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Breeding Wild Rice

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I. INTRODUCTION

A. Origin

Wild rice (*Zizania palustris* L., Poaceae) is the native aquatic grain of the upper Midwestern United States and Southern Canada. The First Americans' name for wild rice was Manomin, which means good berry. The French called it *folle avoine*. Other names for wild rice include Canadian rice, squaw rice, water oats, blackbird oats, and Marsh oats (Oelke 1993). In 1775, Peter Bond, a British explorer, noted that the native stands of wild rice were so thick that the First Americans had difficulty poling canoes through it, and "wild ducks rose up like thunder" from the native stands (Fannucchi et al. 1986).

Wild rice has been harvested by the Ojibway, Menomini, and Cree tribes for centuries from the shallow rivers and lakes in the upper Midwest. The Ojibway and Menomini of Minnesota and Wisconsin believed that wild rice was a sacred gift that would always be there to feed them, and that cultivation of wild rice was desecrating the divine nature of their sacred gift (Steeves 1952). The Cree of Saskatchewan did not hold the same view as their neighbors in Minnesota and Wisconsin, and they have actively managed natural and planted lake stands (Winchell and Dahl 1984). Traditional harvest methods involve one person flailing the grain into a canoe as another person poles the canoe through a lake or river stand.

In 1852 and 1853, both Joseph Bowron and Oliver H. Kelley first suggested that wild rice be cultivated (Oelke et al. 1992). James and Gerald Godward built the first wild rice paddy near Merrifield, Minnesota, in 1950, and had 120 acres of wild rice under cultivation by 1958. The big boost for the fledgling industry came in 1965, when Uncle Ben's started to purchase wild rice on contract. W. A. Elliott started the University of Minnesota wild rice breeding program in the early 1970s. Presently, 11,000 hectares of wild rice are under cultivation in Minnesota, Wisconsin, and California (E. A. Oelke, personal communication). Cultivated wild rice contributed 21.12 million dollars to the 1993 United States agricultural economy (Oelke and Jin 1994).

B. Domestication

According to DeWet and Oelke (1978), the major characteristics of domesticated cereals are (1) loss of natural seed dispersal mechanisms (nonshattering); (2) loss of seed dormancy; (3) uniform plant maturity; (4) uniform population maturity; and (5) strict adaptation

to man-made habitats. Early cultivation and harvest of seed from shattering wild rice populations did not initiate domestication (Hayes et al. 1989). The first step occurred in 1972, when the wild rice breeding project at the University of Minnesota focused on shattering resistance, which had recently been discovered.

Shattering and seed dormancy are naturally selected in continuous paddy production. Shattering still occurs in cultivars and breeding populations selected for seed retention. Plants that shatter lose seeds, which remain dormant in the paddy over the winter and contribute large numbers of plants to the population in the subsequent season. Selection for nondormancy is therefore necessary to allow complete seed replacement by the grower each year, thus reducing selection pressure for shattering.

Tiller asynchrony and nonuniform maturity within a population can also reduce gains in developing shattering resistance. In a population with mixed plant maturity, mature seeds from early shattering plants shatter before harvest, thus contributing shattering genes to the next year's stand. The best approach to the domestication of wild rice is to breed for reduced shattering, decreased seed dormancy, and increased uniformity in tiller maturity.

C. Commercial Production

In the United States, diked paddies are used for commercial production of wild rice. Small paddies have dikes around the perimeter and a water outlet at the lower ends. Paddies larger than 12 hectares usually have cross dikes with water gates in addition to the perimeter dike for more efficient water control. Flooding is required for satisfactory growth, but water depths greater than 12 to 14 inches produce elongated stems susceptible to lodging (Oelke et al. 1982).

Wild rice can be planted in the fall or spring. Fall planting eliminates the requirement for seed storage over the winter; seed for spring planting is stored in bags in flooded seed pits. Spring planting needs to be done as early as possible, before the seed sprouts in storage. Late spring plantings in Minnesota can delay maturation and cause yield losses due to late summer storms and early fall frosts .

Oats are commonly mixed with wet wild rice seed to facilitate adequate flow through planting equipment. Spreaders, grain drills, and airplanes are used to seed the crop. Wild rice is similar to many small grains with respect to planting depth. Seeds should be placed no more than 7 cm deep. Seeding rates vary from 35 to 50 kg/ha, depending on germination rates, which can vary from 15 to 75% (Oelke et al. 1982).

Wild rice paddies can remain in production for more than 10 years, reseeded annually by grain that shatters into the paddy before harvest. In Minnesota, as much as 1 t/ha of seed can shatter, requiring that stands be thinned to a density of about 40 plants/m^2 (Oelke et al. 1992). Thinning is done at the floating leaf stage by airboats with v-shaped knives similar to cultivator knives.

Soil fertility management differs from that for other small grains, and soil testing is recommended to monitor the fertility levels in paddies. Ammonium is the only stable form of nitrogen in flooded soils. Phosphorus and potassium availability differs by soil type, being more available in peat soils than in mineral soils (Oelke et al. 1992).

In Minnesota, paddies are gradually drained in late July and early August, during the grain filling period, to facilitate harvest operations. Harvest begins when one-third of the grain has matured to a black or brown color. This maximizes the processed grain yield by balancing losses due to immature grain and shattering. This corresponds to approximately 35–40% moisture in the grain. In Minnesota, wild rice harvest usually begins in early to mid August to avoid late summer storms. Wild rice growers usually add modified pick-up reels and half- or full-tracks to standard combine harvesters to accomodate the crop height variability and the soft paddy soils.

II. BOTANY

A. Taxonomy

Zizania is a small genus of aquatic grasses in the tribe Oryzeae (Gould and Shaw 1983). Wild rice was first collected in Virginia by John Clayton in 1739 (Aiken et al. 1988), and the binomial, *Zizania aquatica*, was suggested by Linnaeus for Clayton's herbarium sample. Linnaeus (1753), Dore (1969), Dore and McNeill (1980), and Duvall et al. (1993) subdivided *Z. aquatica* into *Z. aquatica* and *Z. palustris*, and separated *Z. aquatica* into 2 subvarieties, vars. aquatica and brevis, and *Z. palustris* into vars. palustris and interior (Warwick and Aiken 1986). Dore and McNeill (1980) and Aiken et al. (1988) based the species' distinctions on differences in the lemma and palea of the pistillate spikelets and number of spikelets per branch. Isozyme work of Warwick and Aiken (1986) and Counts (1993) and scanning electron microscope studies of Terrell and Wergin (1981) agree with separation of *Z. aquatica* and *Z. palustris*. *Z. palustris* is the large-seeded type that grows throughout the up-

per Midwest and Southern Canada, and is cultivated in Minnesota, Wisconsin, Canada, and California. *Z. aquatica* grows from the St. Lawrence Seaway down the Eastern Seaboard to Florida and Louisiana (Warwick and Aiken 1986; Duvall and Biesboer 1989). In addition to *Z. aquatica* and *Z. palustris*, there are two other species of note: *Z. texana* Hitchc., a perennial type localized to the San Marcos river in Texas (Oelke 1993), and *Z. latifolia* (Fassett 1924), an Asian species.

