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Wild Rice Domestication, Fungal Brown Spot Disease, and the Future of Commercial Production in Minnesota

Wild rice (*Zizania palustris* L.) is an aquatic grass native to North America. Its edible seeds are similar in size and shape to those of white rice (*Oryza sativa* L.), but wild rice is not closely related to *Oryza* spp. or to southern wild rice (*Zizaniopsis miliacea* (Michx.) Döll & Aschers). The unusual infloresence of wild rice prevents self-pollination because female florets are produced on the upper part of the panicle and are no longer receptive when the male florets emerge below (Fig. 1). The harvested grain of wild rice is highly prized as a gourmet item because of its unique texture and nutty flavor. Sclerotia of ergot (*Claviceps zizaniae* (Fyles) Pantidou) have also been collected and sold as a source of alkaloids.

Before commercial production began, wild rice was difficult to obtain and always commanded a high price. It was painstakingly hand-harvested from wild stands by Native Americans and a few licensed "ricers," who flailed ripened grain into their canoes with wooden sticks (Fig. 2). The advent of commercial wild rice production has made this practice largely unprofitable, but it continues on a small scale. Most wild rice in Minnesota is now mechanically harvested from intensively managed paddies. Commercial production has begun in many parts of the United States and Canada, and the California industry now rivals that of Minnesota. Wild rice is still considered a gourmet item, but it is no longer scarce or expensive.

Minnesota and the surrounding Great Lakes region is the center of origin for wild rice. It is the only cereal native to North America that has been domesticated from a wild plant. Commercial production of wild rice originated in Minnesota, where it is now grown on over 8,000 ha in 10 counties (Fig. 3). Current production techniques and wild rice cultivars were developed by Minnesota growers in cooperation with the University of Minnesota within the last 40 years.

The industry flourished throughout most of its history but is now threatened. Recently, fungal brown spot (FBS), caused by *Bipolaris oryzae* (Breda de Haan) Shoemaker (Fig. 4A), the anamorph of *Cochliobolus miyabeanus* (Ito & Kuribayashi in Ito) Drechs. ex Dastur, and *B. sorokiniana* (Sacc.) Shoemaker (Fig. 4B), the anamorph of *C. sativus* (Ito & Kuribayashi) Drechs. ex Dastur, has become the limiting factor in production. Although FBS has been a problem since the inception of commercial production, recent changes in pesticide labeling have almost eliminated options for chemical control. Market competition from growers in regions where FBS is not a problem has driven down the price of wild rice, while production costs for Minnesota growers have increased. Thus, the commercial wild rice industry seems likely to diminish in the state where it was born. In this paper we review the history of commercial wild rice production and discuss factors that have made FBS a serious threat to the industry in Minnesota.

Taxonomy

The common name "wild rice" has historically been applied to four different aquatic grasses in the genus *Zizania*, three of which are native to North America. Texas wild rice (*Z. texana* Hitch.) is a short-statured perennial found only in a restricted area of the San Marcos River in Texas. The grain of this wild rice is small and not extensively harvested by man. Manchurian wild rice (*Z. latifolia* (Griesb.) Turcz. ex Stapf.) is a perennial native of Asia. The grain of this species is not harvested, but the lower stems are used as a vegetable when infected by the smut fungus *Ustilago esculenta* Henn. (28). Manchurian wild rice differs from the three North American species in general morphology and chromosome number ($2n$=34 vs. $2n$=30) and perhaps should be placed in a separate genus. The remaining two species, *Z. aquatica* L. and *Z. palustris*, are indigenous to lakes and rivers of eastern and north central North America, and grains harvested from natural stands have been utilized as a food source for centuries (7). The two species recently were subdivided into botanical varieties based on grain morphology and isozyme distinctions (1,8) (Table 1). Some wild rice harvested from natural stands is *Z. aquatica*, but the majority is *Z. palustris*. Only *Z. palustris* var. *interior* is grown in intensively managed paddies.

Evolution of the Commercial Wild Rice Industry

The first commercial field of wild rice was planted in 1950 near Merrifield, Minnesota, using seed from natural stands. After one successful season, the second crop in this field was destroyed by FBS (14). In the next decade, FBS destroyed many other wild rice crops, including a 10-ha stand planted by a large frozen-food company. Hope for quickly obtaining resistance through simple selection vanished when surveys of numerous infected wild rice stands revealed no variation for reaction to FBS (13).

