Pythium 'red rot disease' of *Porphyra*

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Since the early 1600s, several species of the red seaweed *Porphyra* have been cultivated in Japan where they are processed into dried 'nori' sheets. The intensive cultivation of this marine alga has been attended by 2 serious fungal diseases, the 'red rot' (Akagusare) or 'red wasting disease' caused by *Pythium* (Arasaki[1,2], Fujita and Zenitani[3]) and a 'chytrid blight' or 'chytrid disease' caused by an unidentified species of *Olpidiopsis* (Migita[4]).

In Japan, 1 species of *Pythium, P. porphyrae* Takahashi et Sasaki (Takahashi, Ichitani and Sasaki[5], Fujita and Zenitani[3]) appears to be the causative agent of the red wasting disease of the cultivated *Porphyra tenera* and *P. yezoensis.* The pathogen is characterized by having unbranched filamentous sporangia and intercalary, rarely terminal, oosporangia containing 1 usually pleurotic oospore. There most often are 1 or 2, but occasionally up to 4, diclinous antheridia per oogonium (Takahashi et al.[5]). In the first series of papers reporting *Pythium* as the causative agent of the Japanese red rot diesease, Arasaki[1,2] did not identify the pathogen to the species. However, Fujita (personal communication) feels that the *Pythium* observed by Arasaki had characteristics similar to, and may have been, an isolate of *P. porphyrae.*

The alga *Porphyra* on the Japanese coast is a winter annual, and the disease has been reported only on the leafy thalli, not on the *Conchocelis* phase. The pathogen is transmitted via zoospores with relatively warm winter seawater temperatures (24–28 °C), low salinity, and plant overcrowding favoring the occurrence and severity of the disease (Arasaki[1,2]). Zoospores from germinating oospores can initiate infection (Fujita[6]) suggesting that the fungus may, in the absence of the leafy *Porphyra* thalli stage, oversummer in the oospore stage.

Thalli of *Porphyra* infected by *P. porphyrae* show rapidly developing somewhat circular lesions of variable sizes that may coalesce. The central region of the lesion is light green (Fujita, unpublished data). The fungus penetrates through algal cell walls and into the cells causing them to collapse. Fujita and Zenitani[3] reported that fungal hyphae within penetrated cells had thickened walls.

A similar, if not identical, disease to the Japanese red rot has been reported to occur on both the Pacific and Atlantic coasts of North America (Fuller, Lewis and Cook[7], Kazama and Fuller[8–10]). In North America, unlike Japan, *Porphyra* is usually a summer annual. Natural infections of *Porphyra miniata* occur on the Atlantic coast (Massachusetts), while natural infections of *P. perforata, P. lanceolata,* and *P. schizophilla* have been observed on the Pacific coast (California and Washington) (Fuller et al.[7], Kazama, unpublished data). Additionally *P. pulchra, P. nereocystis* and *P. miniata* forma *cuneiformis* are also susceptible to infections in vitro suggesting that all species of *Porphyra,* under certain conditions, may be susceptible to invasion by *Pythium* (Kazama and Fuller[10]).

The lesions on the *Porphyra* species found on the Pacific coast were described as whitened and 1–3 mm on diameter, while the *P. miniata* observed on the Atlantic coast showed 2–25 mm lesions that were mottled pink at the center with an orange periphery (Fuller et al.[7]). Field observations of naturally infected *P. perforata* and *P. lanceolata* that remained submerged at low tide on the Pacific coast showed lesions from less than 1 mm to more than 10 mm in diameter (Kazama, unpublished observations).