B. Cytogenetics

The North American *Zizania* species are all $2n = 2x = 30$ (Bolkhovskikh et al. 1969; Oelke et al. 1992). Fifteen bivalents (8 rods and 7 rings) are present at meiosis (Grombacher et al. 1993). *Z. latifolia*, the Asian species, is $2n = 2x = 34$ (Fassett 1924). In interspecific crossing experiments, Duvall and Biesboer (1988) noted that a crossing incompatibility in *Z. aquatica* required it to be the female parent in crosses with *Z. palustris* in order to obtain seed set.

There are large areas of heterochromatic blocks around the centromeres in wild rice chromosomes. These presumably highly methylated, nontranscribed regions cover 70% of the chromosome arms, corresponding to the estimated percent methylated DNA in the genome (69 to 80%) (Grombacher et al. 1993). The existence of the large heterochromatic blocks on many chromosomes indicates that linkage groups based on restriction fragment length polymorphism (RFLP) linkage mapping will align with relatively small segments of euchromatin.

C. Growth and Reproduction

Wild rice seeds require a 3- to 4-month period in cold water (1–4°C) to germinate (Elliott 1980). Following the cold period, germination occurs when the coleoptile breaks through the pericarp. The primary root extrudes out of the pericarp 7 to 10 days after emergence of the coleoptile. At 3 weeks, the seedlings will have 3 submerged leaves. The next 2 leaves float on the water surface ("floating leaf stage"), while subsequent leaves are aerial. Aerial leaf widths vary from 1 to 3 cm, with lengths up to 75 cm. Ligules present at the leaf blade and sheath junction are 1.0 to 1.5 cm in length. Stem diameters can be up to 1.5 cm, subject to plant densities and soil fertility. The root system is composed of shallow, white, adventitious roots, without root hairs, and often with rust-colored tips. Plants range in

height from 1.0 to 1.5 m, and can have as many as 30 tillers (Oelke et al. 1982). Growth stages of wild rice have been classified by Grava and Raisanen (1978) and Percich et al. (1994).

Wild rice is usually monoecious, with staminate and pistillate spikelets spatially separated on the same panicle, and with occasional hermaphroditic spikelets in the transition zone between the pistillate and staminate portions. The upper 60% of the panicle is composed of the pistillate inflorescence, while the staminate inflorescence with 10 to 15 branches comprises the lower 40%. Each pistillate branch bears from 10 to 30 single-fioret spikelets in *Z. palustris* var. interior, while staminate branches bear 30–60 spikelets, each with 6 stamens (Aiken et al. 1988). Staminate spikelets vary from 0.7 to 15 mm in length and have short awns or none at all. Pistillate spikelets are composed of a lemma and palea surrounding the floret (Weir and Dale 1960) and vary from 2 to 20 mm in length (Aiken et al. 1988). Foster and Rutger (1980) found variation in length from 11.5 to 15.1 mm within the cultivar 'Johnson', not including awns. Awns vary greatly in length and are usually longer than the seed itself.

Panicle branches bearing female flowers emerge first in *Z. palustris* and remain appressed to the rachis, while male branches usually spread to a near horizontal position. Variations of this panicle form include the "bottlebrush" characteristic (often associated with male sterility), in which male branches also remain appressed, giving the panicle the compact appearance of a bottle brush. Another variant is the "crowsfoot" panicle, in which the pistillate branches spread in the same manner as in *Z. aquatica* panicles. In the "pistillate" variant the staminate florets are replaced with pistillate florets, resulting in a gynoecious, or all-female, panicle. H. J. Schumer (unpublished data) found that the average number of pistillate florets was 137 for a normal panicle, and 382 for a pistillate panicle.

Regardless of panicle type, soon after pistillate spikelets have emerged from the boot, lodicules inside open a gap between lemma and palea through which the stigmas are exerted. Page and Stucker (1990) found that the stigmas are receptive under greenhouse conditions until 5–6 days after exertion. Once staminate florets opened, pollen viability dropped dramatically after 2 h. Viable pollen grains landing on the stigma, germinated within 1 h and reached the embryo sac within 2 h (Weir and Dale 1960).

Pollination is usually wind-mediated. Since stigma exertion usually occurs before staminate florets of the same panicle have begun to shed pollen and the staminate flowers are below the pistillate florets, self-pollination within a panicle is unlikely (Weir and Dale

1960). However, asynchronous tillering increases the chances that female flowers of later tillers could receive pollen from male flowers of the mainstem or early tillers. The proportion of natural self-pollination in wild rice has not been investigated directly; however, in experiments at the University of Minnesota (Porter et al. 1990), bulks of seed collected from mainstems, first tillers, and remaining tillers were grown out and compared for yield, flowering date, and plant height. There was no consistent decline in yield, giving no evidence of significant inbreeding depression associated with non-random mating of the tillers. However, there was some tendency of seeds from later-tillers to produce later-maturing plants, probably because of a greater contribution of pollen from later-maturing plants in the population. This implies that as seeds are collected from an individual plant (i.e., to obtain a half-sib family), including seeds from later tillers will likely increase the range of maturity within that family.

Weir and Dale (1960), working with wild populations in Ontario, reported that once pollination occurs (usually in July–August), the caryopsis matures within 10 to 14 days, the pericarp turning from green to dark brown or black at maturity. However, Kurle et al. (1985), report that the nonshattering cultivar Netum required 26 to 33 days from anthesis to physiological maturity, and Everett (1982) reported a range of 25 to 28 days from flowering to maturity for 3 cultivars at two locations.

