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Breeding Perennial Grain Crops

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ABSTRACT: One-third of the planet's arable land has been lost to soil erosion in recent decades, and the pace of this degradation will increase as the limits of our food production capacity are stretched. The persistent problem of worldwide soil erosion has rekindled interest in perennial grain crops. All of our current grain crops are annuals; therefore, developing an array of new perennial grains - grasses, legumes, and others – will require a long-term commitment. Fortunately, many perennial species can be hybridized with related annual crops, allowing us to incorporate genes of domestication much more quickly than did our ancestors who first selected the genes. Some grain crops — including rye, rice, and sorghum — can be hybridized with close perennial relatives to establish new gene pools. Others, such as wheat, oat, maize, soybean, and sunflower, must be hybridized with more distantly related perennial species and genera. Finally, some perennial species with relatively high grain yields — intermediate wheatgrass, wildrye, lymegrass, eastern gamagrass, Indian ricegrass, Illinois bundleflower, Maximilian sunflower, and probably others — are candidates for direct domestication without interspecific hybridization. To ensure diversity in the field and foster further genetic improvement, breeders will need to develop deep gene pools for each crop. Discussions of breeding strategies for perennial grains have concentrated on allocation of photosynthetic resources between seeds and vegetative structures. However, perennials will likely be grown in more diverse agro-ecosystems and require arrays of traits very different from those usually addressed by breeders of annuals. The only way to address concerns about the feasibility of perennial grains is to carry out breeding programs with adequate resources on a sufficient time scale. A massive program for breeding perennial grains could be funded by diversion of a relatively small fraction of the world's agricultural research budget.

KEY WORDS: natural systems agriculture, interspecific hybridization, crop domestication, cereal, legume.

I. THE NEED FOR PERENNIAL GRAINS

Annual grain crops have dominated the Earth's agricultural landscape since the time of the earliest farmers 10,000 years ago. Soil erosion followed tillage agriculture as it spread across the Earth's surface (Lowdermilk, 1953; Hillel, 1991). In the last few decades, one-third of the planet's arable land has been lost to soil erosion (Pimentel et al., 1995). The pace of this degradation will increase as the limits of our food production capacity are stretched to feed a growing population of humans and domestic animals.

It may indeed be possible to expand food production to feed 10 billion people by the year 2050 (Evans, 1998); however, if grain continues to be produced in 2050 by methods that erode soil and waste other nonrenewable resources, the Earth may not have the capacity to sustain adequate food production into the 22nd century. Tillage agriculture on sloping land always brings the risk of soil erosion. The increasingly common practice of no-till production of annual crops, designed to control soil loss, has so far required increased use of herbicides. Furthermore, direct-seeded annual cropping systems have been shown to produce as high or higher nitrous oxide emissions as tillage systems (Mummey et al., 1998). Research on wholly new agricultural systems may provide the means to produce food on otherwise

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marginal lands and arrest or even reverse losses of ecological capital associated with many current systems. Our best examples to follow in developing solar-powered, less-polluting, soil-conserving forms of agriculture are natural systems.

Natural systems agriculture, still in the experimental phase (Piper, 1999), is a new approach to crop production. The principles of natural systems agriculture can be applied to any food-producing landscape, but most research to date has been conducted in central Kansas, USA, aimed at developing a “domestic prairie”, with herbaceous, perennial grain-producing crops grown in polyculture (Jackson and Jackson, 1999; Piper, 1999).

Other, less far-reaching recommendations for reducing soil erosion also involve perennial grains (Wagoner, 1990a; Scheinost et al., 2001). However, all of our major grain crops are annuals, and no current perennial species produce sufficiently high yields. Plant breeders must develop an array of perennial grain crops — grasses, legumes, and plants representing other families — before natural systems agriculture or other methods of producing food without soil erosion can succeed.

Wagoner (1990a) published in this journal a comprehensive review of efforts to develop perennial grains in the grass family. Her article made a convincing argument for the development of perennial grains, provided a thorough history of breeding programs worldwide up to 1990, and recommended approaches to be taken in further research on breeding and crop production. We first reexamine the feasibility of perennial grain crops, building on Wagoner’s discussion. Then we review genetic research and efforts to breed perennial grains in the grass family since 1990 and examine some possibilities for breeding perennial grains other than grasses. Finally, we undertake an expanded discussion of breeding methodology relevant to all perennial grains.

We keep the discussion general, recognizing that the term “perennial” has very different meanings in different environments. We discuss tropical and temperate crops, crops of tropical origin grown in temperate zones, and temperate crops that can be grown in the tropics. However, we discuss only those species on which research aimed at perennial grain production has been done or proposed, with concentration on the environment targeted by each research project.

II. PERENNIALS TO ANNUALS, AND NOW BACK TO PERENNIALS

A. Prevalence of Annual Grain Crops

Whyte (1977) noted that the rapid warming of the Earth’s climate at the end of the Pleistocene Ice Age 11,000 years ago created three large and three small “arid cores” on the Asian continent. On the fringes of these cores there formed concentric “isoexothermic zones”, where the highest annual temperatures occurred during the dry season. The new climatic regime in those belts favored annual grasses and legumes, which could survive long hot, dry periods in the form of seeds. Their seeds were relatively large and could germinate and grow quickly with seasonal rains and moderating temperature. Annuals largely displaced perennial species in isoexothermic zones such as the Fertile Crescent of southwest Asia, becoming “suddenly and abundantly available” to human hunter-gatherers.