Commercial wild rice production is hindered by "shattering," the progressive loss of ripened grain from the panicle following uneven maturation. In 1963, University of Minnesota agronomists discovered a few shatter-resistant wild rice phenotypes in one commercial field that had a significant yield advantage over the more shatter-prone phenotypes despite their susceptibility to FBS. All subsequent commercial cultivars were derived from these selections of *Z. palustris*. Some losses to shattering still occur because commercial cultivars are actually mixtures with varying degrees of shatter resistance.

Shatter-resistant cultivars and improved production techniques allowed the industry to prosper and grow. In 1968, only 365 ha of wild rice were planted in Minnesota, but by 1978, 4,860 ha produced 1.09×10^5 kg of processed wild rice. In 1986, a record 2.32×10^6 kg were produced on 10,125 ha. Total annual production was lower from 1987 through

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1991, but yields as high as 1,138 kg/ha were recorded (18). Much success in commercial production can be attributed to improved cultivars, but the narrow genetic base of commercial wild rice limits the potential variation for certain desirable traits. Because commercial cultivars of wild rice are uniformly susceptible, yield loss to FBS is a major problem for commercial wild rice production in Minnesota.

Etiology of Fungal Brown Spot and Yield Losses

Yield losses can be significant even in well-managed paddies and can be severe or even total in untreated fields (3,15). Epidemics in 1973 and 1974 resulted in complete crop loss in many Minnesota paddies and contributed to the demise of several large wild rice farms. One of the two pathogens, *B. oryzae*, also attacks white rice and was a major factor in the Bengal famine of 1942 (21). Isolates of *B. oryzae* attacking *Zizania* and *Oryza* spp. are believed to be identical (6).

The FBS complex, caused by *B. oryzae* and *B. sorokiniana*, is considered as one disease because the symptoms caused by each organism are not readily distinguishable (13). The first symptoms are small (1–5 mm in diameter) purple-to-brown lesions often observed early in the season on the long, buoyant, floating leaves. Early lesions are similar on aerial leaves, but they later acquire a necrotic tan center and yellow halo (Fig. 5). Lesions on aerial leaves can expand rapidly to as large as 25 mm in diameter and coalesce and may result in necrosis of the entire leaf. The fungi also infect sheaths and stems. Severely infected stems often break, resulting in loss of the entire panicle. Infected panicles can become covered by a dense mass of fungal mycelium and numerous conidia that provide massive amounts of secondary inoculum for dispersal above the canopy.

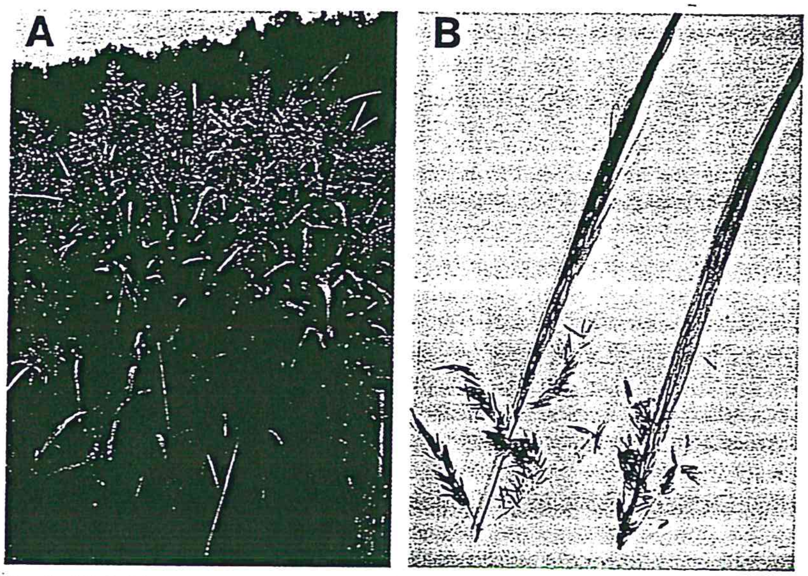

Fig. 1. (A) Cultivated wild rice (*Zizania palustris*). (B) Female florets are produced on the upper part of the panicle, male florets on the lower.