Seed dispersal in natural populations of wild rice is accomplished by formation of an abscission layer in the stalk attaching the spikelet to the pedicel, allowing the mature seed to separate, drop into the water, and sink to the soil surface. Hanten et al. (1980) observed a well-defined abscission zone at anthesis, composed of a 2-celled separation layer with thin cell walls, adjacent to layers of parenchyma cells above and below with thick cell walls. After fertilization, the separation layer began to plasmolyze, and the middle lamellae and cell walls dissolved. Separation pockets developed and coalesced and the process was completed concurrently with embryo maturation. Seed maturation and separation (shattering) proceeded basipetally on the panicle. Staminate florets are also shed in natural populations following pollen dispersal, although the rate of separation zone development is more rapid than in the grain (Hanten 1975).

D. Seed Physiology

1. Dormancy. Seed dormancy and stratification requirements (i.e., the need for cold wet storage to break dormancy) slow breeding

progress by hindering rapid generation advance. The stratification requirement was quantified by Muenscher (1936) and later Simpson (1966) to be between 96 and 182 days in storage at 3°C. Simpson suggested, and Cardwell et al. (1978) later confirmed, that the pericarp barrier as well as chemical factors prevented germination. Albrecht et al. (1979) concluded that dormancy was the result of the wax-covered pericarp and an imbalance of growth promoters and inhibitors, such as abscissic acid.

Other investigations sought the most effective methods for artificially breaking dormancy. Some of the methods included excising embryos (LaRue and Avery 1938); ultrasonic treatment and high (50°C) temperature (Halstead and Vicario 1969); removing, slitting, or puncturing the pericarp covering the embryo (Woods and Gutek 1974; Cardwell et al. 1978); scarifying dehulled seeds in a rock tumbler (Oelke and Albrecht 1978); and adding growth promoters to seeds with embryos exposed by scraping (Oelke and Albrecht 1980; Kovach and Bradford 1992b). Adding growth promoters and tumbler scarification both gave enhanced survival after germination.

Although these methods offer some alternatives to stratification at 1–3°C for 3 or more months, their usefulness in a breeding program is limited because the most effective treatments are either time or labor intensive, limiting the quantity of seed that can be treated, or because the treatments injure the seedlings. Success with the various treatments varies with genetic background and pretreatment handling (e.g., length of time in cold storage prior to treatment).

2. Storage and Drying. It has been difficult to maintain seed viability for more than 1 year, even when storage water is maintained slightly above freezing. Elliott (1980) reported that high-moisture seed (30 or 40%, fresh weight basis) retained 27–58% germination after 9 months storage at –2°C. Kovach and Bradford (1992a) were able to maintain viability of 'NorCal-1' seeds at high moisture (30–41%) for 6 months when stored at temperatures up to 30°C, and for 12 months when stored at 0 to 20°C. Seeds stored in a nonsubmerged, warmer environment at these moistures (30–35%) tended to develop fungal growth which damaged the seeds after about 6 months. However, seeds stored above 10 or below 0°C still required the full stratification period in order to break dormancy. Hydrated seeds (30–35%) that had already been stratified at 2.5°C were able to retain 60–80% germination after being gradually frozen to –10°C; germination dropped off rapidly below –10°C. After storing dormant seeds at

–3°C or in water at 2.5°C for 9 months, seeds showed 87 and 92% viability (tetrazolium assay).

Air-dried seeds (down to 11.5% moisture) stored at –2 or 2°C for 6 months had only slightly reduced germination following stratification (Oelke and Stanwood 1988). In later experiments, 50% of the seeds ('K2') germinated after being air-dried to 9% moisture over a 12-day period at room temperature, stored dry at 3 or –2°C for 9 months, then stored in water at 3°C for an additional 3 months (Oelke et al. 1990). Kovach and Bradford (1992b) dried 'NorCal-1' seeds and embryonic axes to 6–8% moisture; viability was highest when seeds were dehydrated at 25°C or higher and rehydrated slowly (over 3 weeks) at 10 to 25°C prior to stratification or dormancy breaking treatments. They reported that improper dehydration and rehydration temperatures, failure to break dormancy, and imbibitional injury during viability testing were the likeliest explanations for reports of intolerance to dessication. Based on seed-drying experiments on several seed sources, Vertucci and coworkers (1994) developed a model to predict the optimum temperature and seed moisture based on two varieties ('Johnson' and 'Franklin'). The optimum conditions differed, depending on the maturity of the seed. The most mature seed examined (hard brown) showed an optimum embryo moisture of 20 to 26% (fresh weight basis) at a temperature of –22 to –26°C. Less mature seed (hard green) had an optimum of 28 to 35% embryo moisture at –16 to –8°C. Soft green seed was the least tolerant of drying and did not survive below –8°C. The cultivar 'Johnson' was more dessication and freezing tolerant than 'Franklin'.

Few researchers have reported on the longevity of seed stored at various moistures and temperatures. Oelke and McClellan (1992) reported that a small proportion of seed was viable (2–8% germination) after storage at –2°C for 18 months. Cryopreservation of seed in liquid nitrogen (–196°C) could be the most reliable long-term storage method, but Oelke and Stanwood (1988) reported that liquid nitrogen freezing of seeds at various moistures severely reduced germination after post-treatment stratification. However, K. J. Bradford and D. A. Kovach (personal communication) have successfully frozen dried seed in liquid nitrogen and recovered a high percentage of viable seed. Their success probably was attributed to drying and rehydrating seed under controlled conditions. Research is continuing at the National Seed Storage Laboratory and at the University of Minnesota to develop a more reliable protocol for storage of germplasm both for breeding purposes (short- and medium-term)

and for long-term, in vitro preservation of basic seed lots of new cultivars.

III. GENETICS AND BREEDING

A. Germplasm Resources

Wild rice germplasm available for a breeding program is limited to seed that has been harvested within the past 1 to 2 years because of the limitations of seed storage. This mandates yearly grow-outs of all available germplasm populations and cultivars, thereby prohibiting maintenance of large germplasm collections. All of the cultivars and most breeding populations are *Z. palustris* var. *interior*. In Minnesota and other Great Lakes states and provinces (center of origin for *Z. palustris*), seed is still occasionally collected from wild populations of *Z. palustris* var. *interior* for immediate use in breeding and agronomic research. The variability within this taxon, and even within populations collected from a single site can be quite high. Cultivars have been developed primarily though population improvement of wild populations, as opposed to inbred lines, or other methods that reduce genetic variability. Heterogeneity is a characteristic of all wild rice cultivars. Genetic variability within cultivars is more than sufficient to allow for selection progress for most traits (Foster and Rutger 1980).

