The Domestication of American Wildrice (*Zizania palustris*, Poaceae)[1]

P. M. HAYES,[2] R. E. STUCKER,[3] AND G. G. WANDREY[4]

*The expansion in wildrice (*Zizania palustris*) production and the associated research efforts represent the largest modern effort to domesticate a cereal grain. Wildrice growers brought the species under cultivation, but plant breeding and agronomic research have accelerated the domestication process. The domestication and commercialization of this diploid (2n = 30), protogynous, cross-pollinated, annual, aquatic cereal present an opportunity to examine crop evolution and domestication theory. Traits associated with the domesticated cereal grains are shattering resistance, tiller synchrony, and increased seed size. This syndrome of traits may result from automatic selection, the selective force applied by repeated cycles of planting of harvested seed. Positive responses from deliberate selection for these traits in wildrice populations indicate that a domestication ideotype is attainable through plant breeding and that founder effect in this diploid species may be negligible. Continued commercial production of wildrice in the Great Lakes region is not likely to further the domestication process, whereas automatic selection may be initiated in the emerging California wildrice industry.*

Domesticación del Arroz Silvestre Americano (*Zizania palustris*). *El incremento en la produción de arroz silvestre (*Zizania palustris*) y la investigación realizada en esta especie representan el esfuerzo más grande en la domesticación de un cereal en tiempos modernos. Los productores de arroz silvestre iniciaron su cultivo, pero el fitomejoramiento y la investigación agronómica han acelerado su domesticación. La domesticación y comercialización de este cereal diploide (2n = 30), protoginéo, alógamo, anual, y de hâbito acuático presenta una oportunidad para examinar la teoría de la evolución y domesticación de cultivos. La resistencia al desgrane, sincronización del amacollamiento, y el incremento en tamaño de grano son características comunes en los cereales domesticados. Estas características pueden ser el resultado de una selección automática debida a la siembra de semilla cosechada. Respuestas positivas a la selección directa de estas características en poblaciones de arroz silvestre indican que un ideotipo domesticado se puede lograr por medio del fitomejoramiento, y que el efecto del tamaño en la población base en esta especie diploide puede ser de poca importancia. Es probable que la produción de arroz silvestre en la región de los Grandes Lagos de los Estados Unidos de América no adelante el proceso de domesticación. En cambio, selección automática puede ser iniciada con la produción de arroz silvestre en el estado de California.*

Within the past 20 yr wildrice (*Zizania palustris* L., Poaceae) has emerged as a crop of commercial importance. Distinct production systems—natural stands, managed natural stands, and paddy—are found in the principal wildrice regions of the U.S. and Canada. Production statistics for 1983–1985 are provided in Table 1 as tons of unprocessed wildrice. Paddy wildrice accounted for more than 95%

---

[1] Received 25 September 1987; accepted 27 July 1988.

[2] Department of Crop Science, Oregon State University, Corvallis, OR 97331.

[3] Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108.

[4] Asgrow Seed Company, Redwood Falls, MN 56283.

Economic Botany, 43(2), 1989, pp. 203–214

TABLE 1. PRODUCTION OF UNPROCESSED WILDRICE CATEGORIZED BY CULTIVATED PADDIES AND NATURAL STANDS, 1983–1985[1]; FIGURES REPRESENT TONS OF UNPROCESSED GRAIN.

	Cultivated—U.S.		Natural stands—Minnesota and Canada	
Crop year	Minnesota	California	Minnesota	Canada
1983	3632	1362	545	476
1984	4130	3514	613	851
1985	5870	8641	183	442

[1] Data from Table 2 in Nelson and Dahl (1986).

