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POLARITY OF ELONGATION GROWTH
GENERATED AND SUSTAINED
BY ANISOTROPIC DISTRIBUTION
OF THE PROTONS EJECTED FROM MITOCHONDRIA
INTO THE CYTOSOL OF HYPHAL APICES
(*NEUROSPORA* MODEL) ?

PAR

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ABSTRACT

The acropetal gradient of decreasing pH detected in hyphal apices might originate from a localized anisotropic distribution of the protons ejected around respiratory-active mitochondria, randomly and asymmetrically displaced below the thus determined site of germ tube emergence from fungal spores.

Using semi-vital staining with standard pH indicators, we have repeatedly observed a lower pH in the tips of elongating vegetative hyphae of a few Fungi (Turian, 1978a, b, 1979). Recently the staining of vegetative hyphae of *Neurospora crassa* with bromcresol purple struck us by the contrast observed between their yellowish amitochondrial tips (pH around 5.2) and the purple colour (pH around 6.0) of their elongated granules, corresponding to the mitochondria located in the subapical zone. With bromcresol green, mitochondria have been seen bluish-green (pH 5.8) by comparison with the pale green ultimate hyphal tips.

We were thus led to confront these observations with the predicted lower pH of the hyaloplasm around the mitochondria according to the chemiosmotic theory (Mitchell, 1977) based on proton ejection out of mitochondria through energy input of their respiratory electron chain. Since then, we have been comforted in such a correspondence by the experimental confirmation of such a pH differential (up to one unit) cytosol/mitochondria by Shulman et al. (1979). The idea then came to us that Mitchell's chemiosmotic theory implies what we decided to consider an

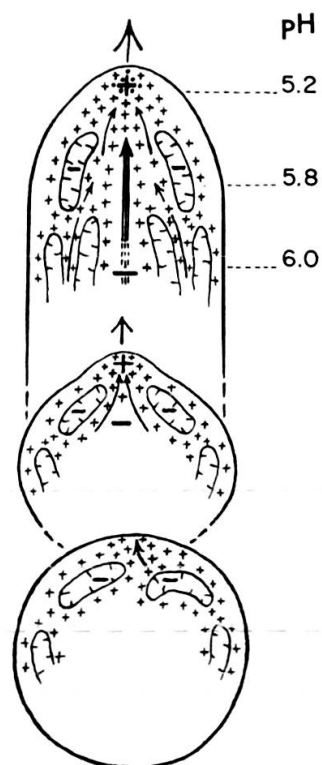
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isotropic situation, protons being predicted to be ejected in a symmetrical manner along *all* the axes of the mitochondrion into the surrounding hyaloplasm to determine the proton motive force for internal ATP synthesis following re-intrusion of protons. In our case, however, we are confronted with what could be viewed by contrast as an *anisotropic* situation. Indeed, and because of the localized accumulation of mitochondria forming a kind of frontier below the so-called exclusion, amitochondrial zone at the subapical limit (Turian, 1978), there is a possibility that part of the protons ejected from such frontier mitochondria can no longer be re-intruded (H^+ influx) into the mitochondria according to the now celebrated theory of the reversal synthesis of ATP from $ADP + P$. Such protons are thus anisotropically dissipated into the hyaloplasmic material and therefore create a positive polarization sink zone with lower pH (figure 1). The known acropetal cytoplasmic currents

FIG. 1. — Spanning diagram from germ tube inception to hyphal elongation in *Neurospora*.