Wild rice populations were first introduced from Minnesota lakes into paddies in 1950 (Oelke et al. 1982), all of which shattered. The first nonshattering cultivar, 'Johnson', was put into production in 1968 (Stucker 1982). Minnesota cultivars, developed by growers and by University of Minnesota breeders, are summarized in Table 8.1. Hayes et al. (1989) reported that the initial collection of nonshattering plants was the germplasm base for all current varieties. However, growers who developed cultivars have indicated that they developed their cultivars from independent collections. The exact pedigrees of some grower-developed varieties remains unclear. Since 'Johnson' was late-maturing, potentially high yields were greatly reduced by frost in some years. Once earlier varieties were developed, cultivation of 'Johnson' was abandoned in Minnesota; however, California growers continue to grow various reselected versions of 'Johnson'. Currently, the most widely grown cultivars in Minnesota are 'K2' 'Petrowske Bottlebrush', 'Voyager', and 'Franklin'.

Other North American taxa of *Zizania* can be used as sources of genetic material for breeding programs. Duvall and Biesboer (1986,

Table 8.1. Summary of wild rice cultivars released in Minnesota.

Cultivar	Description
Johnson	Tall, late, some nonpurple panicles. Released 1968.
M1	Medium to late maturity. Developed by Manomin Dev. Co. in 1970.
K2	Early to medium maturity, medium to high yield. Developed by Kosbau Bros. in 1972.
M3	Medium to late maturity, having a mixture of gynoecious and monoecious panicles. high yield. Developed by Manomin Development Co. in 1974.
Netum	Early maturity, low to medium yield. Developed by Minnesota Agricultural Experiment Station and released in 1978.
Voyager	Short to medium height, early maturity, and medium to high yield. Released by Minnesota Agricultural Experiment Station in 1983.
Meter	Short height, very early maturity, and reduced foliage in the canopy. Large seed size and low to medium yield. Released by Minnesota Agricultural Experiment Station in 1985.
Petrowske Bottlebrush	Medium to late maturity, high yield. Up to 50% of plants can have bottlebrush panicle type. Developed by K & D Wild Rice.
Franklin	Medium to early maturity, more shattering resistant than other varieties. Released by the Minnesota Agricultural Experiment Station in 1992.

Source: Adapted from Stucker (1982), Mayes et. al. (1989), and Porter (1993).

1988) found that nonreciprocal crosses between the different varieties of *Z. palustris* and *Z. aquatica* could produce viable seed from which fertile plants developed. This germplasm showed additional gene pools from which to introgress new traits. For example, a *Z. aquatica* population collected in northern Florida shows greatly reduced or absent seed dormancy, robust stature, and more pistillate florets per panicle (R. Porter, personal communication). Another useful source of traits could be *Z. aquatica* var. *brevis*, characterized by short awns, short seeds, short height, and adaptation to the higher salinity of a tidal habitat (Aiken et al. 1988). Some populations of *Z. palustris* (var. *palustris* and var. *interior*) and *Z. aquatica* var. *aquatica*, as well as *Z. texana*, have been obtained and are being used by breeders to make wide crosses with *Z. palustris*. The potential for incorporating useful genes from *Z. latifolia* into *Z. palustris* has not been explored.

Currently, the University of Minnesota and Lakehead University in Thunder Bay, Ontario, have wild rice breeding programs that are developing varieties for Minnesota and Canada. One private breeding company (NorCal Wild Rice) is developing cultivars for California's Sacramento valley. Minnesota growers continue to practice mass selection to improve their own seed.

B. Procedures and Techniques

Elliott (1980) reviewed greenhouse and field plot culture methods and pollination techniques. Subsequent improvements have been incorporated in the following descriptions.

1. Field Plot Technique. Limited research paddy space often constrains fallow periods to 1 or 2 years, which is not enough time to ensure death of shattered, dormant seed under Minnesota conditions. Currently, soil is fumigated with 450 kg/ha of methyl bromide to kill remaining seed; however, an alternative product or an effective rotation scheme may be needed, given the uncertain future availability of this product. Survival of dormant seeds is reduced in paddies kept dry and tilled for 1 or 2 years of fallow. An alternative practice followed by Minnesota growers, flooding fallow paddies for 1 or 2 years to germinate dormant seed followed by tillage prior to flowering, could also be adapted to research paddies in cool, wet areas. In California's Sacramento valley, temperatures are high and minimal precipitation after harvest effectively eliminates seed carryover.

Research plots are fertilized primarily on the basis of soil test results for P and K. Grava and Raisanen (1978) reported that plants contained 120 kg/ha of N, 40 kg/ha of P, and 290 kg/ha of K at harvest. Organic soils require higher levels of potassium, often in excess of 100 kg/ha, than mineral soils that already contain moderate levels of potassium (P. Bloom, personal communication). Tissue samples from young whole plants indicated sufficiency levels of 3% K and 0.3% P (Bloom 1993, 1994). Phosphorus is applied at 0–45 kg/ha, depending on soil tests (Grava, in Oelke et al. 1982). Nitrogen requirements were estimated by Bloom and Zanner (1992) to be 40–50 kg/ha prior to boot stage, applied preplant in the form of ammonia or urea and incorporated. Prior to flooding, soil temperatures greater than 5°C led to nitrification of at least 4 kg/ha per day, requiring that plots be flooded as soon as possible after fertilizing and planting. Since 60–70 kg/ha of N are taken up by plants after boot stage (Bloom and Zanner 1992), research plots are topdressed one or two times, depending on soil ammonium tests, tissue analyses, or leaf nitrogen estimates with a chlorophyll meter. Typical production practices now include topdress applications during boot and early flowering.

Until recently, research plots have been hand-planted. A plot drill can be used, provided the containers and pathways are sufficiently wide (i.e., no less than 30 mm inside diameter). Wild rice seed is routinely mixed with dry oats just prior to planting, at a ratio be-

tween 4:1 and 6:1 (oat:wild rice) to promote seed flow. Yield test plots are usually 4 rows by 1.5 m, with 30 cm between rows. Since germination is often variable, plots are overseeded and thinned to 20–40 plants/m² soon after first aerial leaf stage. After end-trimming plots, only the center two rows are harvested to reduce border effects. Nursery rows are planted in 1.0- to 1.5-m rows, with alternating 25- and 50-cm spacing between rows to allow access by research personnel. Lower stand densities in nursery rows permit greater tillering and more seeds per plant. Research paddies are flooded immediately after spring planting or may be flooded in the fall or early spring if fall-planted. A water depth of 25 cm gives the optimum growth and yield (Oelke 1975).