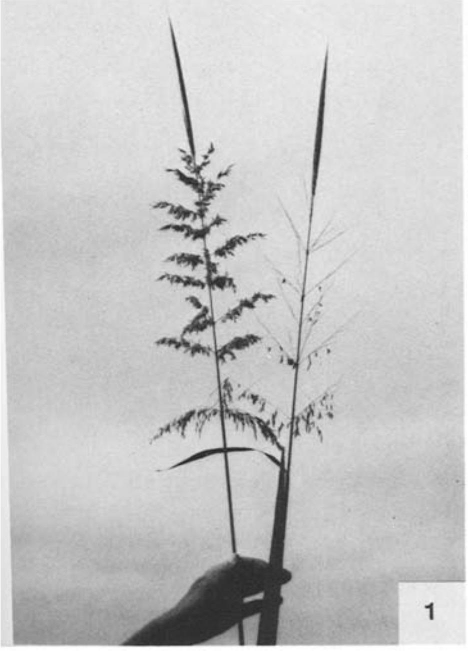
of the 1985 world production of 15,200 t of unprocessed grain. Cultivated wildrice (paddy) production from Minnesota and California is predominantly from shatter resistant cultivars (Fig. 1); natural stand production is from shatter susceptible varieties. An estimated 12,000 ha of natural stands are harvested annually in Minnesota, an area comparable to that under commercial production in the state. The cultivated wildrice producing areas of Minnesota are shown in Fig. 2. Minnesota paddy yields average 0.53 t/ha, while natural stand yields range from 0.02 to 0.14 t/ha, depending on the season. Wildrice is not native to California, the leading producer since 1985, with more than 6200 ha of paddies and yields averaging 1.4 t/ha. In Canada, managed natural stands are the predominant production system and account for approximately 3% of total annual world production (Nelson and Dahl 1986). Almost 70% of all processed wildrice, regardless of provenance, is marketed in mixes and prepared foods (Winchell and Dahl 1984). The remaining 30% is marketed as pure wildrice.

The purpose of our paper is to review the continuing process of wildrice domestication with reference to key crop evolution concepts. Although cereal crop evolution theory is largely based on wheat, barley, and oats (Harlan et al. 1973), these taxa show a commonality of evolution with *Oryza* (Chang 1985) that supports Vavilov's Law of Homologous Series (Vavilov 1951) and justifies our discussion of aquatic cereal domestication in terms usually applied to the terrestrial cereals.

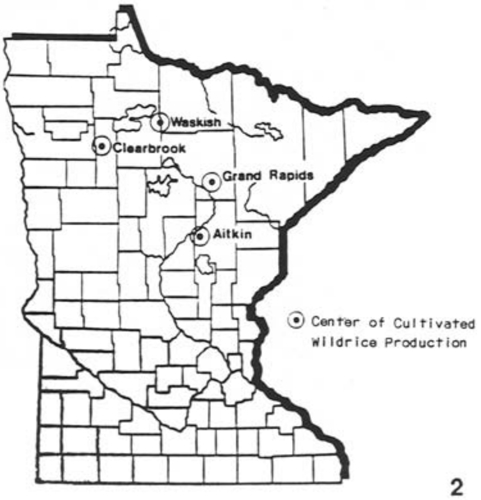
HISTORICAL CONTEXT

Despite the importance of wildrice to Indian groups in prehistoric (Johnson 1969; McAndrews 1969) and historic times (Steeves 1952), the domestication of wildrice was not initiated until the 1960s (Oelke 1982). The traditional Indian method of harvest, in which one person flails mature grain into a canoe propelled by another, will not lead to domestication. The repeated harvest of natural stands does not lead to the syndrome of traits conferring adaptation to an agroecosystem; repeated cycles of planting harvested seed (automatic selection) initiate the domestication process (Harlan et al. 1973). As Wilke et al. (1972) observed, harvests by seed beating, even if followed by sowing, reinforces wild-type seed dispersal mechanisms.

Many crops may have originated as aggressive colonizers of the disturbed habitats surrounding hunter-gatherer campsites (Schwanitz 1966). Camp-follower populations of wildrice did not arise because (1) seed had to be kept in cold water to remain viable and break dormancy and (2) seed had to be parched to safeguard



1



2

Fig. 1-2. Wildrice. **Fig. 1.** Shatter-resistant wildrice plants (panicle on the left) retain staminate spikelets, and shatter-susceptible plants (panicle on right) lose staminate spikelets shortly after pollen shed. **Fig. 2.** Location of centers of cultivated wildrice production in Minnesota (from Nelson and Dahl 1986).

quality and flavor in storage. According to Steeves (1952), Indian groups may have been responsible for disseminating wildrice throughout the Great Lakes region. Dissemination suggests an understanding of storage conditions needed to maintain seed viability, but dissemination alone, because of the harvest techniques subsequently employed, would not lead to domestication.

