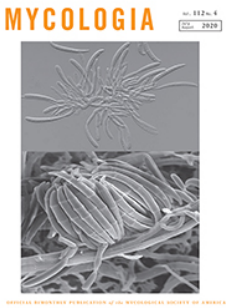

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Students remember Joseph Gerard Hubert (Jos) Wessels as an excellent, charismatic lecturer teaching a wide variety of courses, including plant and fungal biology and cell and molecular biology. Jos was an expert making difficult topics simple to understand, wearing a lab coat when lecturing. As a PhD student, I remember Jos smoking his pipe while reading articles in his spacious room. He was always happy to discuss new results but also to discuss science in general. Once he told me, "Do not read too much scientific literature, it will kill your imagination." I have used this excuse ever since for my failure in actively following the literature.

Jos was born in Roermond in the southeastern part of the Netherlands. Being so close to the Ruhr area in Germany, this city became part of the war front in 1944. Men were forced to work in Germany. Woman and children, including 10-year-old Jos, were evacuated to the northern part of the Netherlands after being in shelter for months. This traumatic experience was probably the basis of his strong support for a united Europe.

Jos studied biology at Leiden University and did an internship with Prof. Albert Kluyver in Delft, linking him directly to the Delft School of Microbiology. During this internship he studied oxidative phosphorylation in *Schizophyllum commune*, resulting in his first publication in 1959 (Wessels 1959). He continued his studies on *S. commune* as a research associate at the Department of Botany of Leiden University, supervised by Prof. Anton Quispel, and defended his PhD dissertation on morphogenesis and biochemical processes in *S. commune* in 1965 (Wessels 1965). He then spent a year in the USA working together with Donald Niederpruem (Indiana University) and Salomon Bartnicki Garcia (University of California at Riverside). Jos and Salomon became friends, accompanied by decades of intense discussions on cell wall synthesis and tip growth (see Bartnicki Garcia 1999).

Jos was appointed associate professor in microbiology at Leiden University in 1969, followed by an appointment as professor in plant biology at Groningen University in 1970. Although he did work on plants (peas) for several years, he mainly continued working with fungi, in particular *S. commune*, until his retirement in 1999. Jos established an important center for fungal research at Groningen University in close collaboration with Hans Sietsma and Onno de Vries. The steady-state growth theory, the concept of bulk flow secretion of proteins, and the discovery of hydrophobins were among their main discoveries. Less known, but also of high impact, were the studies on enzymes of *Trichoderma viride* to protoplast fungi (de Vries and Wessels 1972). The recipe they formulated continues to be used to prepare fungal protoplasts. The work on double-stranded RNA (dsRNA) viruses in the white button mushroom *Agaricus bisporus* was also of great importance. Viral particles were isolated from fruiting bodies affected by la France disease (van der Lende et al. 1994). Based on their work, a diagnostic kit was developed to monitor presence of the virus in colonized compost, an important tool to prevent spreading of the virus in commercial mushroom production.

Filamentous growth and cell wall assembly were the main topics of study for Jos in the 1970s and 1980s. A widely held view, also supported by Salomon Bartnicki Garcia (1999), was that wall lytic enzymes were involved in plasticizing the wall at the apex, thus allowing new wall material to be inserted and enabling expansion of the hypha by turgor pressure. In this view, cell wall growth at the hyphal apex would be the result of a delicate balance between cell wall synthesizing and cell wall lysing activities. Jos proposed an alternative model without the need of such a delicate balance (Wessels 1986). His steady-state model holds that cell wall polymers formed at the hyphal apex are inherently plastic, enabling turgor pressure to expand the hypha. Continuous addition of new cell wall polymers at the tip would maintain the plastic nature of the cell wall at the apex. At the same time, cell wall polymers interact with each other once secreted into the cell wall. As a result, the cell wall becomes more and more rigid in the subapical direction. The rigid cell wall in the subapical part and the plastic wall at the apex would ensure that hyphal extension

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only occurs at the apex. As far as I know, Jos and Salomon never agreed on which of the models was actually correct. Perhaps both models work in conjunction.

