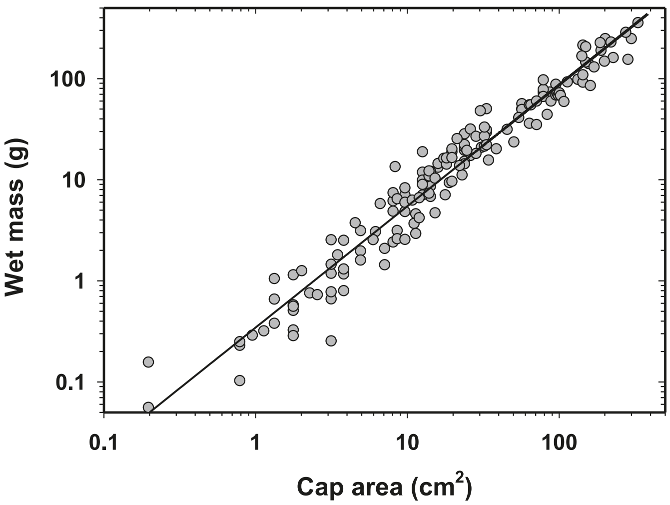
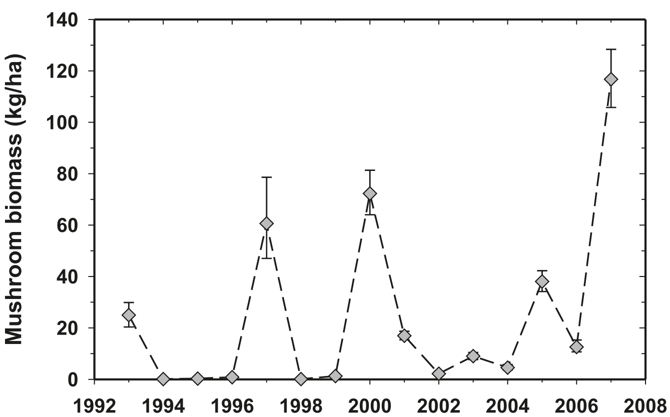


Fig. 2. Observed aboveground mushroom biomass (wet weight as kg/ha) for 1993 to 2007 with 95% confidence limits for variation among sites. More sites were counted after 1999, as indicated in Table 1.



20–40 small and medium mushrooms to estimate the average biomass of a single mushroom for these two size classes. Because large mushrooms contain most of the biomass on a plot, all large mushrooms were individually measured and their biomass individually computed from the regression shown in Fig. 1. We were not able to identify the species of mushrooms we counted. We did not count puffballs (which were relatively rare on our sites) because we were interested in mushrooms that animals used as food and we had no observational evidence that puffballs were ever eaten by animals once they are above ground in this part of the boreal forest.

These study sites were all located in areas of moderately open spruce forest (55%–70% canopy cover) with a well developed (>80% cover) herbaceous and moss understory. The Shakwak Valley has a patchwork of vegetation caused by fire (Francis 1996; Dale et al. 2001), but there were no fires on any of our sites during the study interval. We counted the same plots year after year, and adjusted the wet biomass (kg) of mushrooms to a standard area of 1 ha (g per 10 m^2 = kg per ha). Values in the literature are typically presented as kilograms per hectare. The conversion factor to dry weights for mushrooms in our area was estimated as 11%–13% (SD = 4%, $n = 82$, P. Carrier, unpublished data).

Table 2. Correlation of total monthly rainfall with square-root transformed aboveground mushroom biomass in the same year and with time lag of 1 year.

Variable	Correlation coefficient	*P*
May rainfall of year *t*	–0.25	0.37
June rainfall of year *t*	**0.68**	0.005
July rainfall of year *t*	0.14	0.63
August rainfall of year *t*	0.06	0.82
May rainfall of year *t*–1	**0.75**	0.001
June rainfall of year *t*–1	–0.15	0.59
July rainfall of year *t*–1	–0.43	0.11
August rainfall of year *t*–1	0.21	0.45

Note: Correlations that were statistically significant at 5% are in bold face.

Analyses

The experimental design was a nested design with the measurement variable as standing crop in each year, with sites as the primary units of subsampling within the year, and plots as the secondary units of subsampling within the sites. We are concerned here with variation among years in standing crop. Multiple regression analyses were used to derive the best set of weather variables that could predict epigeous mushroom crop estimates for each of the 15 years of data. We used only mean monthly temperature and total monthly precipitation in summer as weather variables because a preliminary analysis showed that no measures of winter snow depth or accumulation were related to mushroom production in the following summer. All analyses were done with NCSS (www.ncss.com). The best of a suite of alternative regression models was determined using AIC_c (Anderson 2008). All confidence limits given in this paper are 95% confidence limits.