Cultural as well as biological factors prevented the prehistoric and historic domestication of wildrice. The Menomin, believing the plant was a sacred gift that would always provide for them, actually forbade any sort of wildrice husbandry. To cultivate the crop would signify that they no longer believed in the divine nature of the gift (Steeves 1952). The resistance of some Native American societies to wildrice cultivation surfaced as the commercial wildrice industry developed in Minnesota, and little commercialization of wildrice has taken place on Ojibway lands in the U.S. and Canada. On the other hand, the Cree, for whom wildrice did not have the same cultural and religious significance, are actively managing natural stands in Saskatchewan (Winchell and Dahl 1984).

COMMERCIALIZATION AND INCIPIENT DOMESTICATION

The commercial value of wildrice and its importance in providing waterfowl feed and habitat prompted numerous efforts at propagation and management (Brown and Scofield 1903; Chambliss 1922; Fyles 1920). Efforts were made to re-establish and extend natural stands. In the 1930s the CCC Indian division engaged in extensive lake re-seeding in the Great Lakes region (Steeves 1952). Overall, these early ventures were of limited success, probably due to the strict ecological requirements and seed dormancy mechanisms of *Zizania* species.

The commercial value of wildrice also led to the use of mechanical harvesters and broad boats in natural stands. Destructive harvesting techniques were effective in recovering more grain than traditional Indian methods, but they led to the decline of native wildrice populations. To protect Minnesota's natural stands and ensure a sustainable harvest, legislation was passed in 1939 that required natural stand harvests be conducted in the traditional Indian manner. Today approximately 60% of Minnesota's lake wildrice is regulated by the Minnesota Department of Natural Resources (DNR), which issues wildrice harvest permits and sets opening and closing dates for the wildrice season.

Failing to commercialize natural stands, entrepreneurs focused their attention on wildrice cultivation and thrust the wild species into an incipient agroecosystem. Rindos (1984) argued that establishing agroecology sets the stage for differential species destruction and protection, leading to what he called specialized domestication. Specialized domestication was initiated in 1950, when a 1-acre paddy was planted at Bass Lake, Minnesota, with seed collected from natural stands (Oelke 1982). This was a non-replacement planting; the stand was harvested with a modified pull-type combine similar to that shown in Fig. 3. Because the paddy was allowed to perpetuate from shattered seed, automatic selection was not initiated. Other growers followed the Bass Lake example, although not all attempts were successful. One grower who gave up is quoted by Rossman (1973) as saying "There's nothing wilder than wildrice." By 1965 Uncle Ben's Inc. was contracting wildrice production, providing economic incentive for cultivation. These initial efforts at commercialization culminated in a conscious effort at domestication through plant breeding.

PLANT DISEASE IN THE INCIPIENT AGROECOSYSTEM

Plant disease played a key role in the early years of commercial wildrice production. In the early wildrice agroecosystems, typified by the Bass Lake paddy, more grain was lost to shattering than was actually harvested. This led to dramatically increased plant densities, a suspected contributor to devastating foliar disease epidemics. The Bass Lake paddy, for example, produced excellent yields of wildrice for 3 yr. The fourth year the crop was destroyed by an epidemic of brown spot (*Bipolaris* spp.) (Oelke 1982). The agroecosystem obviated the natural ecosystems' resistance mechanisms, including genetic resistance and inter- and intra-specific genetic diversity.

Cyclical variation in yield is not unique to agroecosystems. Natural stands are characterized by cyclical yield patterns, with a poor yield one year out of four. The difference between the agroecosystem and the natural ecosystem is the magnitude of oscillation. There are no reports of devastating foliar epidemics in natural stands, although ergot (*Claviceps zizaniae*) infections are frequently mentioned in historical accounts (Dore 1969). While Moyle (1944) ascribed natural stand productivity cycles to fluctuations in water depth, reduced production in the low years is more likely due to dense stands resulting from heavy reseeding during the preceding year of good production.

3

4

Fig. 3-4. Wildrice. **Fig. 3.** Example of a wildrice harvester that can make repeated trips through a cultivated stand of shatter-susceptible wildrice without destroying the plants. Repeat harvests of shatter-susceptible varieties are necessary to collect kernels as they mature. **Fig. 4.** Retention of mature seed on shatter-resistant cultivars permits once-over harvest with rice (*Oryza sativa*) combines.

IMPLICATIONS OF PLANT DISEASE FOR WILDRICE DOMESTICATION

People, by generating imbalances in agroecosystems, are responsible for most, if not all, epiphytotics (Harlan 1976). Extensive foliar disease epidemics in cultivated wildrice may result from a disturbance of the equilibrium achieved through host-parasite coevolution. A stable long-term domestication strategy in wildrice may be one that would preserve, rather than alter, this equilibrium. Multilines, cultivar mixtures, and other strategies have been suggested as mechanisms to approximate natural ecosystem stability in the production environments of domesticated cereals (Browning 1974; Robinson 1980).