- Swollen conidium: initial, random event of the asymmetric displacement of a peripheral mitochondrion creating a cytosolic sink zone for anisotropic distribution of ejected protons and presumed first local lowering of the pH.
- Germ tube emergence: self-entrained increased compartmentation between the more positive and acidic apical cytosol and the more negative and alkaline mitochondria excluded from the gelified tip.
- Elongating hypha: equilibrium between the gelified exclusion zone and subapical mitochondria. Acropetal cytoplasmic streaming continuously and anisotropically "washing off" protons toward the tip and its "Spitzenkörper" from the axially orientated front mitochondria.

pH averaged from semi-vital stainings with bromcresol purple and bromcresol green.



could well be a secondary motive force for acropetal dispersion of the acidifying protons into the hyaloplasmic tip. As to the origin of the separation of the electric charges and therefore pH differential, this could be sought for as an early event occurring in the relatively iso-organized content of the spore: the random momentary retreat during their limited, internal displacements of one or a few adjacent mitochondria from the proximity of the cytoplasmic membrane would create an asymmetrical distribution of respiratory-ejected protons (figure 1) which, on that « free side » (proton sink) of the mitochondria, would then escape to their normal secondary influx proposed in Mitchell's chemiosmotic theory. Such a transient, aleatory event

could be visualized as sufficient to initiate charge separation leading to cytosolic acidification. As low pH is known to favor cytoplasmic gelation (Condeelis & Taylor, 1977), slowing and then excluding mitochondrial penetration, conditions are therefore created for electrochemically-driven cytoplasmic streaming from the mitochondria maintained at the back to the progressively extending cytosol-hyaloplasmic zone (amitochondrial or exclusion apical zone, see Turian, 1979). The system can thus be visualized as being self-entrained, the self-reinforcing cytoplasmic currents acropetally displacing acidifying protons along the flanks of "frontier mitochondria" toward the gelating hyaloplasmic tip zone. It can be added that the lower pH of the emerging tip has been checked by its turning to clear yellow when germinating conidia of *N. crassa* were bathed in bromcresol purple.

As seen above, the content of the hyphal tip has an average pH of 5.2 in *Neurospora crassa*. According to Slayman's experiments (1962), the apices of *N. crassa* have a lower negative membrane potential than distal portions of hyphae. Such a less negative inside potential means relatively more positive charges which could thus be provided by the acropetal movement of excess mitochondrially-extruded protons chased toward the tips by cytoplasmic currents. Such a relatively positive hyphal tip can then previsibly attract negatively charged vesicles (anionic wall precursors) toward the extending plasmalemma and continuously newly-formed tip wall.

From all the above assumptions it can be deduced that the efficient functioning of the mitochondrial respiratory electron chain conditioning the efficiency of the proton extrusion process similarly conditions the quality of the electrochemical gradient inside the apices of hyphae and the speed and normality of their cylindrical elongation growth. In consequence, respiratory mutants such as the "poky" strains which mostly rely on the alternative cyano-insensitive pathway (Lambowitz et al., 1972), should have a lower extension growth rate than wild type, as recently confirmed (Michéa et al., 1979). Along the same line of thinking, it could be predicted that mutants more deeply lesioned in their mitochondrial apparatus such as « amycelial » (Oulevey et al., 1978) should grow, as it is well known, with a deviated, vesiculated hyphal growth form as also shown by the very slow growing colonial-mutants (col-2 and col-3) in which preliminary tests with bromcresol purple have revealed a dissipated apical pH gradient (from 6.2 to 5.6 at the most in the wide tips). In the same line of thinking, and in support of the importance of an efficient proton extrusion process for the normality of polarized elongation growth of hyphae, we have also found that the growth of those of *N. crassa* is slowed and deviated to excessive branching (colonial type) in the presence of the uncoupler 2, 4-dinitrophenol (10^{-3} M), well known for its disruptive effect on the vectorial transfer of protons through the mitochondrial internal membrane (Mitchell & Moyle, 1967; Harold, 1977).

As an interesting consequence of our new views, it would appear that the variously induced losses of apical polarity in vegetative hyphae leading to conidiogenesis in

Neurospora, zoosporegenesis in *Allomyces*, etc. should be related to a destruction of the electrochemical polarization gradient presumably following some suspected change at the level of mitochondria, implicating dissipation of the proton-motive force.

Finally, we have some reason to suspect that our anisotropic resulting proton ejection model has a value of generalization for the other types of cellular elongation growth, among which are pollen tubes and root hairs.

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