Results

Mushroom biomass varied greatly over the 1993 to 2007 period. Average wet biomass was 24 kg/ha with a coefficient of variation of 143% and a range from 0.0 to 117 kg/ha. Figure 2 shows the year to year changes. The years 1997, 2000, 2005, and 2007 were years of high mushroom abundance and there were never two years in a row with high mushroom abundance in these boreal forest sites.

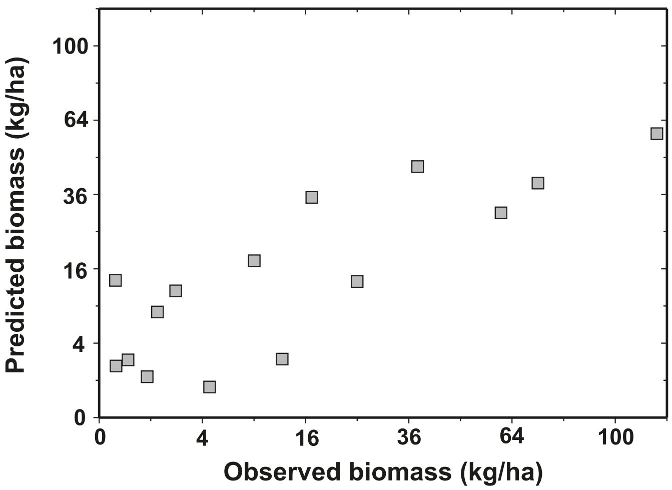
Summer weather conditions were measured at the Haines Junction meteorological station, and we used monthly temperature and rainfall data from May to August as potential explanatory variables to predict mushroom crops. We investigated whether adding the time lagged weather variables from year *t*–1 would improve predictability. For all the models tested, we found from an analysis of residuals that a square-root transformation of mushroom biomass was re-

Table 3. Multiple regressions of square-root transformed aboveground mushroom biomass with June rainfall in the same year and May rainfall with time lag of 1 year.

Model	No. parameters	Log likelihood	AIC_c	Weights	Evidence ratio	R^2
No intercept	4	–9.338	30.68	0.87	1.0	0.85
With intercept	5	–8.950	34.57	0.13	7.0	0.68

Note: Terms as defined in Anderson (2008). The best regression model is, square root (biomass) = 0.0409 June rainfall + 0.1632 May rainfall of t–1, with R^2 = 0.85, n = 15 years, with standardized regression coefficients of 0.57 for May rainfall of t–1 and 0.39 for June rainfall of t, and biomass measured as kilgrams of wet weight per hectare, rainfall in millimetres.

Fig. 3. Observed aboveground mushroom biomass (wet weight) in relation to predicted biomass from June rainfall of the current year and May rainfall of the year before. The scales are square root transformed. Each point represents one year of data.



quired to satisfy the normal distribution requirement of regression analysis, so all subsequent analyses were done with this transformation of mushroom biomass. None of the temperature variables showed a significant correlation with aboveground mushroom production, and we deleted these from further analysis. Table 2 gives the simple Pearson's correlation coefficients between summer rainfall and transformed mushroom wet biomass. Two variables stand out: June rainfall of the current year and May rainfall of the previous year.

We computed a multiple regression of transformed mushroom biomass on June rainfall of the current year and May rainfall of year t–1. The main decision was whether to include an intercept in the regression analysis or to assume that the regression goes through the origin (0 for all variables). Table 3 presents the two best regressions along with their AIC_c analysis. The multiple regression without an intercept has the highest weight and the best evidence ratio and thus appears to be the best model for the existing data.

Figure 3 shows, for each year, the observed mushroom biomass and that predicted by the regression given in Table 2. There is room for improvement in this fit, particularly in the high mushroom years like 2007 when there were 117 kg/ha observed and only 64 kg/ha predicted. One reason for the lack of fit is the apparent rule that a high mushroom year cannot be followed immediately by another high production year. Thus the negative deviations of 1994, 1997, and 2001 (predicted much higher than observed) can be partly explained by this rule. Adding a lag variable to mushroom production (similar to delayed density dependence) did not however improve the fit of the multiple regression model.

