The Austere *Tomentella*

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Many fungi form mutualistic partnerships with specific plants, called ectomycorrhizal relationships. 'Ecto' means that the relationship takes place outside the root (i.e. the fungal strands cover the root tips but do not penetrate root tissue), 'myco' refers to the fungal partner and 'rhiza' refers to the root of the plant partner, usually a tree. Figure 1 shows an example of root tips covered with fungal 'mantles'. The commonest ectomycorrhizal fungi we encounter in our woods are the boletes, russulas, lactariuses, entolomas and cortinariuses. In 2008 we had Urmas Kõljalg, a keen student of Genus *Tomentella*, as one of the faculty at our foray. He told us that when root tips are analyzed, it turns out that Genus *Tomentella* is the most plentiful colonizer, more abundant at the root tips than the big five combined [1].

Figure 1. Root tips of larch (*Larix laricinus*) dramatically covered by thick white mantles of mycelial tissue. Fungus species not determined in this case. (Photo: Roger Smith)

Tomentella? What is this genus that has slipped completely under our radar screen to gain such prominence in our woods? How can something that common and successful elude the attention of even most dedicated mycophiles? Surely the *Tomentella* story served as model for Horatio Alger: an unassuming little genus looks diligently for the better way and is crowned with success beyond its wildest dreams, but remaining true to its humble origins, eschews ostentation and demonstrative flamboyance of success.

To understand this, let us first look at mushrooms as we know them. A mushroom is the fruiting body of a fungus; its job is to make spores and ensure their effective spread. Consider the stately *Russula paludosa*, shown in Figure 2. It spreads its spores by the aid of gravity and wind. Therefore it has to raise the spore-bearing surface (the hymenium) above the ground cover. For this it creates a sturdy stem to raise and support the hymenium and cap structures. Gravity causes the spores to fall from the raised hymenium, and on their way down they are wafted away by wind currents. The cap needs strength to keep the hymenium away from the stem

Figure 2. *Russula paludosa*, a very common, stately and tasty ectomycorrhizal mushroom in Newfoundland and Labrador.

and substance to protect it, including a tough skin to shed the falling rain and ward off falling debris. Because propagation by sporulation is inefficient, myriads of spores have to be released. Even though they are small in size, a very large surface area is required to make the required amount of spores. However, the mechanics of the structure is such that the area the stem and cap can support has very real limits. Thus, in order to increase hymenial surface area without increasing total structure size proportionately, our *Russula* makes gills under the cap to bear the hymenium. This formal structure (the gills, in this case, covered with the sporulating surface) created to increase the surface area of the hymenium, is the hymenophore, and the entire structure, the mushroom or fruiting body, is the sporocarp.

Quick calculations on the back of a napkin show how effective our russula's efforts are. Let us assume that the cap Diameter is 8 cm and that of the stem is 2 cm. The footprint Area left for sporulation under the cap is (Area of cap) - (Area taken up by stem). Using Area = π times the Radius squared, A = πr^2, footprint Area for sporulation is [π x 16cm^2] – [π x 1cm^2] = 47 cm^2. Now, suppose we insert 5 radial gills for every cm of Circumference. The cap Circumference is Diameter x π = 8 cm x π = 25 cm. This will accommodate 125 gills. Let us assume an average gill height of 1 cm. Gill length is Radius of cap minus Radius of stem = 4cm – 1 cm = 3 cm. Thus Area of each gill side is 1 cm x 3 cm = 3 cm^2. Each gill has 2 sides, so the area per gill is 6 cm^2. Total gill Area is 125 x 6 cm^2 = 750 cm^2. Thus, gills increase the surface area more than 15 times the available footprint.

Seems very efficient, does it not? However, consider the energy cost involved. Imagine how much energy the organism must expend to create such magnificent sporocarps. And think of the energy required to create such a precisely engineered hymenophore. We, of course, know that this requires energy, because we pick these mushrooms and eat them, thus assimilating their stored energy for our own purposes. In fact, it has been well demonstrated that mushrooms have made significant dietary contributions to many cultures and have facilitated survival during times of famine[2]. So, our *Russula* spends a lot of energy to build a fruiting body to spread its spores.

There must be a better way.