Despite considerable effort to refine cultural techniques, the undomesticated nature of the species places severe constraints on breeding progress: (1) Labor and other resource requirements, including maintenance of bird-exclusion netting on paddies, limit the number of trial locations to either one or two for individual experiments, (2) very few isolated population maintenance paddies are possible, and maintenance by hand pollination is limited by the labor required to stake and adjust bags, and (3) stand density and quality of growth are quite variable, despite extensive preventive measures, leading to large experimental errors.

2. Greenhouse Procedures. Plants are grown in standard pots submerged in water. The pots are filled with soil, topped with a 1-cm layer of sand to reduce particulate flotation, and placed in tanks or boxes which are then filled with water to a depth of 1–4 cm above the soil. Pots may be submerged for at least 1 week prior to planting to bring soil to a reduced state and make iron and other nutrients more available. If pots are not preflooded, iron chelate may be mixed with the soil prior to flooding and planting, especially if the soil has been sterilized.

Viable nondormant seed or dormant seed that has been treated to break dormancy (see Section II.D.1) is pregerminated in pans of water. Seed in the initial stage of germination is placed in the submerged pots so that the caryopsis is anchored in the medium and the crown is at soil level.

Fluorescent lights, kept just above the highest leaves and supplemented with incandescent lights, provide sufficient light to prevent premature flowering and stunted growth. Planting before 1 November in Minnesota usually promotes more normal growth, since daylengths are short and natural light is low during midwinter. Oelke

and Jin (1994) found that reducing photoperiod in growth chambers reduced the time to flowering, even in very late maturing populations of *Z. aquatica*. They suggested that manipulation of daylength could facilitate crosses between populations with differing maturities. Greenhouse temperatures are maintained between 21 and 30°C during flowering. Pollen viability is greatly reduced below 21°C and above 35°C (Elliott 1980). Maintaining the water level within 1–4 cm of the soil surface forces the seedlings into the aerial leaf stage earlier than if they were in the field, reducing seedling vulnerability to competition by algae or possible foraging by ostracods.

Monitoring plants for nitrogen deficiencies is necessary. Several topdresses of urea should be applied, beginning at tillering, at a rate no greater than the equivalent of 30 kg/ha per application to prevent leaf burning. Topdressing with potassium may also be beneficial (P. Bloom, personal communication). Wild rice grown in a greenhouse is susceptible to mites and aphids.

Plants that are to be hand-pollinated are attached to stakes at least 1 m in length, to minimize the space that tillers occupy and to support pollination bags. Populations that are to be open-pollinated may be enclosed in a composite barrier of clear plastic film and cloth. The plastic allows natural light to be transmitted, while the cloth keeps excessive humidity and temperature from building up inside the chambers. The cloth must be woven tightly enough to effectively prevent passage of pollen grains, which are 30–40 μm in diameter (R. Porter, personal observation).

3. Pollination Methodology. When the plant is in the boot stage, a lightweight pollination bag is placed over the boot and flag leaf. This is necessary to prevent outcrossing, since stigma exsertion begins soon after panicle emergence. When the pistillate inflorescence has emerged fully into the bag, staminate branches are excluded prior to anthesis, so that only the pistillate branches remain in the bag. The pollination bag is folded over at the base, stapled, and labeled. Stapling through one of the pistillate branches inside the bag enables the bag to remain in place during the wind and rain. Poles and tapeners can be used to hold heavier bags in place in spaced planting or thin stands. The pistillate portion of the panicle is ready to be pollinated when the stigmas have just emerged from the florets.

Panicles used as a pollen source are bagged in the afternoon before the pollination. Wild rice pollen is short-lived, and bagging the day before or earlier in the same day negates the effects of foreign pollen contamination (Page and Stucker 1990). The pistillate inflo-

rescence is clipped off, leaving about 3 cm of the inflorescence to act as a brush to support the bag. The pollination bag is placed over the staminate inflorescence, stapled through the pistillate brush, and folded over at the bottom.

Elliott (1980) noted that during high temperature and low humidity in summer, early morning pollinations are the most successful at setting seed. After the morning dew has evaporated, the pollen is collected by shaking the pollen off the bagged panicle into small cups placed under the opening, or by shaking the pollen into the bag itself, which is removed to carry the pollen to the seed parent. The pistillate bag is slit with scissors at the top, the pollen poured in, and the top of the bag folded over and stapled shut.

For self-pollinations some staminate branches are included in the bag. Wind action and manual movement of the bags are sufficient to move the pollen in the bags (Bush and Elliott 1977), but manual agitation will increase seed set (Elliott 1980).

4. Seed Storage Procedures. Freshly harvested seed is submerged in water and refrigerated. Awns are removed prior to storage if the seed is to be planted with a mechanical planter. Seed may be pretreated with 1–2% NaOCl for up to 2 h (Oelke and Albrecht 1980; Kovach and Bradford 1992a), to reduce microbial growth during storage and to reduce dormancy to some extent. Containers are rinsed and filled with water, and then placed in a coldroom or refrigerator at 1–4°C for at least 90 days, or until seeds are treated to artificially break dormancy. After air-drying, seed from individual heads (e.g., heads from controlled crosses or half-sib seeds) may be placed in a coldroom in the pollination bags until threshing: seed will remain viable for at least 6 months in this manner. Seed from individual families or lines can be stored in water-filled plastic bags or in perforated plastic petri dishes submerged in water. Seed is then placed in cold storage until stratified or otherwise stimulated to germinate. Limiting exposure of seed to light may help to prevent premature germination once dormancy is broken in cold storage.

5. Molecular Genetics. A molecular genetics project on wild rice was initiated in 1993 at the University of Minnesota as an adjunct to the breeding program (Grombacher and Phillips 1994). The goals of the project are to develop an RFLP linkage map and to identify RFLP markers for important agronomic traits.

A wild rice genomic library was constructed using DNA from 'Franklin', a 'K2'-derived cultivar (Grombacher et al. 1993). The li-

brary was designated pAWG (Plasmid Aquatica Wildrice Genomic). Genomic DNA was digested with *Pst*I and fractionated on a sucrose gradient. The DNA was inserted into PUC18, and the recombinant plasmids were transformed into *E. coli* strain DH10B. The average insert size is 3.25 kb with an insert range of 0.5 to 6.0 kb.

Of the pAWG library (4365 clones), 70% were single or low copy, with the potential of 3000 probes available to map the genome. Mapping populations are being developed, and mapping techniques are being adapted to wild rice.

