Cycles in the Forest: Mammals, Mushrooms, Mycophagy, Mycoses and Mycorrhizae

by Gary A. Laursen, Dr. Rodney D. Seppelt, and Maggie Hallam

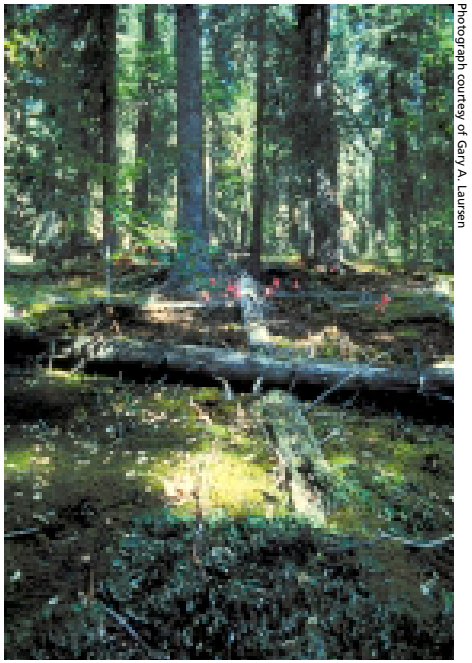

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Figure 1. Interior mixed deciduous/conifer boreal forest stand and small mammal habitat.

Figure 2. Left: Boreal forest landscape mosaic with underlain permafrost.

Photograph courtesy of Gary A. Laursen

Cycles in the Forest

Cyclic interactions are omnipresent in natural ecosystems. In the northern boreal forests like those found in Denali National Park, such interactions involving the smaller microtine and sciurid rodents are vital to the health and survival of the forest ecosystem. These small mycophagous (mushroom eating) mammals consume selected above and below ground mushrooms (gilled agarics, false and true truffles) and distribute the fungal spores through their droppings along prescribed runways. Squirrels utilize spruce trees to dry and preserve these fungi aerially and then make storage caches in old nest sites hollowed out of "witch's brooms," the tangle of small branches and twigs that result from rust fungus infections (mycoses) of tree crowns. Extensive spruce stands could not exist in Alaska's northern boreal forests if it were not for symbiotic mycorrhizal associations with above and below ground fungi that are eaten and dispersed year round by the rodents. Ironically, similar fungi are responsible for the forests' demise and decomposition, which return vital nutrients to the relatively poor soils. (Glossary at end of article with select terms included)

Introduction

Alaska's far northern interior boreal and taiga deciduous broadleaf and conifer forests *(Figure 1)* present a mosaic landscape with discontinuous permafrost *(Figure 2)*. These forested landscapes, such as those seen in Denali National Park and Preserve, support a host of animal, plant, and fungal inhabitants and their associated biological interactions *(Laursen et al. 2001, 2002)*. Forest growth, propagation, regeneration, disease, death, and decomposition are continual processes, and each is important to different components of the total forest cycle.

Both biotic and abiotic factors play a significant role in determining the interaction between components of the ecosystem. Such interactions may have positive or negative influences on the landscape. These complex interactions, or "cycles in the forest," result in the development of complex ecological communities *(Figure 3)*.

Abiotic influences on the forest ecosystem include drying or desiccation, frost, freeze-thaw action, lightning strike, fire, and flood.

Extensive spruce stands could not exist in Alaska's northern boreal forests if it were not for symbiotic mycorrhizal associations with above and below ground fungi that are eaten and dispersed year round by the rodents.

