# Which way is Up?

## Mushroom Gravitropism

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*The images of* Ganoderma applanatum *were provided by Patrice Benson who passed away suddenly a few months ago. She is sorely missed by so many in the mycological community.*

Figure 1a.

Once a mushroom is cut or picked, it's dead right? Wrong! A number of things tell you that the cells making up the picked mushrooms in your basket or refrigerator are still very much alive. They may continue to "drop" spores for a few days after being picked. (Spore release is actually a very active process—as the name for it, ballistospory, implies—requiring living cells.) Some mushrooms, for example Amanitas, may continue to elongate and bend upwards, away from the surface upon which they are placed. This, of course, ensures the cap is up in the air column so that discharged spores may be carried away on the air currents. Furthermore, the gills (or tubes in boletes and polypores) must be exactly vertical or spores will not drop free of the cap.

A growth response to gravity is called gravitropism (sometimes, geotropism). I recall first noting this as an undergrad studying under the mycologist Sam Mazzer at Kent State University. (Ironically, it was at the same time that I was taking a plant physiology course with Professor Rollo dela Fuente, one of the co-discoverers of phototropism in plants. Phototropism is the process that causes plants to bend toward sunlight, thus more efficiently collecting the sun's energy on the surfaces of leaves.) I had made a nice collection of *Amanita muscaria* and brought the specimens into the lab for all to enjoy. The following day I returned to the table where I had left my mushrooms and was surprised to find them—no longer pencil-straight. During the night they had continued to "grow." Or so I thought. The stems had become curved with the mushroom caps no longer resting on the table, instead resuming a position above and horizontal to the surface.

The phenomenon of negative gravitropism, wherein the mushroom stem is moving away from the source of gravity, so to say, is to ensure the mushroom cap will be in the air column so that the spores may be carried away. (See Figure 1; Fig.1a is of *Pleurotus dryinus* on a tree; Fig. 1b is of a shiitake growing on a log.) The mushroom's hymenophore (be they gills of agarics, tubes of boletes and polypores, or teeth in hydnoid forms) hang down from the cap, indeed they *grow* perpendicular to the cap, exhibiting positive gravitropism. The cap itself is an ingenious structure, for it protects the hymenium of Basidiomycetes from rainfall; any moisture would disable the spore discharge mechanism of Basidiomycetes.

Figure 1b.

Figure 3a.

Figure 3b.

If the cap is repositioned to anything but perfectly horizontal, the hymenophore will continue to elongate and bend so that they will again be vertical. (See two Amanita species in Figure 2.)

Bracket fungi probably are more correctly termed gravimorphogenic, rather than gravitropic, as the entire bracket does not bend or reshape. If repositioned other than perfectly horizontal (as when a standing tree with brackets falls down) a new bracket is formed horizontal to the surface. (See views of *Ganoderma* in Figure 3.)

In the case of gilled mushrooms, both the positive and negative geotropism exhibited by the gills and stem, respectively, ensures that the spores will be ejected from the hymenium (the surface of the gills), then fall straight down without landing on an adjacent gill (see Figure 4, an illustration from A.H.R. Buller, 1909.) Probably all mushrooms demonstrate this while intact. Amanitas demonstrate this beautifully even after being picked or cut (most other mushrooms will wither or dry soon after cutting and don't show this as dramatically). *The Mushroom Handbook* by Louis Krieger (1936) is the only book I know of that points out this habit of Amanitas (Figure 5). If you are involved with setting up wild mushroom displays, you would be wise to store all Amanita specimens fully upright, lest they become bent and distorted from their natural shape found in the wild.

Figure 2a.

Figure 2b.

Figure 3c.

How do mushrooms grow "up?" As mentioned earlier, plants bend towards a light source by a process called phototropism. In a sense, fungal gravitropism is by a somewhat similar process. In plants, the side of the plant stem receiving the strongest light sends a plant hormone signal (auxin)

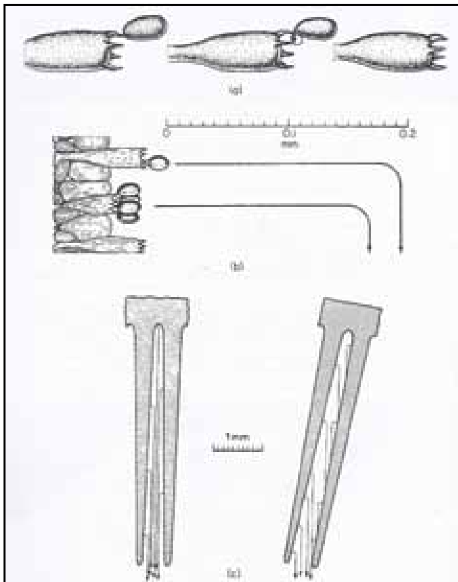

Figure 4.