Central to host-parasite coevolution theory is the idea that centers of diversity, coevolution, and/or origin are primary sources of host resistance genes (Leppik 1970; Nelson 1978). However, Kernkamp and co-workers (1976) failed to find any brown-spot resistant germplasm after 4 yr of screening over 15,000 wildrice plants. This failure to identify resistance in germplasm at the center of diversity may be attributable to the selection criteria employed, as well as to the epidemiological characteristics of the *Bipolaris* disease complex.

Since 1976, the Minnesota breeding program has emphasized traits other than disease resistance, and phytopathological research has been directed toward chemical control (Percich and Nickelson 1982). The domestication process may be affected by reliance on fungicides to control diseases. An imbalance in the host-parasite coevolution process may develop; host resistance alleles will have no selective advantage, and intense selection pressure for fungicide resistance will be applied to the pathogen.

GENETICS OF DOMESTICATION TRAITS

Shattering resistance

Simply inherited recessive shatter resistance is characteristic of many domesticated crops (Ladizinsky 1985), and the loss of seed dispersal mechanisms is a first step in the domestication process (de Wet and Harlan 1975; Harlan et al. 1973). Seed shattering, even more than brown spot epidemics, caused the most obvious and consistent annual economic losses in the incipient wildrice agroecosystems, and deliberate selection for shattering resistance initiated the plant breeding effort.

Shattering resistance in wildrice is conferred by a two-gene complementary system in which shattering is dominant (Elliott and Perlinger 1977). Shatter resistant phenotypes are readily identified by their retention of staminate spikelets (Fig. 1); in wild type plants, the staminate spikelets are shed after pollen release, leaving naked panicle branches. A few cycles of mass selection led to fixation of this simply inherited recessive trait.

In Minnesota environments, except when harvested seed is used to initiate new plantings, there is no further automatic selection for shatter resistance within the bounds of the two-gene system. Rather, since the stand arises from shattered seed, there is natural selection for quantitatively inherited seed dispersal. As de Wet and Oelke (1978) recognized at the outset of the domestication effort, commercial production in the Great Lakes region would not further the domestication process.

Present wildrice cultivars with some resistance to seed shattering trace to a

TABLE 2. DESCRIPTION OF WILDRICE SHATTER RESISTANT CULTIVARS RELEASED FOR MINNESOTA WILDRICE GROWERS, AND CULTIVAR PERFORMANCE FOR YIELD, HARVEST DATE, PLANT HEIGHT, AND 100-SEED WEIGHT BASED ON REPLICATED EXPERIMENTAL TRIALS IN MINNESOTA.

Cultivar	Description
'K2'	Medium height, early to medium maturity, and medium to high yield. Developed by Kosbau Bros., Aitkin, MN, in 1972.
'M3'	Medium height, medium to late maturity, and high yield. Diverse in plant and panicle type. Developed by Manomin Development Co., Aitkin, MN, in 1974.
'Netum'	Medium height, early maturity, and 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. Should equal or exceed K2 in yield and mature a few days earlier. Developed by Minnesota Agricultural Experiment Station and released in 1983.
'Meter'	Short height, very early maturity and reduced foliage in the canopy compared to other varieties. Large seed size and low to medium yield. Developed by Minnesota Agricultural Experiment Station, St. Paul, and released in 1985.

Agronomic performance[1]

Cultivar	Yield[2] (Mt/ha)	Harvest date	Plant height (cm)	100-seed weight (g)
'K2'	1.76	23 Aug	185	2.38
'M3'	1.80	27 Aug	185	2.31
'Netum'	1.67	17 Aug	175	–
'Voyager'	1.68	18 Aug	168	2.42
'Meter'	1.21	2 Aug	130	2.51

[1] Results of experimental trials in 1981–1986, except 100-seed weight, which was based on paddy-produced seed in 1986.
[2] Green weight of grain at 40% moisture.

single collection of shatter resistant plants made in a paddy planted with wild type seed (Stucker 1982). This initial collection served as the germplasm base for an emerging wildrice industry. In 1967 the Manomin Development Company was formed with the objective of producing and marketing seed of shatter resistant varieties that could be combine harvested. Recognizing the crop's commercial potential, the Minnesota legislature in 1969 initiated continuing appropriations for wildrice research.