2. In the traditional two-stick method of harvesting wild rice from natural stands, senger bends panicles over the canoe with one stick and knocks the ripened the bottom of the canoe with the other.

Disease Cycle and Epidemiology

Primary inoculum in established commercial paddies comes mainly from infested crop debris. The harvest index (proportion of total plant mass represented by grain) of wild rice is low compared with that of other crops, and a great quantity of infested debris remains after harvest. Even after debris is plowed into the soil, degradation is very slow because of relatively limited microbial activity in the cold, wet, acidic (as low as pH 4.5) peat soils of most paddies. When paddies are flooded in the spring, infested crop debris floats to the surface and conidia of *B. oryzae* and *B. sorokiniana* infect leaves and stems of wild rice as they emerge from the water. Additional sources of primary inoculum are the many upland grass hosts of the fungi, some of which grow on the dikes surrounding paddies. Airborne conidia from infected grasses are deposited on the wild rice plants throughout the growing season.

Relative humidity is a principal determinant of FBS severity. The disease is absent or unimportant in the less humid California wild rice paddies, despite the presence of FBS organisms (31). Fungal brown spot is also of minor importance in Minnesota's natural stands, where plant densities are much lower than in commercial paddies. In Minnesota paddies, periods of 100% RH occur almost nightly within the plant canopy from early June until harvest. Infection spreads readily from primary lesions so that all floating and aerial leaves often are infected. Differences in severity among leaves of individual plants are probably due to vertical variation in humidity within the canopy (15).

Host-Parasite Interaction

The fast rate at which FBS infects, colonizes, and sporulates undoubtedly contributes to the rapid development and severity of FBS epidemics. When viable conidia of *B. oryzae* are inoculated onto wild rice leaves at 28–30 C and 100% RH, one to three germ tubes are produced within 8 hours (25). The host may be penetrated through stomates or through the epidermis. When stomates are invaded, hyphae grow through stomatal apertures (Fig. 6) and prolifpenetrate in substomatal cavities. When cells are penetrated directly, appressoria form over cell junctures and produce infection hyphae that penetrate the cuticle and cell wall. Lesions are visible on infected hosts within 24–36 hours of inoculation. Sporulation and dissemination of secondary inoculum via wind or rain splash can occur within 10 days of primary infection.

Disease Losses

A disease loss model for FBS developed by Kohls and Percich (15) used multiple linear regression analysis of final yields and disease severities on the upper three leaves at the medium milk growth stage. Yield was not significantly affected by infection of leaves formed before the antepenultimate. Also, fungicide applications after the milk stage of plant development did not significantly affect yield. The model showed clearly that the upper three aerial leaves are most important for yield and must be protected until the milk stage to reduce yield loss due to FBS.