Biotic influences include the building of squirrel and bird dwellings; bark stripping by woodchuck, bear, and porcupine; and browsing by hare and moose. Less obvious biotic influences include the interactions between heart and root rot fungi, broom rusts *(Figure 4)*, and other fungi that cause blights, cankers, casts, crooks, galls, and the "diamond-formations" that are found in some diamond willows. A multitude of insects also invade forest canopies, laying eggs, causing galls and minor lesions, drilling into the damaged stems, and ejecting a form of fecal "sawdust" (frass). Insects forage on young plant parts and carve extensive galleries under the bark where they lay eggs and deposit yeasts and other fungi. These fungi may also subsequently invade host plants, altering

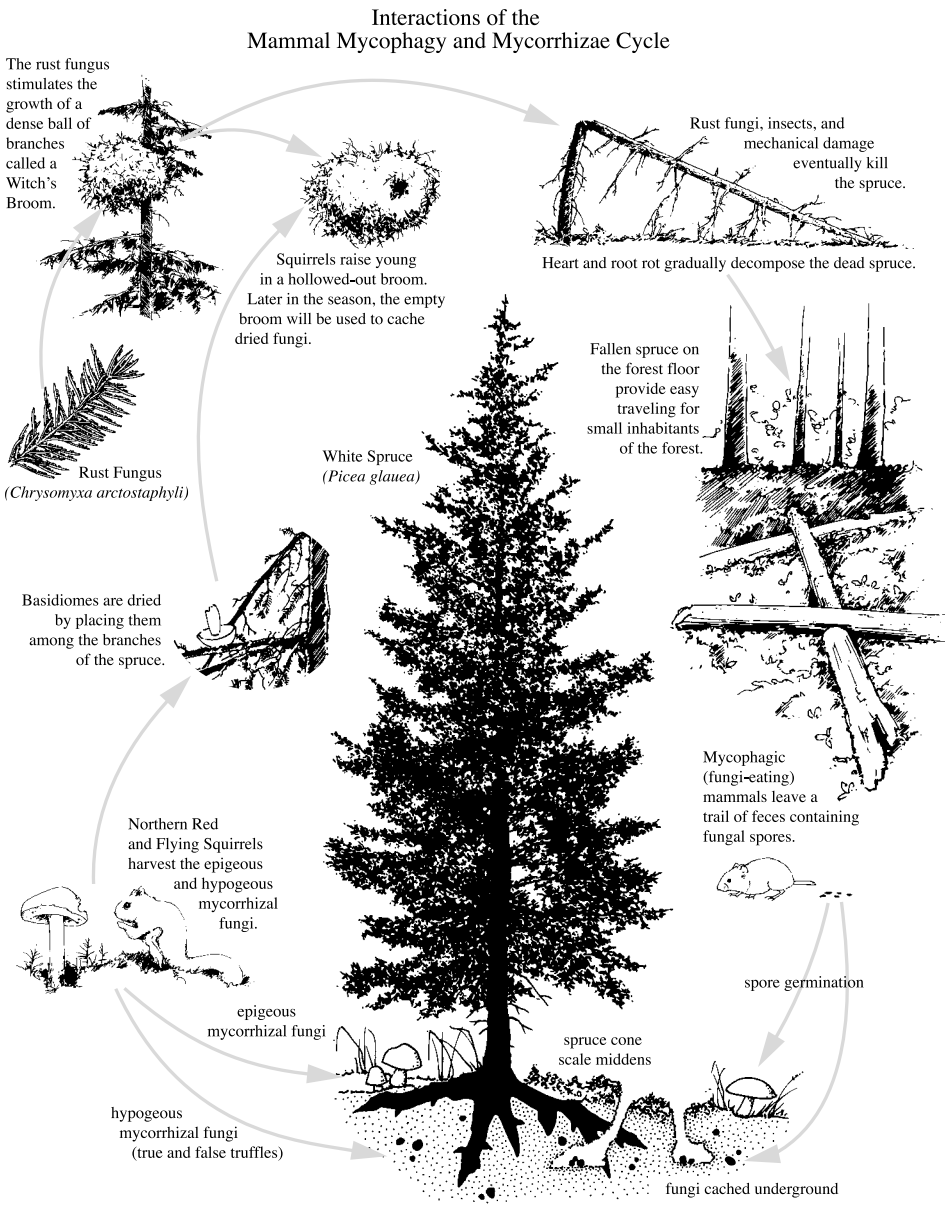


Figure 3. Mammals, mushrooms, mycophagy, mycoses and mycorrhizae boreal forest cycle.