By 1972, when a wildrice breeding program was initiated at the University of Minnesota, three shatter resistant cultivars, all privately developed, were available: Johnson, Manomin 1 (M1), and Kosbau 2 (K2). Manomin Development Co. released M3 in 1974 (Stucker 1982). The University of Minnesota Agricultural Experiment Station released Netum in 1978, Voyager in 1982, and Meter in 1985. More than 95% of commercial paddies in Minnesota are planted to the shatter resistant cultivars whose agronomic characteristics are given in Table 2. These cultivars are sufficiently shatter resistant to allow for once-over combine harvest (Fig. 4), but shattering losses still remain high. Since 1982, two privately developed cultivars, 'Nor-Cal 1' and 'Nor-Cal 2', have been released in California.

Selection for quantitatively inherited shatter resistance beyond the two-gene system is effective, but tedious. Everett and Stucker (1983) used a tensile strength meter to measure the strength of retention of individual seeds in an array of half-sib families derived from shatter resistant cultivars and reported a 49.6% gain from two cycles of mass selection. Realized heritabilities for quantitatively inherited shatter resistance ranged from 50 to 60%, depending on test location. Since shatter resistance was not correlated with flowering or maturity date, greater shatter resistance appeared attainable without lengthening the growth cycle. If catastrophic selection for shatter resistance were practiced by harvesting only seed remaining on plants long after the optimum harvest date, as suggested by de Wet and Oelke (1978), there would be a rapid and inadvertent shift toward unacceptably later maturity; only the latest-maturing plants would contribute viable seed.

Tiller synchrony

Tiller synchrony—the uniform maturity of mainstem and tillers—is said to be characteristic of domesticated cereals (Chang 1985; Harlan et al. 1973; Schwanitz 1966) and has been used as evidence for prior domestication (Nabhan and de Wet 1984). However, there are few reports in which tiller synchrony has actually been measured in domesticated cereals (Faris and Klinck 1982; Paroda 1972) and no reports in which synchrony has been quantified in a wild species or protodomesticate. Selection for heading date synchrony was initiated in wildrice with the objective of increasing recovered yield. Because mainstems mature and shatter before tiller maturity, the amount of grain recovered at harvest is substantially less than the amount actually produced. Under plant densities per unit area commonly found in Minnesota paddies, plants produce one to three tillers that have mature seed at harvest.

Wildrice is more asynchronous than domesticated cereals, and there is substantial genetic variance for the trait (Hayes and Stucker 1987). The difference in heading date between the mainstem and third tiller in wildrice half-sib families derived from cv. Voyager ranged from 12 to 14 da, while the differences between the flowering date of the mainstem and fifth tiller in wheat and oats ranged from 4 to 6 da (Faris and Klinck 1982). Predicted gains of 3–7% per cycle from selection for heading date synchrony indicated that synchrony could be attained within 10 cycles of selection. These predicted gains also indicated that even at the low selection intensities of automatic selection, greater synchrony could readily be achieved. In light of the assertion that there would be "considerable linkage" of traits controlling wild type vs. cultivated morphology (Harlan et al. 1973), the correlation between heading date synchrony and other domestication traits such as shattering resistance, loss of seed dormancy, and increase in seed size would be of interest. However, these correlations have not been measured.

Seed size

Harlan (1975) argued that intentional selection for seedling vigor—i.e., for seedlings able to survive in highly competitive agroecosystems—frequently leads to larger seed size. At the same time, plants producing greater quantities of seed are likely to contribute more progeny to subsequent generations. Given the negative correlation between seed size and seed number, an equilibrium between these yield components will eventually be reached. Overall, however, automatic selection leads to an increase in seed size (Harlan et al. 1973). The wildrice processing industry prefers smaller grain. Shorter wildrice seed is preferred in packaged blends with white or brown rice, because the more uniform length allows for better texture, a more consistent cooking time, and a higher proportion of wildrice kernels in a given blend.

There is substantial genetic variance for seed size in relatively narrow-based wildrice populations. Estimates of seed length heritability in wildrice range from 58 to 70% and predicted gains from selection from 2 to 4% (Foster and Rutger 1980; Wandrey 1988). Deliberate selection for smaller seed size, however, may run counter to the effects of automatic selection.