A solute-exclusion technique indicated that pores in cell walls do not exceed a width of 2–3 nm, thereby preventing diffusion of proteins larger than 15 000–20 000 Da (Money 1990). This finding raised the question of how proteins would traverse the cell wall to be released into the culture medium. Based on the steady-state growth theory, Jos proposed that proteins would traverse the wall together with viscoelastic wall polymers (Wessels 1989, 1990). These polymers are released at the inner part of the cell wall and are driven to the outside of the wall by turgor pressure and the continuous release of new wall polymers at the plasma membrane. This "bulk flow" does not require pores that would enable proteins to traverse the wall. After co-migration with the viscoelastic wall polymers, proteins would simply diffuse into the medium from the most stretched, and thereby most porous, outer region of the wall. Indeed, evidence was obtained that secretion only occurs at apices of growing hyphae in *Aspergillus niger* and *Phanerochaete chrysosporium* (Wösten et al. 1991; Moukha et al. 1993). In fact, these studies were the first to show that proteins were secreted at tips of hyphae and not along the whole hyphal surface. It should be noted that 20 years after publication of these results, the collaborators found that nongrowing parts of colonies of *A. niger* can also secrete proteins (Krijgsheld et al. 2013). Possibly, secretion from nongrowing hyphae is facilitated by cell wall lytic enzymes that create pores in the cell wall large enough to enable diffusion of proteins.

In the 1980s, Jos's group began to implement molecular biology in their work, using differential hybridization to identify genes that are strongly up-regulated during aerial growth of *S. commune*. Sequencing of differentially expressed mRNAs revealed a class of proteins, hydrophobins, never described before (Schuren and Wessels 1990). Hydrophobins were shown to be highly insoluble in cell walls of aerial structures such as aerial hyphae and fruiting bodies (Wessels et al. 1991). Purification and subsequent characterization of hydrophobins revealed that these proteins self-assemble at hydrophilic-hydrophobic interfaces, such as those between water and air, the cell wall and air, and the cell wall and a hydrophobic solid surface such as that of an animal or plant (Wösten et al. 1993, 1994a, 1994b, 1999). Hydrophobin self-assembly is important in the formation of aerial hyphae and mushrooms, the dispersion of spores, and the attachment of hyphae of beneficial and pathogenic fungi to the surface of their host. It was also hypothesized that hydrophobins would mask fungal spores from detection by the immune system (Wösten 2001), which was later shown experimentally (Aimanianda et al. 2009). Notably, hydrophobins also affect cell wall composition (van Wetter et al. 2000). "Hydrophobin" revealed 11 000 hits in Google Scholar (February 14, 2020), and these proteins are still widely studied (see, e.g., Appels et al. 2018). Hydrophobins are not only of interest from a fundamental point of view but have also been shown to have potential for use in a wide variety of applications, as described almost 20 years ago (Scholtmeijer et al. 2001).

As a young, ambitious scientist, I was highly excited when we found that hydrophobins form amyloids upon self-assembly. I suggested submitting the manuscript to *Nature* with an eye-catching title stating that mushrooms are coated with amyloid films. Jos did not agree with this title because he was worried that the press would relate mushrooms with amyloid-related human diseases such as Alzheimer's, making consumers no longer willing to buy edible mushrooms. In the end, the article was published with a descriptive title not including "amyloid" (de Vocht et al. 2000) and was hardly noticed by the press, thus safeguarding the Dutch mushroom industry.

Jos was co-founder of *Experimental Mycology* (now *Fungal Genetics and Biology*) and was involved in many other editorial boards. Moreover, he was head of the Department of Biology and dean of the Faculty of Sciences of Groningen University; he was part of the scientific committee of the Centraal Bureau voor Schimmelcultures (now Westerdijk Institute) and honorary member of the British Mycological Society (1991) and the Mycological Society of America (1994).

After his retirement in 1999, Jos switched his focus from fungal biology to the relationship between religion and science. He was studying physics, cosmology, and church fathers, St. Augustine being his favorite. He wrote the book "Wetenschap en Religie zijn Bondgenoten" (*Science and Religion Are Allies*) (Gopher, Harderwijk, The Netherlands, 2007), describing that there is no conflict between science and religion. Jan Dijksterhuis and I visited Jos every year at his beautiful house, Heidehof, situated south of Groningen and surrounded by forests and heaths. We did not particularly like to be exposed to the intimate interactions with his Newfoundland dogs (FIG. 1) but enjoyed his shiitake farm, his arboretum (FIG. 2), dinners and wine, but most of all the inspiring discussions about religion and cosmology. We also discussed the concept of heaven and his belief that he would meet his beloved wife Janneke again after her death in 2005. Jos Wessels passed away October 30, 2019, at the age of 85 years. We miss our friend.

Figure 1. Jos loved his Newfoundland dogs, including the new puppy he welcomed in July 2019 (photograph by Jan Dijksterhuis, with permission).

Figure 2. Jos lecturing Han Wösten about *Wollemia nobilis* in his arboretum, July 2019 (photo by Jan Dijksterhuis, with permission).

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