Photograph courtesy of Gary A. Laursen

Squirrels utilize spruce trees to dry and preserve these fungi aerially and then make storage caches in old nest sites hollowed out of "witch's brooms", the tangle of small branches and twigs that result from rust fungus infections (mycoses) of tree crowns.

Figure 4. *Chrysomyxa arctostaphyli* broom rust.

their morphology, inducing disease, and eventually contributing to their slow demise and decomposition. Plant parasites, such as mistletoes, also play a part in influencing these cyclic interactions in the high latitude forests.

Role of Small Mammals in the Forests

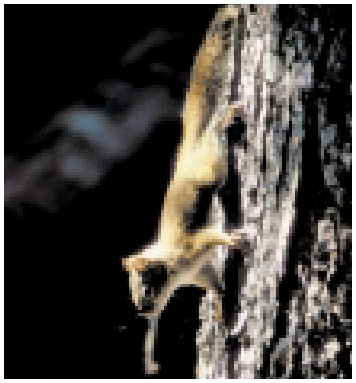
At least three mycophagous small mammals—the northern flying squirrel *(Glaucomys sabrinus, Figure 5)*, the red squirrel *(Tamiasciurus hudsonicus, Figure 6)*, and the redback vole *(Clethrionomys rutilus, Figure 7)* play important roles in the dynamic reshaping of arctic woodlands and forests. By their foraging, voles and squirrels, as well as moose and caribou, play vital roles in transporting and transferring microscopic spores of important ectomycorrhizal fungi, without which forests would die.

Importance of Fungi in Forests

In northern high latitude forests, white spruce *(Picea glauca var. albertiana)* and black spruce *(Picea mariana)* are important symbiotic hosts to numerous ascomycete (sac) and basidiomycete (club) fungi, both as above ground (epigeous) and below ground (hypogeous) ectomycorrhizal forms *(Treu et al. 1996)*. The fungal filaments or hyphae *(Figure 8)* have an intimate association with the outside of small roots of trees and greatly assist nutrient uptake into the roots of these host plants. The hyphae coalesce on the outside of the root to form a "mantle" of fungal tissue *(Figure 9)*. This is also true for boreal forest elements of the expansive temperate coastal rain forests of southeast Alaska *(Bruner et al. 2001)*.

Mycorrhizal fungi (myco = fungus; rhiza = root. Literally, root fungi) are essential to the survival of Alaska ecosystems. No tree species would exist in Alaska without this symbiotic or mutually beneficial relationship.

Healthy white spruce live in a mutually beneficial symbiosis with their mycorrhizal fungal partners. The hair-like fungal hyphae or mycelium surround the spruce root tips *(Figure 9)* and invade between cells inside roots *(Figure 10)*. The mycelial filaments are much finer than the roots and root hairs, and greatly increase the surface area available for absorption of nutrients and water