Loss of dormancy requirements

In addition to shattering resistance, tiller synchrony, and seed size, the loss of dormancy requirements is characteristic of the domestication process in cereals (Harlan et al. 1973). The physiology of seed dormancy in wildrice has been investigated (Cardwell et al. 1978), but concerted selection against dormancy requirements has not been attempted. Wildrice grain must be stored in water at low temperatures (0–3°C) to remain viable and break dormancy. Dormancy, once broken after 3–6 mo of storage, is irreversible. Some kernels, however, have been shown to remain viable in the soil for as long as 6 yr (Oelke 1983).

Differences in dormancy requirements between *Oryza sativa* L. and its putative progenitor *O. perennis* (sensu Oka) were reported by Oka and Chang (1961), but these dormancy requirements do not include one for moisture. In terms of seed dormancy mechanisms, there appears to be no direct parallel between *Oryza* and *Zizania* domestication.

Seed storage requirements, as well as the length of the dormancy period, affect the breeding methods available to a wildrice breeder. Dormancy can be broken on a limited scale by seed coat scarification (Elliott 1980), but breeding methods requiring progeny testing and recombination of plants grown from remnant seed are precluded; the remnant seed loses most of its viability during the prolonged storage period. The dormancy and storage requirements of wildrice, more than any other factor, have hampered the species' domestication. Storage requirements prevented the development of camp-follower populations and have prevented the initiation of automatic selection in Minnesota production environments.

GENETIC VARIATION IN A NARROW GERMPLASM BASE

High estimates of additive genetic variance for shattering resistance (Everett and Stucker 1983), tiller synchrony (Hayes and Stucker 1987), seed size (Foster and Rutger 1980; Wandrey 1988), and grain yield (Palm 1984) in a narrow wildrice germplasm base discount the importance of founder effect in the evolution of this diploid. While Ladizinsky (1985) justifiably argued that seed crop plants evolving from a limited number of shatter resistant mutants would exhibit less genetic variability than their wild progenitors, the key issue, from a selection standpoint, is the amount of genetic variance remaining in the population. Wildrice germplasm tracing to a single sampling of shatter resistant mutants shows substantial genetic variance for all agronomic traits measured. There is, of course, evidence for ample genetic variance within relatively narrow germplasm pools subjected to long-term selection, such as the Illinois oil and protein experiment in maize (Dudley et al. 1974). The existence of such variation is documented, but its causes are not understood.

DISRUPTIVE SELECTION AND WEEDY RACES

Within the area in which wildrice is indigenous, dormancy requirements and shattering susceptibility prevent continuing species domestication in commercial wildrice paddies. Stand establishment from seed lost due to shattering, while eliminating the need for annual planting, reinforces adaptation to the natural ecosystem rather than adaptation to an agroecosystem and makes changing varieties difficult for growers. Thus, disruptive selection, in which natural and artificial selection operate in different and contradictory ways (Doggett and Majisu 1968), is of little consequence within the area of adaptation.

Although reproductive isolation has yet to be demonstrated in wildrice, geographic isolation generally restricts gene flow between cultivated and natural stands of the plant. Dore (1969) considered both *Zizania palustris* L. var. *palustris* and *Z. palustris* var. *interior* (Fassett) Dore to be the taxa producing the wildrice of commerce. More recently, Warwick and Aiken (1986) argued, based on electrophoretic analysis of 33 *Zizania* populations, that cultivated wildrice is most closely related to *Z. palustris* var. *interior.* The possibility of gene flow between *Z. palustris* and *Z. aquatica* has been considered by Duvall (1987), through use of isoelectric focusing profiles; he speculated that introgression is a causal agent of variation in the genus.

Within the aquatic ecosystems, wildrice is a fastidious species, showing stringent water depth and quality requirements as well as poor competitive ability with other aquatic species. Given apparently restricted gene flow and the fact that wildrice is not an aggressive colonizer of disturbed habitats, weedy races of wildrice probably will not arise in the immediate future. Weedy populations provide an opportunity to assess gene flow from crop to wild relative, a phenomenon of potential importance in a number of weed-crop complexes (Ladizinsky 1985).

GEOGRAPHIC EXPANSION AND AUTOMATIC SELECTION

If domestication in its most general sense is considered to be the process by which one species becomes dependent on another for its survival and dispersion (Rindos 1984), then geographic expansion has considerably accelerated the domestication process. Certainly the propensity of humans to move plants out of their native habitat has been a potent force in crop evolution (de Wet and Harlan 1975). With the expansion of wildrice production outside the area of adaptation, particularly into the rice (*Oryza*) production areas of California, the domestication scenario is altered.