C. Breeding Objectives

1. Seed Shattering. Extensive commercial cultivation of wild rice was enhanced with the discovery of shatter-resistant selections in shattering populations in 1963 (Stucker 1982). The correlated trait of staminate floret retention allowed rapid identification of nonshattering types in the field.

Hanten (1975), in comparing the abscission zone development of shattering and nonshattering types, reported that plasmolysis of cells in the separation layer proceeded in both types, but that cell wall dissolution and formation of separation pockets was restricted in the nonshattering types. She suggested that these cells did not produce and secrete the lytic enzymes necessary for complete separation in the nonshattering types. Jin et al. (1994) also reported lack of development of separation pockets in nonshattering types, and noted that neither shattering nor nonshattering types contain the lignified sclerenchyma cells supporting the vascular channel found in domesticated *Oryza* but also missing in wild, shattering *Oryza* species.

Woods and Clark (1976) crossed 6 shattering collections with a nonshattering cultivar, and evaluated the F_2 population for shattering and nonshattering based on staminate floret retention. They concluded that shattering was dominant and simply inherited, although they were not able to determine if it was controlled by one or two genes. They also remarked that there were notable differences in firmness of seed retention within the nonshattering class.

Elliot and Perlinger (1977) made plant-to-plant crosses between 5 shattering ecotypes and 5 nonshattering S_1 families. Parental plants were concurrently selfed, F_1 progeny were advanced to F_2, and progeny were scored. Nonshattering was defined as plants whose main tiller retained a majority of seed on a panicle after striking the mature main tiller panicle against a solid surface. Staminate floret re-

tention was also scored into 4 classes. Segregation ratios indicated that a two-complementary-gene system controls the seed shattering trait, where seed retention is conditioned by homozygous recessive alleles at either locus. All plants with 100% staminate floret retention were nonshattering, and all plants with 100% staminate floret drop were shattering, however, intermediate levels of staminate floret drop did not consistently fall into either shattering class.

The two-gene qualitatively inherited shattering resistance is sufficient to permit combine harvest in paddy production, but still shows considerably less seed retention than other domesticated grains. Strength of retention declines rapidly after seed maturation, and measured shattering losses prior to harvest range from 26% (Schertz and Boedicker 1977) to over 40% (Porter et al. 1994). To maximize recovered yield, harvesting is recommended when 60 to 65% of the kernels are still green (Strait et al. 1977; Strait and Boedicker 1978). To provide additional shattering resistance, Everett and Stucker (1983) compared mass and half-sib family selection for seed retention gain in a population containing major gene shattering resistance. A tensile strength meter was used to measure retention strength of individual seeds, permitting selection for quantitative resistance. Progress from selection was 15.9% from one cycle of half-sib selection and 49.6% from two cycles of mass selection. Estimates of narrow sense heritability based on gains from mass selection were 0.58 and 0.55 at two locations, respectively. Based on realized gain from selection and components of variance analysis, mass selection was recommended for improvement of seed retention. Boze (1985), also measuring retention strength, estimated broad sense heritability in 8 of 10 shattering-resistant populations to be above 70%. Porter et al. (1990, 1993) reported correlations of −0.63 and −0.66 between tensile strength and actual shattering losses at harvest in yield trials, indicating that selection for tensile strength would result in reduced harvest loss. This method is labor intensive, however, requiring measurements of multiple seeds per panicle and multiple panicles per plot, while controlling for uniform stage of maturation of kernels tested.

In 1986, the University of Minnesota program began a project of selection for reduced shattering that combined panicle tagging at flowering with a subjective rating of resistance to hand stripping of seed from the panicle at maturity (Stucker et al. 1987). Several cultivar populations have been cyclically improved using this technique, with primary emphasis on mass selection, but also using half-sib family selection in some populations.

Since 1989, actual seed shattering losses at harvest have been estimated in yield trials by weighing kernels caught in pans or 10-cm split PVC pipe troughs suspended between rows above the water surface prior to maturity. Populations selected for seed retention strength consistently show less shattering loss at harvest than nonselected populations (Porter et al. 1990–1994).

The inability to maintain viable seed for more than 1 year, combined with the cross-pollinated habit of wild rice, complicates the comparison of cycles of selection for shattering resistance. Reference (original) populations cannot be economically maintained by hand pollination, so seed is usually obtained from commercial paddies. These paddies are self-seeded each year from shattered seed, and are thus under negative selection pressure for shattering resistance (Porter and Schumer 1991).

2. Yield. Yield has not been a major selection criterion in the Minnesota program because of the larger influence of shattering on yield recovery. Yield-related selection studies have been conducted.

Palm (1984) was the first to assess heritability and gain from selection for yield using half-sib family selection. He evaluated 114 half-sib families from 'K2', another 144 from 'Voyager', and 96 from bottlebrush plants of 'Voyager' in replicated single-row plots. Narrow sense heritabilies for yield were estimated at 0.78 to 0.83 in a single environment, and no phenotypic correlations of yield with other traits measured were high enough to be of practical value. Expected gain from selection was 9% per cycle.

Actual gain from selection was not as clear. The highest and lowest yielding 10.5% of the 'K2' families were selected and the open-pollinated seed from the half-sib rows was saved to form high- and low-yielding populations. These were compared to check populations of a random bulk from all 'K2' families. Realized gains from selection for these two populations were 12%, and –10%, respectively, as a percentage of the random bulk. Palm was unsuccessful in yield testing populations intermated from stored remnant seed, because of incomplete breakage of dormancy of the winter-grown intermating generation of seed.

Hutomo (1986) evaluated 150 half-sib families of a population formed by crossing 'Meter' (an early, short cultivar) with 'Johnson' (late and tall), intermated for 3 generations prior to the experiment. These families were not randomly selected, but consisted of 42 families phenotypically mass-selected for short height and early maturity, 48 families selected for medium maturity short height, and 60

milies selected for medium maturity and medium height. The short-
rly population was lower yielding than the other two. Yield of
ese three showed genetic correlations of 0.61 to 0.75 with plant
ight. Heritabilities of yield were 0.75, 0.78, and 0.84, respectively.
sing a selection intensity of 0.33 to 0.25, expected gains from half-
b family selection for yield were 12, 17, and 22%. In a third study,
ritabilities of yield on a fresh weight and dry weight basis were
38 and 0.46 (Stucker et al. 1989), based on covariance among 140
lf-sib families of 'K2'.