Enter the lowly *Tomentella* (Figure 3). As you see, it is a thin layer of fungal tissue, spread flat on rotten wood. This habitus is called corticate, which means like a covering, or resupinate, which means upside down, in this case indicating that the "back" of the sporocarp is fastened to the supporting structure, exposing the sporulating surface in "front". Many saprophytic organisms have a similar habitus, spread over the wood they are rotting. *Tomentella* does not rot wood but merely uses it for rigidity or substance for its hymenium. It is just as happy to use leaves, grass, hay or any organic matter on which a few layers of cells can be plastered. The entire sporocarp is only a few cell layers deep. The gray surface is the hymenium, one cell layer thick. It does not quite reach the edges, which is why this sterile margin is a different colour, that of the underlying cell layers. There is no stately sporocarp and no formal sporulating structure or hymenophore.

Figure 3. *Tomentella botyroides* from Central Newfoundland. Note the resupinate habitus (plastered onto rotten wood, sporulating side outwards), total lack of stem or cap structure and lack of any significant hymenophore (structure to aid in spore dispersal). Any shape it has is derived from the supporting material. Compared to the *Russula* of Figure 1, tomentella's plain looks are inescapable. (Photo: Roger Smith)

Consider the matter of sporulating surface area some more. The sporocarp in Figure 3 (broken in two parts) has an approximate footprint area of 24 cm^2; indeed, although they can extend over quite an area, 20-50 cm^2 is a reasonable average surface area for most tomentellas. Even if one were to quadruple the effective sporulating area due to the irregularity of the underlying structure and granularity of the heaped-up hymenium, the average sporocarp would have about 100 cm^2 of hymenium for spore dispersal. This is approximately one-half the fertile surface of one of the smaller of common mycorrhizal mushrooms from the big gerera familiar to us, *Cortinarius acutus*, shown in Figure 4. *Cortinarius* sporocarps are much more common in our woods than *Tomentella* sporocarps, even were one to seek out the latter specifically. The number of *Cortinarius* species in our woods exceeds several hundred, while the total number of *Tomentella* species is probably less than 25. Yet, when it comes to the root tip, where the rubber meets the road for ectomycorrhizal mushrooms, *Tomentella* has *Cortinarius* beat hands down! How is this possible? Of course, we do not know. However, one can't help but wonder if the energy that *Tomentella* saves by not building a structure for sporulation becomes available to surpass its rivals in colonizing the root tip.

Four secrets of *Tomentella*:

1. *Tomentella* does not expend energy to create a stately sporocarp. Just a sporulating surface with a minimal support layer to attach it to other structures is enough. It utilizes the static energy stored in other structures for its shape. It does not use gravity and wind for spore dispersal, but leaves that to various invertebrate vectors.

The spores, just like those of *Russula*, which also uses some insects for additional spore dispersal, have sharp projections to stick to the crevasses, fur or slime of invertebrates. The spores also have a thick wall to withstand a trip through invertebrate digestive tracts.

2. *Tomentella* does not expend energy to erect a complicated hymenophore. There is no need, really. If it wants more surface area for increased spore production, all it has to do is spread a bit further. Since it is not responsible for holding up its own hymenium, there is no need to worry about efficient use of surface area.
3. *Tomentella* gains additional advantages by using earthbound organic matter for support, especially rotten logs. These can store considerable moisture to moderate the effect of dry periods, thus reducing the number of dormant periods and saving the energy of a new start-up.
4. *Tomentella*, if it does dry up, has the ability to survive dry periods and revive with the next wet spell, saving the energy required to create a new sporocarp each time it dried.

Figure 4. *Cortinarius acutus*. These small, pretty and common mycorrhizal mushrooms are more common than tomentellas and have at least twice the sporulating surface per sporocarp than an average Tomentella. Yet at the root tip, tomentella mantles are more abundant than those of all cortinariuses combined.

This is the story of *Tomentella*: keep a low profile; live an austere, humble and ascetic life; avoid show and ostentation; do not turn up your nose at decay, but seek it out for an abode and turn it to your advantage; do not squander energy but reuse, renew and recycle; and focus all your energies only on your goal. A specific lesson, topical in view of the current housing, banking and economic crisis: avoid debt for a mansion you can ill afford and you will outcompete your peers. A heroic tale: imagine a Verdi opera 'Tomentella!' on the subject, with lofty tunes and noble characters. If you like to get better acquainted with this genus, see the monograph by Kõljalg [3].

Acknowledgment:

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References

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