In the California production environment, relatively high temperatures and low moisture after harvest preclude reseeding by seed from shattering losses as a management practice. This has implications for the domestication of wildrice. First, intense selection is applied to sizeable populations of seed (from shattering) for the ability to overwinter, i.e., for a diminution of dormancy requirements. Second, since paddies are re-planted annually with harvested seed, automatic selection is initiated. Control of seeding rates has obvious advantages from a production standpoint; California growers use high plant densities to limit tillering, and thereby minimize the importance of tiller synchrony. Crop management, coupled with a climate unfavorable for *Bipolaris* spp. epidemics creates, temporarily at least, a disease-free agroecosystem.

CONCLUSION

Wildrice exhibits many of the characteristics associated with progenitors of cultivated cereals. These traits, including shatter resistance, tiller synchrony, and seed size, are under genetic control. There is substantial genetic variance for domestication traits in wild rice cultivars tracing to a single collection of wild germplasm. Given the heritabilities of these traits, deliberate selection may accelerate the domestication process. Continued wildrice production in California, coupled with directed plant breeding efforts, may accelerate the domestication process through automatic selection and rapidly bring wildrice into the pantheon of cultivated cereals.

LITERATURE CITED

Brown, E., and C. S. Scofield. 1903. Wild rice: its uses and propagation. U.S.D.A. Bur. Pl. Industr. Bull. 5:8–24.

Browning, J. A. 1974. Relevance of knowledge about natural ecosystems to development of pest management programs for agroecosystems. Proc. Am. Phytopath. Soc. 1:191–199.

Cardwell, V. B., E. A. Oelke, and W. A. Elliott. 1978. Seed dormancy mechanisms in wild rice (*Zizania aquatica*). Agron. J. 70:481–484.

Chambliss, C. E. 1922. Wild rice. U.S.D.A. Circ. 229. Washington, DC.

Chang, T. T. 1985. Crop history and genetic conservation: rice—a case study. Iowa State J. Res. 59: 425–496.

de Wet, J. M. J., and J. R. Harlan. 1975. Weeds and domesticates: evolution in the man-made habitat. Econ. Bot. 29:99–107.

———, and E. A. Oelke. 1978. Domestication of American wild rice (*Zizania aquatica* L., Gramineae). J. Trad. Biol. Agric. 25:67–84.

Doggett, H., and B. N. Majisu. 1968. Disruptive selection in crop development. Heredity 23:1–23.

Dore, W. G. 1969. Wild rice. Canada Dept. Agric. Res. Publ. 1393:1–84.

Dudley, J. W., R. J. Lambert, and D. E. Alexander. 1974. Seventy generations of selection for oil and protein concentration in the maize kernel. Pages 181–212 *in* J. W. Dudley, ed., Seventy generations of selection for oil and protein in maize. Crop Sci. Soc. Am., Madison, WI.

Duvall, M. R. 1987. A systematic evaluation of the genus *Zizania* (Poaceae). Ph.D. dissertation, Univ. of Minnesota, St. Paul.

Elliott, W. A. 1980. Wild rice. Pages 721–731 *in* W. R. Fehr and H. H. Hadley, eds., Hybridization of crop plants. Amer. Soc. Agron., Madison, WI.

———, and G. J. Perlinger. 1977. Inheritance of shattering in wild rice. Crop Sci. 17:851–853.

Everett, L. A., and R. E. Stucker. 1983. A comparison of selection methods for reduced shattering in wild rice. Crop Sci. 23:956–960.

Faris, M. A., and H. R. Klinck. 1982. Comparison between different methods of measuring synchrony of ear emergence in barley, oat, and spring wheat cultivars. Z. Pflanzenzücht. 88:79–88.

Foster, K. W., and J. N. Rutger. 1980. Genetic variation of four traits in a population of *Zizania aquatica*. Canad. J. Pl. Sci. 60:1–4.

Fyles, F. 1920. Wild rice. Dominion of Canada, Dept. Agric. Bull. 42.

Harlan, J. R. 1975. Crops and man. Amer. Soc. Agron., Madison, WI.

———. 1976. Disease as a factor in plant evolution. Annual Rev. Phytopathol. 14:31–51.