to the “darker” side of the stem, and this induces a physiological change in the cell walls there. Cells on the dark side of the stem release enzymes called expansins that partially break down the cell walls of dark side cells, allowing those cells to be less rigid and to expand. Cells furthest away from the light source receive the strongest auxin signal and expand the most, thus impart a disproportionate elongation force, causing the plant to bend in the opposite direction. Bending towards the light, which is more efficiently captured by the upper leaf surfaces.

Fungal gravitropism was poorly known until recently (Moore, 1991). A number of experiments, some producing inconclusive results, have been published over the past 100 years

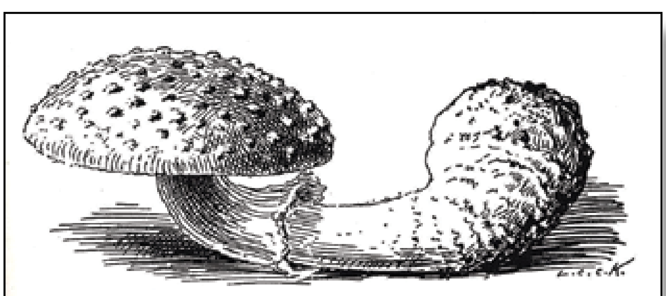

Figure 9 A specimen of *Amanita muscaria* that has lain in the horizontal position over night. Note the effect of gravity in causing the stem to bend so that the cap will again be horizontal

Figure 5.

using gravistat devices and centrifuges to negate gravity’s effects on mushroom formation, and to see the results. Mushroom cultures have even been taken into Earth’s orbit! In the 1970s, the Soviet Union’s unmanned Cosmos 690 was the first; Salyut-5 and Salyut-6 soon followed. Among the experiments aboard were those to test the effects of space, primarily zero gravity, on mushroom fruitbody formation (for a review see Moore, 1991). A decade ago Gruen (1991) performed careful grafting experiments on developing *Flammulina* basidiocarps to test the effects on gravitropism. In fruitbodies of *Flammulina velutipes* growing on sawdust the mushroom caps were removed and replaced with either caps, or caps with stem apices (and sometimes inverted stems) and it was found that the part of the mushroom most sensitive to gravity’s effects is the apex of the stem. Furthermore, the effects of the various grafts demonstrated “acropetal transport” of mycelial metabolites through living hyphae of the stem which induced the bending of the mushroom stems in response to gravity. Those metabolites—a signal of gravitational forces—have yet to be elucidated.

Monzer (1996, 1995) more recently proposed a more simple explanation for how gravitational sensing is accomplished in fungi. And that it’s very similar to the system of otolith organs (technically the utricle and saccule) of humans. Within all of us, deep inside our inner ear, there are organs that contain a liquid filled with tiny stone-like particles called otoliths or otoconia (they really are stony, essentially made of limestone and a protein) that rub against tiny hairs that line the inside of the otolith organ. Most of the time, the particles are uniformly settled telling us which way is down. If you are spun around or shaken like a snow globe, the particles move all about giving you a feeling of disorientation, even dizziness. And this, Monzer has concluded, is similar to how fungal cells sense gravity. Within hyphal cells, nuclei act as fungal otoliths; their sedimentation within the cells in response to the direction of the gravitational forces tells the fungal cells which way is up. The nuclei are enmeshed in proteinaceous actin filaments that make up the cell’s internal “skeleton” (the cytoskeleton). As these nuclei settle, they tug on actin filaments, which in turn tug on the cell walls at their points of attachment. This tension triggers cellular changes in response to gravity, and on the side of the cell feeling gravity’s force, microvesicles begin to fill and expand, vacuoles expand, and the entire process causes the expansion of hyphal cells. The net result is that the mushroom stem bends away from the gravitational sensation.

And finally, one more note. While it seems to be common knowledge that fungi have no need whatsoever for light, there are in fact many fungi that show a phototropic response. The zygomycete *Pilobolus* is well-known for “throwing” its “hats” in the direction of light and away from the dung upon which it grows. The common stalked polypore *Polyporus brumalis* will grow towards light. And shiitake mushroom (*Lentinula edodes*) growers know that this species will not form mushrooms at all in the absence of light. Furthermore, many other mushrooms will fail to form caps or produce malformed fruitbodies in the absence of light.

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