Two qualitatively inherited traits have been investigated for pos-
ble benefits to yield potential. The bottlebrush panicle character
thought by many Minnesota growers to be higher yielding, but
lm (1984) found no significant difference between the yields of
ttlebrush and nonbottlebrush half-sib families of 'Voyager'. Porter
d Schumer (1991, 1992) also found no difference between two
pulations consisting of randomly selected normal or bottlebrush
ants. However, within the 'Petrowske Bottlebrush' (selected for
gh-yielding bottlebrush plants), bottlebrush panicles yielded 24%
ore grain than normal panicles. The variety is increasing in popu-
rity among Minnesota growers. We have observed that this trait,
ith the associated male sterility, behaves under selection as if con-
olled by a single recessive gene for nuclear male sterility, reaching
equilibrium of 50% after 2 generations of selection.

The other quantitative trait affecting yield is the pistillate
ynoecious) panicle. Through the Minnesota Agricultural Experi-
ent Station, Schumer (1989) and Schumer and Stucker (1989, 1990)
veloped and released Pistillate M3 as a germplasm having approxi-
ately 50% pistillate plants. The pistillate trait also appears to be a
ngle nuclear gene for male sterility (Schumer 1989), so a 50% fre-
ency of pistillate plants would be the theoretical maximum if only
eds from pistillate plants are selected in each generation. The pis-
late plants usually have no staminate flowers and, therefore, are
fectively male sterile. Subsequent studies (Porter and Schumer
91, 1992; Porter et al. 1993, 1994) have confirmed that the pistil-
te panicle is high yielding, producing 10–70% more grain per
nicle than monoecious plants. Pistillate panicles may have almost
times as many female florets as nonpistillate panicles, so not all
e florets produce grain. Nitrogen may be a limiting factor in yield;
periments have shown a strong nitrogen response for yield in popu-
tions with more than 25% pistillate plants (Porter et al. 1993, 1994).
me pistillate populations added more than 1000 kg/ha of grain
eld in response to three 33-kg/ha topdresses of nitrogen during the

early reproductive stages of growth, achieving almost 3700 kg/ha grain yield at the 100-kg/ha rate (compared to 2200 to 2800 kg/ha for nonpistillate populations). However, since the frequency of this phenotype would not be maintained at 50% when artificial selection is stopped (i.e., after release), special procedures may need to be developed for seed increase and release of a pistillate cultivar.

3. Tiller Synchrony. Harvestable yield is reduced as a result of asynchronous flowering and maturation of the main stem and tillers. Yield loss occurs both from the main stem, which matures earlier than the tillers, as well as from late-maturing tillers, which are harvested prior to completion of grain filling. Everett and Stucker (1983) calculated an average of 7 to 9 days difference between maturation of the main stem and the first tiller, and 3 days between the first and second tiller in 3 populations. Hayes and Stucker (1987) reported an average of 12.1 days between the main stem and the average of the first 3 tillers in 2 populations. They indicated that main stem grain yield, most of which is lost in commercial cultivation, accounted for 15 to 19% of total grain yield at one site, and 30% at a test site with higher temperatures and reduced tillering.

Foster and Rutger (1980) and Everett and Stucker (1983) both noted substantial variability for synchrony period. Hayes and Stucker (1987) performed one cycle of mass selection within half-sib families and one cycle of replicated half-sib family selection for tiller flowering synchrony in the 'Voyager'. They reported narrow sense heritabilities ranging from 32 to 56%, using two synchrony indices. Predicted gain, based on half-sib family variances, ranged from 3.4 to 6.7% per cycle of half-sib family selection. Synchrony index scores were generally not correlated with plant height, main stem yield, tiller yield, or total yield in their study. Heritability estimates and predicted gains for tiller synchrony were lower than those for yield in 2 populations selected from 'Voyager', ranging from 7.1 to 9.0%, which suggested that selection for yield would be more effective in populations like 'Voyager' where yield had not been a primary selection criterion.

4. Maturity. Reduction of days to maturity has been a breeding objective in Minnesota in order to reduce exposure of the crop to late-season storm damage and early frost. Foster and Rutger (1980), working in California with 'Johnson', reported single plant heritability for main stem heading date to be near 100% and estimated gain from one cycle of mass selection for earliness to be 12% of the mean at 10% selection intensity. Phenotypic correlations were 0.66 between days to heading and plant height, 0.40 between days to heading and

tiller number, and –0.38 between days to heading and seed length in this population.

Palm (1984) determined days to flowering in replicated half-sib families of 'K2' in 1982 and 'Netum' in 1983. Estimates of narrow sense heritability were 88% for both populations, with expected gains of 4.1 and 1.7%, respectively, per cycle of half-sib family selection at 10% selection intensity. Comparison of 'Voyager', which was obtained by two cycles of mass selection for earliness in 'K2', with a population resulting from one cycle of replicated half-sib family selection for earliness in 'K2', led Palm to conclude that the methods were equally effective. Realized gain was 7.4% for the half-sib family selected population. Selection for earliness did not result in reduced yield in this one-cycle experiment.

Hutomo (1986) studied 3 subpopulations of a recombined cross between the tall, late-maturing 'Johnson' and the short, early-maturing cultivar 'Meter'. Narrow sense heritabilities for days to flowering ranged from 47 to 64%, based on variances among half-sib families. Predicted genetic gains ranged from 7 to 11% per cycle using selection differentials ranging from 33 to 25%, respectively, with half-sib family selection. Genetic correlations between yield and maturity score were small and nonsignificant. Results indicate that progress can be obtained in reducing days to maturity without sacrificing yield over a few cycles, but concurrent selection for yield would be recommended with long-term selection for earliness (Palm 1984; Hutomo 1986).

5. Seed Size. Wild rice is marketed both as mixtures with white rice (*Oryza sativa*) and as pure wild rice. Short and narrow-grain wild rice is preferred for the mixtures, to match the length and cooking time of the white rice component. Long grains are preferred by consumers of pure wild rice. Sorting and grading by size for target markets is accomplished at processing plants following curing, drying, and dehulling.

Although considerable variability for seed length exists in wild populations and commercial varieties, development and commercialization of varieties specific to the two types of markets have not occurred. Elliott (1976) reported mean seed length from Minnesota lake accessions ranging from 9.5 to 19.1 mm, with an average of 13.3 mm. Industry has proposed three classes: long (greater than 12 mm); medium (8 to 12 mm); and short (less than 8 mm) (Anonymous 1984).