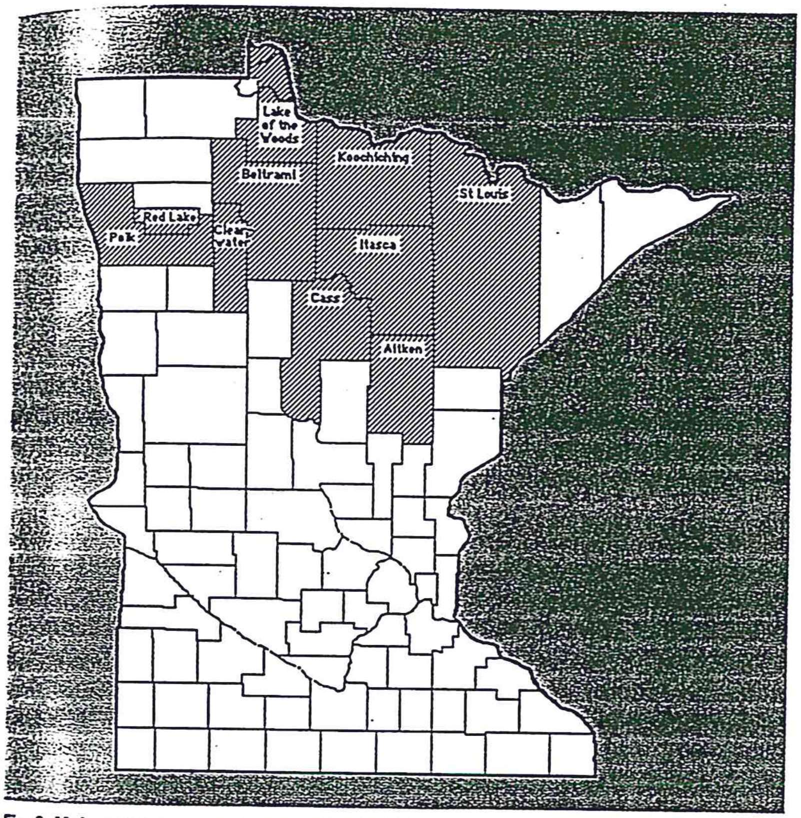

Fig. 3. Major wild rice-growing counties in Minnesota.

Production Practices as Predisposing Factors

Production of wild rice on highly organic soils may adversely affect plant health. Wild rice is adapted to certain soil types common to lakes and rivers (16). Cultivated wild rice is grown in artificially flooded paddies under conditions of high fertility (up to 45, 45, and 67 kg/ha of N, P, and K, respectively) and high plant density (about 100 plants per square meter) that facilitate development of FBS. Paddies typically are constructed on peat soils because they occur on perched water tables and near the river water necessary for controlled flooding. These flooded peat soils have less available oxygen than natural lake and river habitats. Wild rice nutrition under these conditions is complex and poorly understood.

Agronomic practices typical of commercial wild rice production may predispose wild rice to FBS infection. At least 3 weeks before harvest, paddies are drained slowly to induce grain maturation and permit mechanical harvesting with rice combines. Since wild rice regulates internal water potential poorly, plants are water-stressed during drainage, which encourages development of FBS. Massive infection of the three topmost leaves that usually occurs during drainage reduces grain fill. Shattering

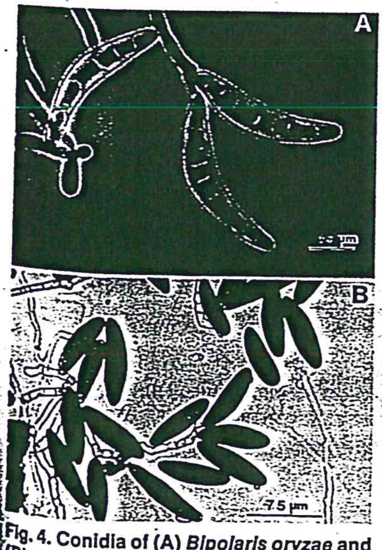

Fig. 4. Conidia of (A) *Bipolaris oryzae* and (B) *B. sorokiniana*, causal organisms of fungal brown spot of wild rice.

Fig. 5. Symptoms of fungal brown spot on aerial leaves of wild rice.

Table 1. Botanical varieties of annual North American *Zizania* species and their distribution

Species and variety	Distribution
Z. aquatica var. *aquatica*	Widespread along southeastern and eastern seaboards from Louisiana to Florida to Quebec and along shores of the Great Lakes
var. *brevis*	St. Lawrence River estuary
var. *subbrevis*	Southeastern Ontario
Z. palustris var. *palustris*	Widespread in rivers and small lakes in southern Canada and northern United States from coast to coast
var. *interior*	North central United States and southern Manitoba

that always occurs to some extent before harvest increases on FBS-infected plants, resulting in additional yield losses. Losses are probably compounded by the practice of raising each successive crop from shattered seed that remains in the field after harvest. This inadvertent selection of shattering phenotypes from the genetically heterogenous cultivar must result in a more shatter-prone crop. The practice continues because a stand cannot be raised from new seed without intervening fallow to kill plants from the shattered seed.

Role of Silicon

Silicon, which can be deficient in Minnesota peat soils, is an important factor in wild rice development and FBS severity. White rice produced on organic, low-silicon soils in Florida often has below-average yields, excessive sterility, lodging, and severe fungal brown spot (26). Difficulties with growing wild rice on low-silicon peat soils and increased FBS severity in Minnesota led to the investigation of silicon's role in wild rice development.

In greenhouse studies, the addition of 1.4×10^3 kg/ha of reagent grade sodium silicate ($Na_2SiO_3 \cdot 5H_2O$) or calcium metasilicate ($CaSiO_3$) to silicon-deficient peat soils significantly increased growth and development of wild rice plants. Plant height and dry weight of stems were increased significantly with either silicon additive (24) (Table 2). Development was accelerated and plants flowered 12 days earlier than those grown without silicon added. Since significant yield loss to FBS occurs between pollination and one-quarter grain fill, accelerated growth and earlier maturity (10–14 days) with adequate silicon might help avoid the most damaging infection periods in early to mid-July.

