Title Ammonium secretion by *Colletotrichum coccodes* activates host NADPH oxidase activity enhancing host cell death and fungal virulence in tomato fruits

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Abstract

Colletotrichum pathogens of fruit and leaves are known ammonium secretors. Here, we show that *Colletotrichum coccodes* virulence, as measured by tomato (*Solanum lycopersicum* cv. Motelle) fruit tissue necrosis, correlates with the amount of ammonium secreted. Ammonium application to fruit tissue induced hydrogen peroxide (H_2O_2) accumulation. To examine whether the tomato NADPH oxidase, SlRBOH, is a source for the ammonium-induced H_2O_2, wild-type and antisense lines abrogated for SlRBOH (SlRBOH-AS) were examined. Wild-type lines produced 7.5-fold more reactive oxygen species when exposed to exogenous ammonium than did SlRBOH-AS lines. *C. coccodes* colonization of wild-type tomato lines resulted in higher H_2O_2 production and faster fungal growth rate compared with colonization in the SlRBOH-AS mutant, although the amount of ammonium secreted by the fungi was similar in both cases. Enhanced ion leakage and cell death of fruit tissue were correlated with H_2O_2 accumulation, and treatment with the reactive oxygen scavenger *N*-acetyl-l-cysteine decreased H_2O_2 production, ion leakage, and cell death. Importantly, the activation of reactive oxygen species production by ammonium was positively affected by an extracellular pH increase from 4 to 9, implying that ammonium exerts its control via membrane penetration. Our results show that *C. coccodes* activates host reactive oxygen species and H_2O_2 production through ammonium secretion. The resultant enhancement in host tissue decay is an important step in the activation of the necrotrophic process needed for colonization.