Foster and Rutger (1980), studying variation in seed length among 100 half-sib families of 'Johnson' in California, reported mean seed lengths ranging from 11.5 to 15.1 mm. Narrow sense heritability was

58%, and predicted gain from selection was 4% of the population mean. Phenotypic correlations indicated that large-seeded plants tended to be earlier, shorter, and had fewer tillers and seeds per panicle than small-seeded plants.

Wandrey (1988) evaluated 147 half-sib families in 'K2' in Minnesota. Mean seed lengths ranged from 9.6 to 11.8 mm. Narrow sense heritability was estimated at 70%, and predicted gain from selection was 2.3% of the population mean. In a subsequent selection experiment, realized heritability for longer seeds was 83% at a southern Minnesota location and 67% at a northern location. Realized heritability for shorter seed length was not conclusive in this study. The correlation between seed length and seed weight was 0.56, indicating that selection using the more easily measured seed weight would be less effective than direct selection for length. The correlation of seed length with plot yield was 0.34, indicating that yield would need to be monitored during selection for shorter seed length. The high narrow sense heritabilities reported in both of these studies indicate that that both half-sib family and mass selection would be effective in selection for seed size.

6. Seed Nondormancy. Because seed nondormancy is a key trait in domestication, selection for seed nondormancy within cultivars has been attempted on several occasions. Stucker et al. (1987) describe two previous unsuccessful attempts to initiate a selection program for reduced seed dormancy. They also described initiation of a third selection program using seeds that had been cold-stored for 98 days. A population of 250 plants was established. Selection within this population continued, with the cold-storage period being shortened by 1–2 weeks each year (G. Linkert, personal communication). Selection in another population was initiated in 1988 using a large quantity of seeds from 4 varieties (Stucker et al. 1989). Seeds that germinated from all 4 cultivars after 60 days in cold storage were used to form the new population. Seed from the first cycle was stored for 45 days before germination was attempted. Both of these populations, however, progressed slower than expected and were abandoned when a genetic source of almost complete nondormancy was found.

In 1990, Porter and Schumer (1991) obtained seeds from a *Z. aquatica* population in Florida that germinated within 1 week after harvest. Since Duvall and Biesboer (1988) reported that *Z. aquatica* and *Z. palustris* crosses produced viable seeds if *Z. palustris* were the pollen parent, the Florida population was crossed with 'K2'; F_1 seed germinated within 1 week after harvest. That initial hybridization has since been backcrossed to *Z. palustris* cultivars available

in the greenhouse when the hybridized population was flowering (Porter and Schumer 1992; Porter et al. 1993, 1994). Nondormancy was still expressed the BC4 generation, suggesting dominance and simple inheritance. These results were similar to studies on dormancy in *Oryza sativa*, where 1 or 2 dominant genes have been shown to control the trait (Seshu and Sorrells 1986). Backcrossing to Minnesota cultivars is continuing in order to achieve the goal of developing a nondormant, Minnesota-adapted, shattering-resistant cultivar.

7. Insect and Disease Resistance. Peterson et al. (1981) observed that the wild rice worm, *Apamea apamiformis* (Guennee), is the major insect pest of wild rice in Minnesota. The major control measure of the rice worm is through applications of malathion. No cultivars are resistant to the wild rice worm. Field observations by R.A. Porter indicate that rough awns (awns with pubescence oriented downward) may serve as a physical deterrent to the rice worm. No populations are available with this trait.

Chemical and cultural control are the principal methods of minimizing fungal brown spot (*Bipolaris oryzae* and *Bipolaris sorokiniana*), from which wild rice suffers substantial economic loss. No resistant cultivars exist, but effective laboratory and field screening techniques have been developed for fungal brown spot disease reaction Johnson (1991) and R. F. Nyvall (personal communication.) In addition, field observations of 2 *Z. aquatica* strains indicated a differential response to the pathogens. Crosses have been made between the *Z. aquatica* strains and *Z. palustris* cultivars to initiate a backcrossing system for incorporation of fungal brown spot resistance into these cultivars.

IV. FUTURE BREEDING RESEARCH NEEDS

The long process of wild rice domestication has begun. A basic foundation has been laid on which to build future plant improvement efforts. Future breeding efforts must include a wide range of traits, including nonshattering, nondormancy, lodging resistance, and disease resistance.

Shatter resistance will continue to be the major breeding objective in Minnesota. Since all wild rice germplasm shatters, a genotypic recurrent selection program will be necessary to eliminate shatter genes from breeding populations. Quantitative shattering resistance has been studied in populations segregating for qualitative nonshattering genes. Therefore, the available estimates of heri-

tability and response to selection for seed retention may be biased. Shattering resistance needs to be reassessed in future populations after they are fixed for qualitative nonshattering.

Lodging is another problem in many production paddies. Lodging is being evaluated in variety trials, and stem sturdiness is an important selection criterion in some breeding populations. Inheritance of stem sturdiness needs to be determined.

Fungal brown spot diease will continue to be the primary emphasis in resistance breeding. Yield per se will also receive increasing attention. The development of pistillate populations should help improve yields. However, that will require research on how to best maintain the pistillate trait during generations of seed increase.

Nondormancy is a key trait for the future of wild rice production, as it has been for other grains. This will require both physiological and genetic assessment of nondormancy. Nondormancy appears to be simply inherited, but definitive studies have not yet been conducted. Appropriate criteria for assessing dormancy are required. Nondormant populations need to be studied in the field to determine whether nondormant seed survives from one season to the next. Optimum conditions for preserving viability of nondormant seed needs to be determined, as does genetic tolerance to dry seed storage. There is a need to learn if the physiological mechanisms of nondormancy are related to seed abscission or grain quality traits. Wide crosses (*Z. aquatica* × *Z. palustris*) are being used in Minnesota to introgress nondormancy into cultivated populations.

Wild rice is considered to be a specialty or gourmet food. Little attention has been paid to breeding for quality. Seed size has been the only trait investigated. Both uniformity in seed size and maturity are associated with tiller asynchrony and the heterogeneity among populations. Uniform plant maturity should be a selection criterion on population improvement and in the development of hybrid cultivars (Ken Foster, NorCal Wild Rice, Woodland, CA, personal communication). Cooking time and water absorption capacity are important to the consumer. Genetic variability for these traits should be quantified and considered during selection. It will be neccessary for the wild rice industry to identify quality standards prior to incorporating quality traits in a breeding program.

Historically, population improvement has been the preferred method of cultivar development in Minnesota. However, development of inbred lines has begun, and controlled crosses are being made more successfully. Improvement in wild rice pollination methodology will provide new approaches to varietal development, such as hybrid production.

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