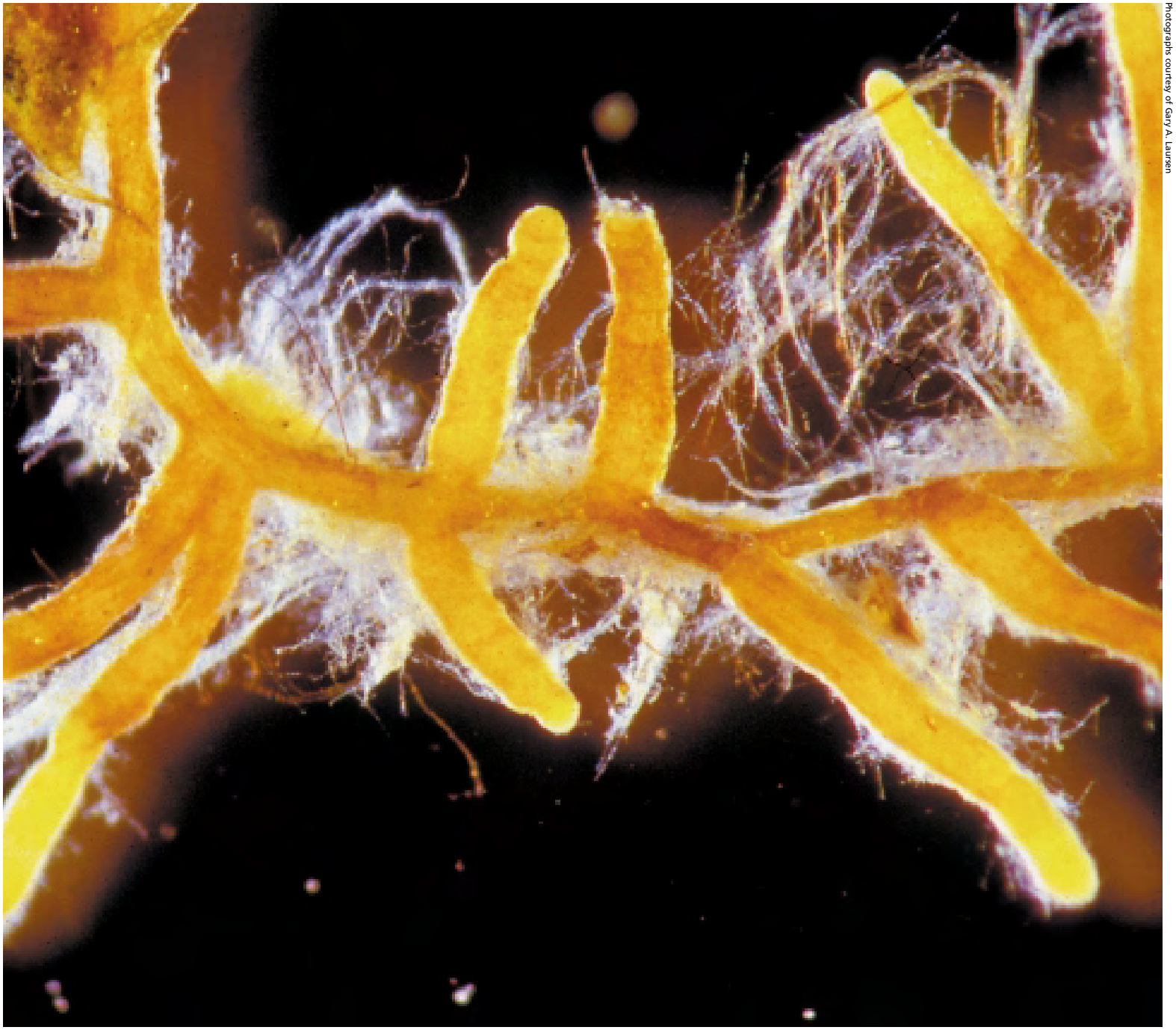


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Figure 5. Inset-top: *Glaucomys sabrinus,* the northern flying squirrel eating a truffle fungus.

Figure 6. Inset-middle: *Tamiasciurus hudsonicus,* the northern red squirrel.

Figure 7. Inset-bottom: *Clethrionomys rutilus,* the red-backed vole.

Figure 8. Right: Extended mantel hyphae of an ectomycorrhiza x100

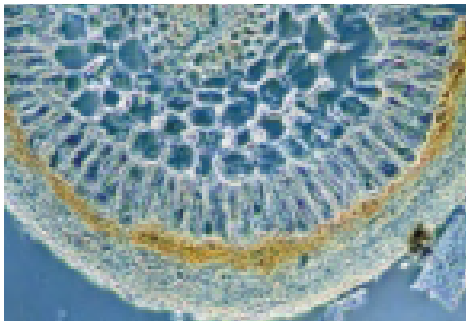


Figure 9. Ectomycorrhizal mantel hyphae, x400.

