Be It Ever So Humble, There's No Place Like Dung

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Although many people shun dung as a subject fit for study, it is a marvelous resource that is constantly being produced and deposited in large quantities at convenient locations. Even though it has passed through an animal's digestive tract, dung retains many nutrients. Thus, it attracts its own fauna and flora consisting of bacteria, fungi, protozoa, platyhelminths, nematodes, annelids, and arthropods. Coprophilous (dung-loving) fungi are uniquely adapted to herbivore dung. They are deposited with dung, and they grow and reproduce there. They disperse their spores from the heap to a location from which they will be consumed by a herbivore, pass through its gut, and again be deposited with the dung heap.

Dung as a Home

Dung consists of the macerated and undigested remains of plant food plus vast quantities of bacteria (mostly dead) as well as animal waste products, such as broken-down red blood cells and bile pigments. The nature of herbivore dung depends on the efficiency of the digestive tract, which, in turn, depends on the animal's digestive anatomy and its microflora. Ruminants produce fine-textured dung of fibrous plant material whereas horses, with a less efficient system, produce much coarser dung. Dung decomposes rapidly because the macerated material has a high nitrogen content, available aeration, and a high water content that is protected from fluctuations.

Although there is little available protein in dung, many other undigested food components are present. Dung is rich in water-soluble vitamins, growth factors, and mineral ions, some of which are metabolic by-products of the microbes in a herbivore's gut. For example, coprogen, an organo-iron compound found in dung, is necessary for the growth and reproduction of the fungus Pilobolus crystallinus. Dung also contains a large amount of readily available carbohydrates.

Fungal Dung Inhabitants

Considering the great variation in the feeding habits, habitats, and digestive systems of herbivores, it is surprising how universal coprophilous fungi are. All classes of the Kingdom Fungi are found on dung, with the Zygomycetes usually appearing first, followed by the Ascomycetes, and finally the Basidiomycetes. Their distribution is influenced locally by the number of herbivores in an area. Some species are restricted to a particular herbivore; for example, Lasiobolus Cainii is found only on porcupine dung. However, many coprophilous fungi grow indiscriminately on any herbivore dung. The greatest variety of fungi have been reported on cow, rabbit, and horse dung, but this could be because the majority of research has focused on these animals.

Adaptations of Fungi to Dung

Coprophilous fungi are highly specialized for growth on dung, and some never occur elsewhere. While some dung fungi show few modifications peculiar to their habitat, most do have some unique features. Many exhibit some very specialized structures to ensure survival in their unique habitat.

Herbivores do not graze near their own dung; therefore, the spores must be propelled beyond this "zone of repugnance." Thus, the spores or spore masses are relatively large and heavy. In the Zygomycete Pilobolus, for instance, the entire sporangium is discharged as a unit. In the bird's nest fungus, Cyathus stercoreus, the peridioles (the "eggs") containing many spores are violently discharged when a raindrop hits the peridium (the "nest"). The spores/masses,
because of their weight, do not remain in the air long, but follow a parabolic trajectory landing on nearby grass without the aid of air currents. The sporangium and sporangiophore of Pilobolus measure about 0.5-1.0 cm, yet the sporangium has been propelled as much as 1.8 m vertically and 2.1 m horizontally.

Some coprophilous fungi exhibit a phototropic response that determines the direction the spore mass will be projected and ensures that the spores clear the substrate. Spore discharge is always during the day. The entire sporangium of Pilobolus, for example, grows toward the light source. To demonstrate this phototropic response, place the mature culture of Pilobolus inside a container with a hole punched into one side of the container top. Wrap the container inside aluminum foil and punch another hole in the foil aligned over the container hole. Place transparent tape over the hole, and set the container in a window. The following day, remove the foil and container. The majority of the ejected sporangia will be found stuck to the tape or around the light source in the container top.

The spores are dark to protect them from ultraviolet light until they are consumed by a herbivore. In some fungi, melanin is present in the spore walls; in others, a dark membrane covers the spore mass. Coprinus comatus, a mushroom that fruits on dung, exhibits these dark spores.