Invasion of the North American species of *Porphyra* cells by *Pythium* results in their collapse, presumably by the loss of cell turgor caused by the penetration of the fungal hyphae. The mucilaginous sheath of *Porphyra* remains intact even after the complete destruction of the cellular contents (Kazama and Fuller[8]). Thalli of different *Porphyra* species range in color from steel grey-green to brownish red. After infection in vitro with an isolate of *P. marinum* sparrow (WH-1) the steel grey-green species (*P. perforata, P. lanceolata,* and *P. pulchra*) gave rise to greenish-white lesions with traces of pink. The lesions were similar to field collected material. The brownish red thalli of *P. miniata* and *P. nereocystis,* after infection with the same *Pythium* isolate (WH-1) showed lesions that were greenish-white with areas that were pink to orange. This suggests that lesion color depends on pigmentation of the host species rather than being due to various isolates of *Pythium* reported in the literature. The mottled appearance of lesions found on *P. miniata* and absence of mottling on *P. perforata* and *P. nereocystis* may be due to the difference in thallus construction. *P. miniata* is distromatic (thallus having two layers of cells) while *P. perforata* and *P. nereocystis* are monostromatic. It is likely that in distromatic thalli wherein only 1 of the 2 layers of cells is infected in many areas of the lesions, the uninfected cells are able to continue dividing. This may give rise to the mottled pink islands observed within the lesions. Experimentally, the diameter of lesions after infection in vitro with zoospores was found to vary with temperature, salinity and the reproductive state of the host (Kazama and Fuller[10]). It thus appears that symptoms of fungal infestation

may vary considerably depending on the nature of the host and prevailing environmental conditions.

So far, very little has been published on the quantitative differences in virulence and pathogenicity between various isolates and species of *Pythium*. Not all marine isolates of *Pythium* have proved to be pathogens of *Porphyra* (Fujita, personal communication; Kazama, unpublished data).

All of the *Pythium* isolates I obtained from lesions of *Porphyra* on both the Atlantic and Pacific coasts were identified as *P. marinum* Sparrow. *P. marinum* was reported by Sparrow[11] to have unbranched filamentous sporangia and 1 antheridium per oogonium. My isolates (on both the Pacific and Atlantic coasts) usually had 1 antheridium per oogonium, however oogonia with 2–4 antheridia were observed, although rather infrequently. The oospores were pleurotic, although in older cultures, apleurotic-appearing oospores with excentric lipid droplets were observed (unpublished observations). Takahashi et al.[5] and Fujita (personal communication) both felt that the Japanese isolates of *P. porphyrae* were nearly identical to *P. marinum* except for the number of antheridia per oogonia. Since Sparrow's[11] description of *P. marinum* was based on naturally infected *Porphyra* thalli, while Takahashi et al.[5], Fujita and Zenitani[3], and Kazama and Fuller[10] described sexual reproduction from pure cultures, but on different media, the differences in number of antheridia per oogonia may not be altogether comparable. Comparisons of the number of antheridia per oogonia should be conducted under similar conditions of culture to determine whether the number of antheridia per oogonia is a constant feature of marine *Pythium* species, since this appears to be the major point of difference between the Oriental and Occidental isolates.

Both *P. marinum* (Kazama and Fuller[9]) and *P. porphyrae* (Fujita and Zenitani[12]) appear to be generally similar physiologically, although differences in methodology prevent detailed comparisons. Both organisms can produce maximal dry weights in 40 to 100% seawater concentration (or artificial seawater of known salt concentrations) (Kazama and Fuller[9]), pH of 7.0–8.5, and temperatures between 15 and 25 °C. The evidence suggests that our isolates of *Pythium* (Kazama and Fuller[10]) are perhaps more similar to *P. porphyrae* than *P. marinum* as previously reported, if the number of antheridia per oogonium is found to be a valid taxonomic criterion. Fuller et al.[7], who first reported the marine pathogenic *Pythium* in North America, were unable to observe or induce sexual reproduction and, hence, were not able to identify their isolates with certainty. The overlap in geographical distribution and similarities in the disease symptoms with other reported cases of the disease in North America would suggest that the same species of *Pythium* is involved.

Until cultures are exchanged and direct comparative studies are conducted, the relationship between the Japanese and North American species of *Pythium* and the disease symptoms they cause on *Porphyra* will remain somewhat uncertain. However, considerable similarities between disease symptoms and the morphological-physiological characteristics of the pathogens would suggest that red rot of *Porphyra* is, with minor variations, identical in all biogeographical locations.

Although reports of the adequacy of *Porphyra* supplies in relationship to demands are conflicting (Woessner[13], Mathieson[14]), consumption in that year of nearly all of the sheets of nori produced in a single nori year (Miura[15]) would suggest that any increase in demand or shortage in production will lead to a shortfall. Potentially, market changes could make *Porphyra* farming in certain areas of North America a profitable family enterprise (Hunter[16]). If these market changes do occur and *Porphyra* farming is undertaken in North America, our data suggests that, as in Japan, the *Pythium* red rot disease will be a serious problem unless preventative measures are undertaken.

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