In 1987, blast furnace slag (47% available calcium silicate), a by-product of phosphate fertilizer manufacturing, was incorporated at 0, 2.5, 7.5, and 15 t/ha into a low-silicon peat soil containing recommended levels of N, P, and K. Disease ratings in wild rice cultivar K-2, expressed as the percentage of leaf area covered by lesions, were recorded for the flag, penultimate, and antepenultimate leaves at boot, early flowering, one-quarter grain fill, and harvest.

The slag treatments increased yield and decreased FBS severity. Trend analysis revealed a strong linear relationship between applied slag and yield according to the F test (Table 3) (4). Wild rice grain yield was 711, 858, 944, and 1,074 kg/ha when plants were grown in soil amended with 0, 2.5, 7.5, and 15 t/ha of slag, respectively. At 15 t/ha, grain yield, panicle weight, number of panicles, and silicon content increased 51, 49, 42, and 210%, respectively, and FBS severity decreased by 43%. Plant maturity was hastened by 7–10 days in slag-treated paddies. The application cost of 15 t/ha of slag was approximately $150, whereas the yield increase was worth approximately $350.

Elements in slag other than silicon, such as copper, sulfur, and zinc, might have affected the plant responses observed. Investigations utilizing various defined hydroponic media are now under way to determine the macroelement and microelement requirements of wild rice and the role of plant nutrition in FBS susceptibility. Additional studies on the effects of silica fertilization on wild rice are also in progress.

Chemical Control

Numerous fungicides have been evaluated for control of FBS (23). Mancozeb, a protective fungicide, was used on wild rice in Minnesota from 1974 to 1988. Applications at 7- to 10-day intervals significantly increased yields and reduced yield loss. Average yield increases in field tests were 160 kg/ha and costs of fungicide and application were $50/ha, resulting in a net increased return to the grower of $352/ha. Commercial growers relied heavily on mancozeb for FBS control until 1988. The voluntary withdrawal of mancozeb by the manufacturer and labeling restrictions imposed by the Environmental Protection Agency have left the paddy wild rice growers in Minnesota with no fungicides registered for use on wild rice.

Propiconazole (Tilt), a systemic ergosterol-biosynthesis-inhibiting fungicide, was evaluated for FBS control during 1985–1987 at the University of Minne-

Table 2. Growth and advancement of maturity of wild rice cultivar K-2 in peat soil amended with silicon in the greenhouse[x]

Treatment	Growth stage 40 days after planting	Plant height (cm)	Total main stem dry weight (g)
Peat + NPK[y]	Boot	62 a[z]	282 a
Peat + NPK + $CaSiO_3$	Inflorescence	70 b	592 b
Peat + NPK + $Na_2SiO_3 \cdot 5H_2O$	Anthers emerged	87 c	721 c

[x] Adapted from Percich et al (24).
[y] Fertilization at planting of 45, 45, and 67 kg/ha of N, P, and K, respectively.
[z] Means in each column followed by the same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

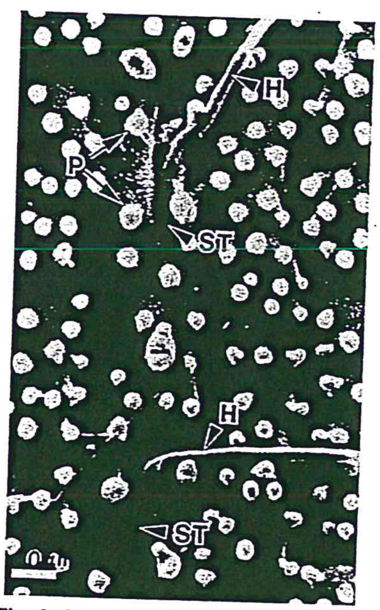

Fig. 6. Scanning electron micrograph of stomatal penetration of wild rice leaves by hyphae (H) of *Bipolaris oryzae* after 48 hours at 28–30 C. Note linear arrangement of stomates (ST) and surrounding papillae (P).