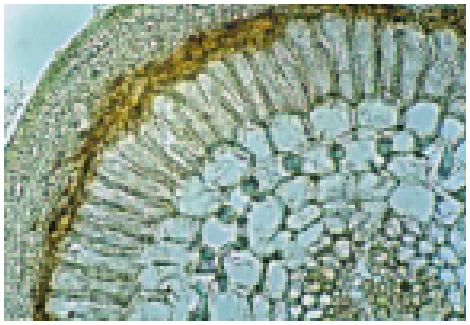


Figure 10. Mantel mycorrhiza and interior Hartig net between cortical cells, x1000.

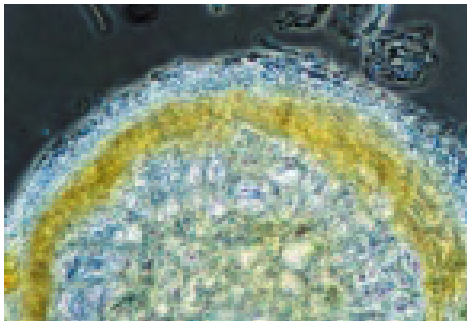


Figure 11. Ectomycorrhizal root xsect., x250.

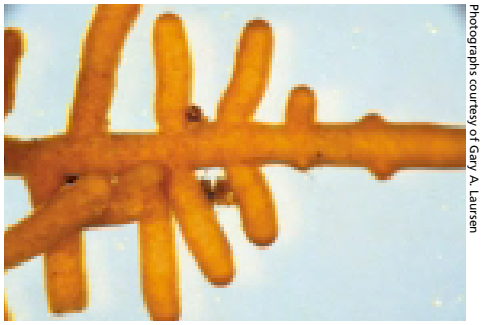


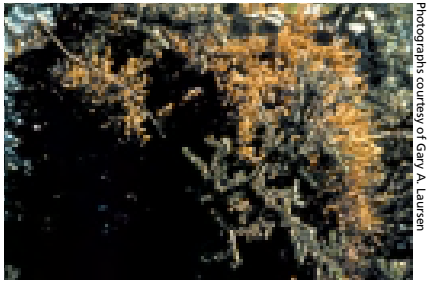
Figure 12. Birch root ectomycorrhizal with pinnate branching habit.

Photographs courtesy of Gary A. Laursen

from the nutrient poor soils. In addition, the glove-like covering of mycelium provides physical protection for the delicate root tips and also a barrier to the entry of soil microorganisms *(Figure 11)*. The mycelium produces antimicrobial compounds that deter competition from other fungi and microbes. In return, the spruce roots provide a supply of essential sugars and amino acids that are necessary for growth of the fungal mycelium and production of fungal fruiting bodies, the mushrooms.

It is possible that the present northern limit of spruce is at higher latitudes than would otherwise be possible because of the presence of mycorrhizal symbioses and, conversely, these fungi would not be present without their host trees. Even broad-leaved birches are not immune from this dependency *(Figure 12)*.

The diversity of these fungal-root associations provides a multitude of plants with a range of strategies for functioning efficiently under seemingly adverse conditions. It has been estimated that around 95% of all plant species characteristically form one of several types of mycorrhizal associations. Significant amounts of organic carbon may also be transferred between different plants through interconnecting fungal mycelia, thereby reducing competition for available resources and maintaining community diversity.



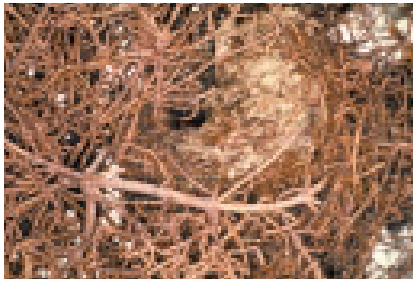


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Figure 13. Left: *Chrysomyxa arctostaphyli* broom at treetop.

Figure 14. Top-right: *Chrysomyxa arctostaphyli* broom with fruiting rust.

Figure 15. Bottom-right: Broom and potential nest/cache site with copious branching.