Discussion

There is good evidence that aboveground mushroom production in the boreal forest responds to rainfall, and the major reason for this study was to define more quantitatively this belief and to determine whether there were any temperature effects. Temperature measures did not add any predictability to the regressions. The observation that June rainfall is closely related to mushroom biomass production is not surprising, but we were surprised to find that May rainfall of the previous year was also highly correlated with subsequent mushroom production. The one-year time lag is difficult to explain. We hypothesize that it involves energy buildup and storage in the year preceding a given sampling of standing crop. Nearly all of the fleshy fungi on our plots are either symbionts (mycorrhiza formers) or saprotrophs. Favorable rain in May would favor better growth of the mycelium, thereby enabling the colony to explore more of the available substrate. It would also favor growth of the feeder rootlets of the mycorrhizal host trees. Thus the mycorrhizal fungi would have more new rootlets to colonize and have better access to host photosynthates and their derivatives. An analogous phenomenon would occur with the saprotrophs, which could explore a greater volume of the organic matter in the soil or fallen trees that nourishes them. Either way, in favorable years the colonies would expand and hypothetically sequester more energy for producing fruit-body primordia in following year.

Epigeous mushroom crops in the autumn in three Douglas-fir forest sites of Washington and Oregon ranged from 2.0 to 4.1 kg/ha dry weight (Luoma et al. 2004). Kranabetter and Kroeger (2001) reported a higher dry biomass of 5–30 kg/ha over a 3 year period for a western hemlock – western redcedar forest in northwest British Columbia, and Vogt et al. (1981) similarly reported high dry biomass of 27–34 kg/ha from two *Abies amabilis* stands in western Washington. Our average biomass converted to dry weight was 2.4 kg/ha, at the lower range of the estimates reported for forest sites in Oregon and Washington.

Martínez de Aragón et al. (2007) reported aboveground sporocarp production over 5 years from 23 pine forest sites in Catalonia, Spain. They found production ranging from 1.2 to 5.8 kg/ha dry weight, and a coefficient of variation of 67% among years. They could predict total annual production of sporocarps from rainfall and potential evapotranspiration in September and October and minimum soil temperature in August, with an R^2 of 0.66. Unfortunately they did not indicate the relative importance of these three variables in their predictive equation. Potential evapotranspiration is computed from temperature, and consequently their predictions flow from temperature and rainfall in late summer and early autumn in these pine forests. We could not find any relationship between air temperatures and mushroom production in our study sites.

Sporocarps in western hemlock stands in Olympic National Park, Washington, averaged a low value 0.58 kg/ha dry weight (range 0–3.8), concentrated mostly in the autumn, and the mushroom crop was correlated with annual rainfall (O'Dell et al. 1999). Straatsma et al. (2001) studied aboveground sporocarp production for 21 years in western Switzerland and found that productivity was correlated with rainfall from June to October. Unfortunately they did not obtain biomass estimates for their plots but counted only the number of sporocarps. They counted on average 226 sporocarps per 100 m^2 (range 12–565) with a annual coefficient of variation of 75%.

A test of the statistical model developed here for the Kluane region of the boreal forest has been provided by Carrier (2003) who irrigated three plots of boreal forest for 5 years. He showed that by increasing summer rainfall an average of 91% via irrigation, mushroom production increased over twofold from an average of 27 kg/ha wet weight to 59 kg/ha. Moreover he verified that even with additional rainfall in 1998, he could get only a very small mushroom crop after a large crop in 1997 (132 kg/ha), indicating that two large crops cannot follow one another no matter what the rainfall.

Our estimates of standing crops of epigeous fungi are slightly biased by the harvesting of sporocarps by red squirrels before we do our sampling and the possible emergence of some sporocarps after the peak of production in early August. Teeth marks from small mammals and red squirrels were often found on the mushrooms we were measuring, and only rarely was the entire sporocarp removed by a squirrel (and the stem left in the ground as evidence of removal). We do not have data on the rate of removal of sporocarps by small mammals but it is certainly not instantaneous. Although both herbivore removals and a prolonged production season are sources of variation in our standing crop estimates, they are dwarfed by the large fluctuations in crops from year to year, which is the main focus of our analysis. Herbivore offtake could be measured with exclosure plots but we have not done these studies.

We do not know the abundance of hypogeous fungi in these boreal forests. The northern flying squirrel (*Glaucomys sabrinus*) is a specialist on hypogeous fungi (Vernes et al. 2004) and these squirrels are rare in the Kluane region. An occasional skull of a flying squirrel has been found in the many great horned owl pellets we have analyzed in this region, and we have caught very few live flying squirrels in traps set for other mammals in these forests (S. Boutin, personal communication).

The next steps in this research program are to identify the dominant species of mushrooms in this part of the boreal forest, and to test the predictive statistical model with additional rainfall data. A sampling program to determine the abundance of hypogeous fungi in these Yukon forests is also needed. Specific diet data for the dominant mammal species could also add an important dimension to our understanding of the role of mushrooms in boreal forest food webs. A quantitative model could be a useful addition to our methods for monitoring the impacts of climate change on fungal fruiting patterns (Gange et al. 2007).

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