———, J. M. J. de Wet, and E. G. Price. 1973. Comparative evolution of cereals. Evolution 27: 311–325.

Hayes, P. M., and R. E. Stucker. 1987. Selection for heading date synchrony in wild rice. Crop Sci. 27:653–658.

Johnson, E. 1969. Archaeological evidence for utilization of wild rice. Science 163:273–277.

Kernkamp, M. F., R. Kroll, and W. C. Woodruff. 1976. Diseases of cultivated wild rice in Minnesota. Pl. Dis. Reporter 60:771–775.

Ladizinsky, G. 1985. Founder effect in crop evolution. Econ. Bot. 39:191–199.

Leppik, E. E. 1970. Gene centers of plants as sources of disease resistance. Ann. Rev. Phytopathol. 8:323–344.

McAndrews, J. H. 1969. Paleobotany of a wild rice lake in Minnesota. Canad. J. Bot. 47:1671–1679.

Moyle, J. B. 1944. Wild rice in Minnesota. J. Wildlife Managem. 8:177–184.

Nabhan, G., and J. M. J. de Wet. 1984. *Panicum sonorum* in Sonoran Desert agriculture. Econ. Bot. 38:65–82.

Nelson, R. N., and R. P. Dahl. 1986. The wild rice industry: economic analysis of rapid growth and implications for Minnesota. Staff paper P86-25. Dept. Agric. and Appl. Econ., Univ. of Minnesota, St. Paul.

Nelson, R. R. 1978. Genetics of horizontal resistance to plant diseases. Annual Rev. Phytopathol. 16:359–378.

Oelke, E. A. 1982. Introduction. Pages 1–2 *in* R. Sherman, ed., Wild rice production in Minnesota. Agric. Extens. Serv., Minnesota Agric. Extens. Bull. 464.

———. 1983. Longevity of wild rice (*Zizania palustris*) seeds in peat and mineral soil under three different flooding regimes. Agron. Abstr. 1983: 120. Amer. Soc. of Agron., Madison, WI.

Oka, H. I., and T. T. Chang. 1961. Hybrid swarms between wild and cultivated rice species, *Oryza perennis* and *O. sativa.* Evolution 15:418–430.

Palm, W. E. 1984. Half-sib family selection in wild rice (*Zizania palustris* L.). Ph.D. dissertation, Univ. of Minnesota, St. Paul. (Diss. Abstr. 45:1378.)

Paroda, R. S. 1972. The impact of synchrony of ear emergence on grain yield and components of yield, and the path coefficient analysis in spring barley. Z. Pflanzenzücht. 67:145–160.

Percich, J. A., and L. L. Nickelson. 1982. Evaluation of several fungicides and adjuvant materials for control of brown spot of wildrice. Pl. Dis. Reporter 66:1001–1003.

Rindos, D. 1984. The origins of agriculture: an evolutionary perspective. Academic Press, New York.

Robinson, R. A. 1980. New concepts in breeding for disease resistance. Annual Rev. Phytopathol. 18:189–210.

Rossman, G. 1973. Wild rice, a delicious food, Northprint, Grand Rapids, MN.

Schwanitz, F. 1966. The origin of cultivated plants. Harvard University Press, Cambridge.

Steeves, T. A. 1952. Wild rice—Indian food and a modern delicacy. Econ. Bot. 26:107–142.

Stucker, R. E. 1982. Varieties. Pages 12–14 *in* R. Sherman, ed., Wild rice production in Minnesota. Agric. Extens. Serv., Minnesota Agric. Extens. Bull. 464.

Vavilov, N. 1951. The origin, variation, immunity, and breeding of cultivated plants. (Trans. K. S. Chester). Chron. Bot. 13:1–364.

Wandrey, G. G. 1988. Genetic variation for seed length in wild rice (*Zizania palustris* L.). Ph.D. dissertation, Univ. of Minnesota, St. Paul.

Warwick, S. I., and S. G. Aiken. 1986. Electrophoretic evidence for the recognition of two species in annual wild rice (*Zizania,* Poaceae). Syst. Bot. 11:464–473.

Wilke, P. J., R. Bettinger, T. R. King, and J. F. O'Connell. 1972. Harvest selection and domestication in seed plants. Antiquity 46:203–209.

Winchell, E. H., and R. P. Dahl. 1984. Wild rice: production, prices, and marketing. Minnesota Agric. Exp. Sta. Misc. Publ. 29.