Parasitic Fungi— Where the Broom Rust Fits In

Parasitic fungi, and especially the spruce broom rust *(Chrysomyxa arctostaphyli, Figure 13)*, occur abundantly in the boreal forests of Interior Alaska, where the geographic ranges of spruce and kinnikinnick or mealberry *(Arctostaphylos uva-ursi var. uva-ursi)*, acting as an intermediate host in one stage of the life of the broom rust, coincide. Germinating rust spores on the spruce result in a perennial systemic infection on the host tree. The rust fungus produces auxins (plant growth hormones) that stimulate prolific branching on the spruce at the site of infection, causing the familiar "witch's broom" *(Figure 14)*. Other parts of the host tree continue to grow normally. Fruiting of the rust fungus occurs on the needles of the witch's broom, causing the telltale rusty-orange coloration. In the fall, needles of infected branches are shed and the broom then appears as a mass of dead twigs *(Figure 15)*.

Northern flying squirrels and red squirrels take advantage of these dense and often massive branch clumps. Squirrels hollow out brooms, construct nest sites *(Fig. 16 a & b.)*, raise their young, and then cache dried epigeous and hypogeous fungal fruit bodies *(Figs. 17a & b.)* in these old nest sites that serve as winter food larders *(Phillips 1998)*.

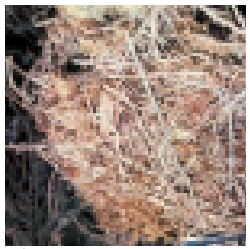
Left behind by these sciurid and microtine rodents and insects are feces and frass that contain viable but dormant fungal spores. During the following spring,

spores germinate and produce new hyphal growth that becomes associated with the rootlets of young plants, once again creating the beneficial mycorrhizal associations. Each summer and fall a new crop of fungal fruiting bodies appear, ready to be harvested by the mycophagous mammals and insects that are attracted to the nutrient rich spores.

Closing the Cycle

So it is that the forest cycle begins anew. Seedling establishment requires the development of a mycorrhizal association for the efficient extraction of moisture and soil nutrients. The fungal root mantle provides a protective physical barrier and microbial defense mechanism for the young and tender roots in a soil that will become, if not already, nutrient poor, yet able to sustain tree growth for 150 to 250 years or more. Soil and litter buildup ensures sufficient organic detritus to harbor the many non-mycorrhizal fungi that break down organic matter and release the otherwise bound nutrients to the soil. The litter also provides shelter for small mammals and insects and a suitable bed for future fruitings of mycorrhizal species of fungi.

Fungi that are harvested, dried, and



16a

16b

17a

17b

Photographs courtesy of Gary A. Laursen

18a

Figure 16a. Flying squirrel nest and cache site.

Figure 16b. Flying squirrel nest opening.

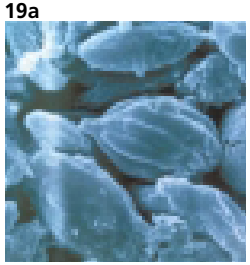
Figure 17a. Drying agarics (gilled mushroom) next to a flying squirrel.

Figure 17b. Drying *Lactarius* sp.

Figure 18a. Cone scale middens with surrounding *Hylocomium spendens* mosses.

18b

19a



19b

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Figure 18b. Cone scale middens with diggings for hypogeous truffle fungi.

Figure 19a. Fecal *Glomus* spores.

Figure 19b. Fecal *Elaphomyces muricatus, Gauteria* sp. and *Hysterangium separabile* spores.

Figure 20a. *Alpova diplophloeus* basidiome (fruitbody).

Figure 20b. *Gauteria otthii* basidiome (fruitbody-field).

stored in the tangled masses of branches of the witch's brooms are consumed throughout the winter months. The spores, after passing through the animals and being deposited in dung, will, in their turn, germinate and grow. Witch's brooms and cone scale middens *(Figure 18)* provide both nesting sites and caches for copious reserves of dried fungal fruiting bodies eaten during the long winter months. Fungal spores pass through the animals and are shed in the dung pellets where they are effectively wrapped in protective nutrient rich packets. As with some flowering plant seeds, passage through an animal not only disperses the seed (or fungal spores in this case), but the digestive chemicals of the animal also prepare the seed (or spore) for germination after defecation *(Figure 19)*. Squirrels also search in middens for hypogeous false truffle fungi *(Figure 20)* and true truffle fungi *(Figure 21)*.

