



Phosphagen kinase function in flagellated spores of the oomycete *Phytophthora infestans* integrates transcriptional regulation, metabolic dynamics and protein retargeting

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Summary

Flagellated spores play important roles in the infection of plants and animals by many eukaryotic microbes. The oomycete *Phytophthora infestans*, which causes potato blight, expresses two phosphagen kinases (PKs). These enzymes store energy in taurocyamine, and are hypothesized to resolve spatial and temporal imbalances between rates of ATP creation and use in zoospores. A dimeric PK is found at low levels in vegetative mycelia, but high levels in ungerminated sporangia and zoospores. In contrast, a monomeric PK protein is at similar levels in all tissues, although is transcribed primarily in mycelia. Subcellular localization studies indicate that the monomeric PK is mitochondrial. In contrast, the dimeric PK is cytoplasmic in mycelia and sporangia but is retargeted to flagellar axonemes during zoosporogenesis. This supports a model in which PKs shuttle energy from mitochondria to and through flagella. Metabolite analysis indicates that deployment of the flagellar PK is coordinated with a large increase in taurocyamine, synthesized by sporulation-induced enzymes that were lost during the evolution of zoospore-lacking oomycetes. Thus, PK function is enabled by coordination of the transcriptional, metabolic and protein targeting machinery during the life cycle. Since plants lack PKs, the enzymes may be useful targets for inhibitors of oomycete plant pathogens.

Introduction

The life cycles of many eukaryotic microbes include a zoospore stage, which is used for dissemination and host infection. Microbes producing these flagellated cells include apicomplexans, brown and green algae, excavates, foraminiferans, myxomycetes, oomycetes and others (Adl et al., 2005). Additional microbes such as alveolates form motile cilia, which are shorter forms of flagella. The movement of cilia and flagella is driven by dynein motors that hydrolyze adenosine triphosphate (ATP), which causes microtubule doublets to slide against each other (King and Sale, 2016). The resulting high rate of ATP use may lead to temporal or spatial mismatches between energy demand and availability.

Understanding how cells meet their energy needs is a major issue in biology. Most ATP in eukaryotes is generated in mitochondria and then diffuses across the cell to its sites of use. However, some cells may periodically use ATP faster than it can be made or transported. Cells cannot stockpile ATP since it must remain within a narrow concentration range to avoid misregulating cellular pathways. To circumvent this challenge, some cells have evolved to replenish ATP using enzymes, such as phosphagen kinases (PKs), which catalyze the reversible transfer of the γ -phosphoryl group of ATP to guanidino acceptors called phosphagens (Ellington, 2001; Wallimann et al., 2011). Most data on this come from studies of vertebrate cells such as muscle, brain and spermatozoa, although PKs have been also identified in bacteria, lower animals and eukaryotic microbes (Walts and Bannister, 1970; Ginger et al., 2008; Ooi et al., 2015). Some cells also use adenylate kinase to replenish ATP, which creates ATP and AMP from two molecules of ADP (Dzeja and Terzic, 2009). PKs and adenylate kinases may also help high-energy phosphoryls diffuse across cells or organelles by raising local concentration gradients in a 'bucket brigade' system (Dzeja and Terzic, 2009). PKs may also accelerate energy diffusion since phosphagens are smaller than ATP, and may relieve thermodynamic blocks to oxidative phosphorylation by siphoning off mitochondrial ATP (Ellington, 2001).

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