Table 3. Yield and disease severity of wild rice cultivar K-2 infected with fungal brown spot caused by *Bipolaris oryzae* and grown in soil treated with 2.5, 7.5, or 15 t/ha of slag

Slag (t/ha)	Yield		Percent leaf area infected (flag/flag-1/flag-2)
	kg/ha	Percent increase	
0	711[z]	...	40/50/80
2.5	858	21	22/44/50
7.5	944	33	17/29/45
15	1,074	51	14/19/40

[z] Significant linear relationship ($P < 0.0001$) with significant quadratic and cubic effects ($P < 0.0001$) between slag and yield according to the F test.

sota North Central Experiment Station in Grand Rapids (22). In 1985 and 1986, propiconazole applications of 186 g a.i./ha at both boot and heading stages of development increased yield 68 and 40%, respectively, and in 1987 applications of 247 g a.i./ha increased yield 113%. In 1990, propiconazole applied at three commercial wild rice–growing locations also increased yields and returned more than the cost of application.

After the propiconazole studies, registration for wild rice was pursued. The label is still pending, but the Environmental Protection Agency permitted use of propiconazole in paddy wild rice for the 1990, 1991, and 1992 growing seasons in a specific exemption under Section 18 of the Federal Insecticide Fungicide and Rodenticide Act. Registration of propiconazole is crucial, because commercial wild rice production in Minnesota without fungicides may not be economically feasible.

Breeding for Resistance

The wild rice cultivars used in commercial production are heterogeneous mixtures having considerable variation for morphological traits but similar reactions to FBS. Because the genetic base of these cultivars is narrow (selected from a relatively small collection of nonshattering phenotypes), there may be no useful FBS resistance in extant cultivars.

The most effective method of improving disease resistance in other cereals has been incorporation of resistance genes from wild relatives. Resistance to FBS has not been reported in *Zizania*, but little screening for resistance has been reported. If the greatest diversity for genetic traits occurs at the plant's center of origin (30), genes for FBS resistance may exist in the wild populations of *Z. palustris* and related species indigenous to the lakes and rivers of the United States and Canada. Short intervals of pollen viability (27) and lack of insect pollinators (29) probably have resulted in genetic isolation of lake populations. There may be numerous discrete populations that might be sources for desirable genetic traits.

Obtaining and screening wild *Zizania* germ plasm is difficult. Limited collections of wild rice have been screened for FBS resistance, but no working germ plasm collections exist. Although FBS is considered one disease, reaction to *B. oryzae* and *B. sorokiniana* must be evaluated separately to exploit any differences in the biology of the two fungi. Germ plasm is difficult to collect because the habitat is aquatic, the distance between natural stands is often great, and the seed requires cold, wet storage. Expeditions must be planned carefully because shattering of ripened seed shortens the period when seed is available for collection. Yeasts and bacteria degrade the seeds in storage, producing phytotoxic by-products and noxious odors.

Germ plasm screening is complicated by seed dormancy, even with cultivated varieties of wild rice. Seed normally remains dormant for 3–6 months after maturity. Although dormancy is vital for survival of *Zizania* spp. in nature, it interferes with crop improvement efforts, such as greenhouse screening of germ plasm and initiation of tissue cultures. Dormancy of wild rice seeds can be broken by chemical treatment (20), ultrasonics (9), or mechanical scarification (19,32), but the resulting seedlings are often weak and fail to survive beyond the floating leaf stage. After dormancy, stored seed cannot be prevented from germinating even in darkness at 1 C. It is therefore difficult to produce plants on demand or maintain germ plasm. Seed dormancy can be overcome using in vitro embryo rescue on tissue culture medium (12), but this method is not practical for large-scale screening.

Tissue Culture

Dormancy has also interfered with induction and maintenance of embryo-derived callus cultures. Callus initiated from immature or mature embryos of wild rice grows slowly and is much more prone to browning than embryo-derived callus of other cereals. Seed dormancy and poor callus growth are partially mediated by the level of endogenous abscisic acid (ABA) in the seed (2,5). The effect of ABA in tissue cultures was partially reversed by amending the medium with the ABA synthesis inhibitor fluridone (10,17), but in wild rice culture, fluridone inhibits morphogenesis and regeneration (11). Perhaps vigorous callus cultures can be obtained from embryos, since no other plant parts are usable as explants. Success may depend on finding embryos that are naturally lower in ABA. Efforts to develop a tissue culture system for wild rice are continuing, so that somaclonal variation and in vitro selection can be used to develop FBS-resistant cultivars.