With age, healthy trees gradually become stressed and, over a period of time, prone to increased attack from insect and fungal infections. With death, the trunks and branches are returned to the debris-choked forest floor to join a host of invertebrate animals and decomposer fungi, which slowly break down the plant cellulose and lignin by mechanical and chemical means, thus releasing nutrients to again be recycled into the ecosystem.

Fallen trees play a significant role on the debris-strewn forest floor by providing convenient raised walkways or highways for travel by smaller animals *(Figure 1)*. These animals, in their turn, deposit spore-laden feces on the logs and upon the forest floor debris. Flying squirrels are particularly important because they disperse mycorrhizal and other fungal spores in their dung pellets in the form of "nutrient pills"—rich in yeasts, nitrogen-fixing bacteria, and the vital nutrients necessary for germination, early growth, and establishment.

Waves of decomposer fungi, in a multitude of different shapes, sizes, and forms, soon become residents in the forest. Examples are the agarics (gilled), polypores (bracket and shelf fungi), tooth fungi, chanterelles, coral fungi, puffballs, and cup fungi. The above ground forms, such as the agarics *Amanita, Cortinarius, Lactarius, Pholiota*, and *Russula*, the boletes such as *Boletus, Fuscobolitinus, Leccinum*, and *Suillus*, and tooth fungi, such as *Hydnum* and *Sarcodon* species, are particularly abundant and striking on the forest floor. These above ground forms are accompanied by their below ground cousins such as the false truffles *Alpova (Figure 20a), Gauteria (Figures 20b)*, and *Hysterangium (Figures 20c and 20d)*, and the true truffle, *Elaphomyces (Figure 21)* and *Geopora* species. Their fruit bodies are harvested, dried, cached, and used for winter food by small mammals.

Conclusion

This complex cyclical biological system is dynamically balanced. Any change in the physical environment will be reflected in the biotic components of the ecosystem. Under the influence of global climate warming, hypothesized increases in microbial activity can only increase concerns for altering the arctic and subarctic carbon pool and contribute to an increase in the emission of greenhouse gases. Climate

warming trends are having adverse effects by increasing plant stress through desiccation. Of concern is the possible decline or demise of the northern boreal spruce forest in the next 50 to 100 years, and what might replace these forests. Any changes in the forest structure will impact the ecosystem at all levels—the large megafauna, small mammals, invertebrates, microbes, trees, shrubs, herbs, bryophytes, lichens, and even microscopic soil algae.

Continued integrated research will assist in comprehending the effects of altering one aspect of these biotic cycles in the ecosystem.

Figure 20d. *Hysterangium separabile* fruitbodies.

Photographs courtesy of Gary A. Laursen

Figure 20c. *Glaucomys sabrinus* with *Hysterangium separabile* fruitbody.

Figure 21. *Elaphomyces muricatus* cleistothecium (fruitbody), a true truffle with roots.

Glossary

abiotic — pertaining to non-living conditions.
biotic — pertaining to life or specific life conditions.
boreal — northern.
ectomycorrhizal—describes when fungi associated with plant roots are external, not within the cell structure of the plant root.
hyphae — vegetative threadlike filaments, which form the mycelium and fruitbody of a fungus.
microtine — small rodents consisting of the lemmings, voles, and mice.
mushrooms — fruiting bodies of fungi that support sexual reproduction.
mycelium — the vegetative part of a fungus, consisting of a mass of branching filaments called hyphae.
mycophagous — mushroom eating.
mycorrhizal — the symbiotic association between fungal mycelium and plant roots.
mycoses — fungus infections.
sciurid — mid-sized rodents consisting of the squirrels.
taiga — intermediate zone between the boreal forest and tundra.

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