Elongation of fungal hyphae
[HyphalGrowth.doc]
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Understanding how hyphae grow in length will make it easier to understand how to interpret sporangial renewal types in watermolds. Hyphae exhibit apical growth (i.e. they grow at the tips only) by constant repetition of a cyclic process described and illustrated below.

1. **The cell wall at the hyphal apex must first be softened so that it can be stretched**: Initiation of this softening involves a cluster of enzyme-containing vesicles (visible only with the electron microscope) that accumulate at the hyphal tip. For fungi whose cell walls are made of chitin, the vesicles contain chitinase but for watermolds (whose cell walls are cellulose) the vesicles contain cellulase. The vesicles fuse with the plasma membrane such that they empty their enzyme contents into the space between the membrane and the wall. Subsequently, some of the wall is dissolved away (hydrolyzed) resulting in its becoming thinner than the wall further back from the apex.

2. **After the wall is softened, the cell absorbs water and elongates**: The pliable cell membrane thus presses outward against the cell wall and stretches the wall in the region where it is thinnest (the apex). The stretched wall will not burst from this force but the overall effect is that the hypha gets longer.

3. **The stretched wall at the hyphal apex is next rebuilt to its original thickness**: The rebuilding process if initiated by a second group of vesicles that aggregate at the apex just as did the first set. The ‘rebuilding’ vesicles, however contain monomers of the macromolecules that the wall is made of (e.g. for chitin cell walls, the monomers are n-acetyl-glucosamine). Fusion of the vesicles with the plasma membrane empties the monomers into the space between the membrane and stretched wall where they then polymerize to return the stretched wall to its original thickness.

4. **This entire process repeats itself continuously resulting is a steady increase in hyphal length**

Understanding this process should enable you to appreciate that the tip of a living hypha (where the elongation process occurs) is an indeterminant apex (IA). We use the term IA to reflect that a growing hyphal tip has the capacity to: grow longer almost indefinitely if it elects to remain vegetative **OR** bulge (following the wall-softening stage) to become an oogonium, sporangium, or gemma.

For those hyphal apices that elect to become sporangia, cytoplasm packs into the apex and then is trapped there by the formation of a septum that will become the base of the sporangium. After spore cleavage begins,
the fate of the hyphal tip is now sealed (*i.e.* it can become only a sporangium). Such a structure is said to be ‘determinant’ and the living tip (indeterminant apex) now is the region of the hypha just below the sporangial septum. This new IA can elect to grow upward (by the cyclic softening/stretching/rebuilding process) into the cavity of the empty sporangium (after the zoospores have been released) as occurs during the internal proliferation-type of secondary sporangial production, *OR* grow to the side as a sympodial branch.

As this relates to distinguishing between primary and secondary sporangia, ask yourself where the original determinant structure is located on a main hypha then follow the path that the new IA took as it continued its growth. In the case of a long chain of sympodially-renewed secondary sporangia, start looking backwards from the uppermost sporangium until you see the sporangium that is most basal and you will have found the primary sporangium. From that point, follow the sympodium back upwards (following the path it took as the new IA elongated) and locate the first-formed secondary sporangium, then further upward the second-formed secondary sporangium *etc.* to the very tip.

Basipetal sporangial renewal is best thought of as the IA below the empty primary sporangium having decided not to grow (although in some species it might grow out to the side for a short distance as if it were producing a sympodial branch), but rather to pack cytoplasm into itself then lay down a basal septum to delimit the secondary sporangium. The secondary sporangium thus will be located just below the primary sporangium in the very same hypha that produced the primary sporangium. If some growth to the side occurred before the secondary sporangium was delimited, the secondary sporangium would have some of its length within the original hypha and its upper portion sticking out to the side (possibly looking like an enlarged spore discharge tube).