Future of Commercial Wild Rice Production

Wild rice was designated the official Minnesota State grain by the state legislature in 1977, but the future of the commercial wild rice industry in Minnesota is in jeopardy because of a plant disease. FBS now looms as the major problem for growers because no fungicides or herbicides are currently labeled for Minnesota paddy wild rice. The special exemption for propiconazole is only a temporary solution because future exemption or labeling of this compound for wild rice is uncertain. Although FBS is prevalent in paddies, lack of selection pressure in natural stands suggests that such resistance may not exist. Further, transfer of resistance or other traits from noncultivated germ plasm into cultivated wild rice would be difficult and time-consuming. Useful germ plasm is scarce and *Z. palustris* is incompatible in certain interspecific matings. Wild rice is also recalcitrant in tissue culture, so obtaining an FBS-resistant somaclonal variant in the near future is unlikely.

Commercial production in California and Canada is not significantly affected by FBS because both climates are unfavorable for the disease. Competition from these sources is increasing while the price of wild rice is declining because of market saturation (Fig. 7). The current average wholesale price of approximately \$3.30/kg of processed wild rice is below the production cost for some

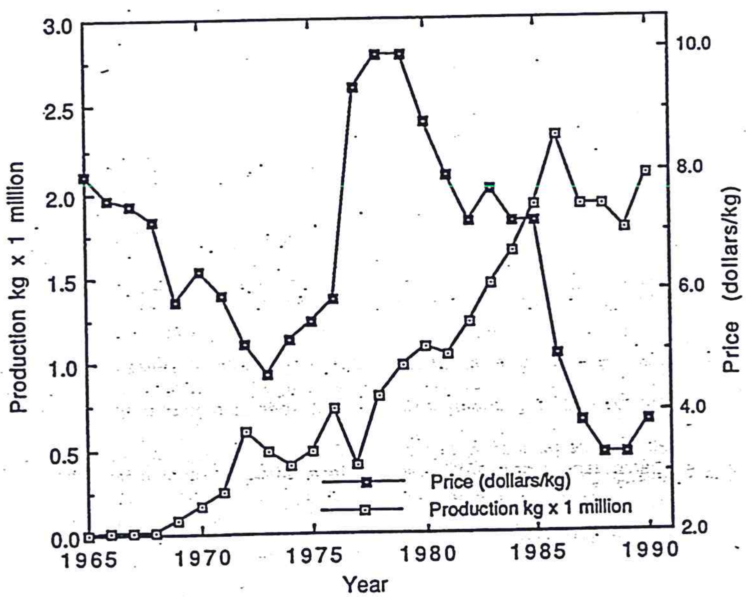

Fig. 7. Wild rice annual production and price of processed grain in Minnesota.

Minnesota growers. Minnesota has been the leading producer of paddy wild rice since the birth of the industry, but without fungicides or genetic resistance, the potential yield loss due to FBS is unacceptable for increasing numbers of growers. If FBS is not controlled effectively, the Minnesota wild rice industry will decline, while production in other areas will expand to replace it.

Acknowledgment

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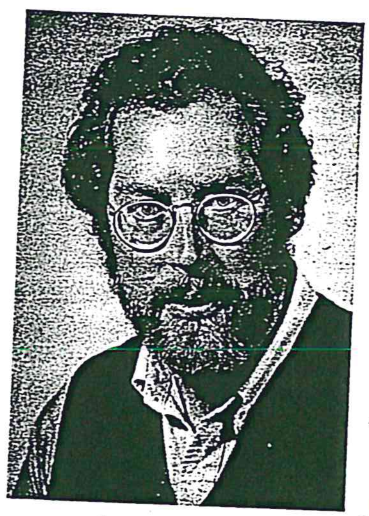

James A. Percich

Dr. Percich is a professor of plant pathology at the University of Minnesota. After obtaining his Ph.D. degree from Michigan State University in 1975, he was a research fellow at the University of Wisconsin-Madison during 1976. In 1977 he moved to the University of Minnesota, where he has been responsible for research on integrated pest management of wild rice and vegetables.