The spores/mass are often mucilagenous so that they stick to vegetation upon impact, and the mucilage, when dry, cements firmly. In Cyathus, the peridiole has a sticky piece of hypha, the funiculus, which attaches to vegetation upon impact and wraps the peridiole firmly around it. Other coprophilous fungi, such as Mucor hiemalis, form a sticky droplet around their spores. When an insect visits the dung, the spores stick to the insect's body. If the insect rests again on other vegetation or another dung heap, the spores rub off and adhere to the new environment. Many of the coprophilous fungal spores will not germinate until after passing through an herbivore's digestive tract: They must be heated inside the gut, digested by the gut enzymes and/or bacteria, or stimulated by the higher pH of dung.

**Fungal Dung Succession**

Some observers have noted a true ecological succession on dung in that first the Zygomycetes, then the Ascomycetes, and finally the Basidiomycetes appear. Early researchers suggested that this succession was a nutritional one. They postulated that the Zygomycetes, or sugar fungi, appear first, because their spores germinate quickly and their mycelium grows rapidly, exploiting the fresh substrate; that is, they utilize the simple sugars and hemicelluloses present in dung. The Zygomycetes are not capable of utilizing the cellulose and lignin found in dung. When the simpler carbon sources are metabolized, the Zygomycetes disappear and are replaced by the Ascomycetes, which can utilize cellulose. These are then replaced by the Basidiomycetes, which can utilize both the cellulose and the lignin.

Although this nutritional hypothesis of dung succession was an attractive one that seemed to fit the observations, it ignored some important ecological and physiological facts. For example, some spores had already germinated or had their dormancy broken in the herbivore gut. Also, no scientist had yet considered the interference/competition/enhancement effects of the various dung inhabitants on each other.

The nutritional hypothesis was based solely on the order of appearance of fruiting structures. Mycelial development and growth may not have been proceeding at the same rate, so a second hypothesis, the reproduction hypothesis of dung succession, was developed. This hypothesis was based on the time it takes each kind of fungus to fruit. The simple sporangia of the Zygomycetes could develop much more quickly and require much less energy than the more
complex Ascomycete fruiting body. The even larger Basidiomycete fruitification would require
the largest amount of energy expenditure and would, therefore, take the longest amount of time to
appear. This hypothesis still neglects the interrelationships between fungi themselves and
between fungi and other dung inhabitants.

The dung heap is not inhabited exclusively by fungi. As mentioned previously, vast
populations of bacteria, protozoa, platyhelminths, nematodes, annelids, and arthropods coexist
with the fungi. These compete for resources, and some parasitize or consume the fungi while
others provide substrates for them. Also, these organisms can deplete the dung of nutritionally
necessary compounds, such as nitrogenous ones, and can produce waste products that enhance or
retard the growth and reproduction of some fungi. For instance, ammonia, a waste product of the
bacterial degradation of proteins, stimulates sporangial production of Pilobolus, which grows
better in the presence of other microbes.

Coprophilous bacteria enhance the growth of some of the coprophilous fungi, but retard
the growth of others. Also, the number of fly larvae, Lycoriella mali (Diptera: Sciaridae) that
survive to pupate increases as fungal competition increases. It could be that as fungal growth is
inhibited, more resources are available to the fly larvae, or that larvae may be favored by the
enzymes produced by fungi to inhibit other fungi!

There is evidence that some fungi excrete products that inhibit fungal competitors. A few
weeks after dung is deposited, the Zygomycetes and Ascomycetes disappear, but the
Basidiomycetes continue fruiting for months. Obviously, the substrate has not been depleted.
Some Basidiomycetes suppress some of the Zygomycetes and Ascomycetes by hyphal
interference. Within minutes of contact, the sensitive species’ hyphae undergo vacuolization and
lose turgor. This is followed by a drastic alteration of cell membrane permeability and subsequent
death of the hyphae.

In the classroom, dung succession is easy to observe and is sure to promote the interest of
students. Fresh or weathered dung can be placed in empty containers. If the dung is dry, add a
small amount of distilled water. Plastic wrap secured with a rubber band will allow observation
and prevent evaporation of the necessary moisture. The dung culture should be observed over a
period of three to four weeks to study fungal succession.

The success of coprophilous fungi, as measured by their ability to produce and maintain a
fruiting body, is not simply a matter of competing against other fungi. Instead, it is a complex
web of interactions, some combative, some inhibitive, some mutually or exclusively beneficial
between and among the bacteria, fungi, protozoans, platyhelminths, nematodes, annelids, and
arthropods. It's a jungle in there!

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