According to Whyte (1977), the wide availability of annuals in the various isoexothermic zones led humans, who previously had relied in part on seeds of perennial grasses for food, to initiate the agricultural revolution and carry it well beyond its regions of origin. Wagoner (1990a) summarized the subsequent events that led to the human species’ almost complete reliance on annual species for use as grain crops, with tiny pockets of perennial grain production persisting into modern times. As she points out, “our ancestors took the easy route” by concentrating on annual grains.

A difficult road lies ahead for breeders intending to develop perennial grains. Breeding herbaceous perennials for adaptation in regions where the vegetation until recently was almost entirely made up of herbaceous perennials (e.g., the prairie of the central United States) should be eminently feasible, but simultaneous selection for persistence and grain yield will require intensive work. To domesticate wild perennials with no genetic input from other species would entail a genetic retreat of 10,000 years. Fortunately, it is possible to shorten this new round of crop development by orders of magnitude. Many perennial species can be hybridized with related annual crops, allowing us to incorporate genes of domestication much more quickly than did our ancestors who first selected the genes.

B. Resource Allocation and Negative Correlations

Breeders have before them the genetic resources for breeding perennial grains, but just beyond lies the question of a "tradeoff" between grain yield and perenniality (Jackson and Jackson, 1999). In the words of Wagoner (1990a), "Yield from a perennial grain will probably never be as high as that from annuals because the life strategies of annuals and perennials are so different". The photosynthetic energy assimilated by a perennial plant over the course of a growing season must be divided among its perennating structures and seeds."

Indeed, high-yielding perennial grains do not exist today. Wagoner's (1990a) survey of 51 experimental studies in 27 species of perennial grasses showed that seed yields most often fell below 1000 kg/ha but could exceed that level. Piper (1999) reported similar yields in perennial grasses; however, two perennial legumes, Illinois bundleflower (*Desmanthus illinoensis*) and wild senna (*Cassia marilandica)*, yielded up to 2000 kg/ha. Suneson et al. (1963) reported that their 25 years of work with perennial wheat (*Triticum aestivum* hybridized with perennial grasses) in California had produced lines whose first-year yields fell "within the range of the lowest yielding commercial wheat varieties" of the time, with a rapid yield decline in subsequent years. Recently, eight intergeneric wheat lines selected for regrowth ability in Washington state, USA, yielded between 1600 and 5800 kg/ha, compared with almost 9000 kg/ha for the popular annual wheat cultivar 'Madsen' (Scheinost et al., 2001).

Is a tradeoff between perenniality and grain yield inevitable? The fundamental assumption of tradeoff theory — that the pool of carbon to be shared by reproductive and vegetative structures is fixed and cannot be increased by breeding — is open to question (Jackson and Jackson, 1999). Grain production can be sink limited (Slafer and Savin, 1994); for example, shading during development of wheat inflorescences (i.e., during determination of sink size) depressed grain yield, whereas shading during grain filling (once sink size was fixed) had much less effect (Evans, 1978). When yield is sink limited, more or larger reproductive structures will induce greater production of photosynthate, resulting in little competition with perennating structures. Basal- or rhizome-derived tillers on a grass plant are largely self-sufficient (Nyahoza et al., 1973; Jackson and Dewald, 1994), and their own inflorescences can supply much of the photosynthate for seed development (Blum, 1985). Perennials also may be able to maintain green tissue and continue to photosynthesize late in the growing season, after the photosynthetic tissue of annuals has senesced (Scheinost et al., 2001). For all of these reasons, there need not be a gram-for-gram tradeoff between grain and perennating structures.

Most experimental studies have addressed the question of grain yield per hectare vs. persistence over seasons only indirectly (see Jackson and Jackson, 1999). Jackson and DeWald (1994) compared half-sib populations from a population of *Tripsacum dactyloides* segregating for a 'pistillate' mutation that causes a large increase in seed production per inflorescence. The increased seed yield did not come at the expense of plant vigor or longevity. Piper and Kulakow (1994) found no correlation between seed and rhizome production in a population of unreplicated, winterhardy F_3 plants from an interspecific cross between tetraploid *Sorghum bicolor* and *S. halapense*; however, rhizome production was all but lost in backcrosses to *S. bicolor*, the cultivated species.

Any tradeoff between yield and perenniality should occur only during establishment of the first year's crop from seed. Once perennating structures are developed, they can serve as a source of carbon for plant establishment in subsequent years (Jackson and Jackson, 1999). By way of comparison, Wagoner et al. (1993) computed the energetic costs of sowing and establishing a hectare of annual wheat, including all energy required to produce the seed (Heichel, 1980), cultivate the land, and sow the seed. The resulting cost of "annuality" was equivalent to the usable energy contained in 715 kg of wheat grain, amounting to 32% of the crop's yield in that study. Wagoner (1995) provided a table of calculations by Watt (1989) showing that intermediate wheatgrass yielding only 673 kg/ha/yr over 4 years without resowing would have a break-even price of $3.60 per bushel, similar to that of spring wheat at the time.

The negative relationship assumed to exist between perenniality and grain yield is largely based on life-history theory (e.g., Gadgil and Solbrig, 1972; Jackson and Jackson, 1999). Gardner (1989) has provided a physiological application of the theory to crop plants. However, these theories are based on observation of existing species, which are products of natural and artificial selection in divergent directions (Figure 1). High-seed-yielding herbaceous perennials are not found in nature — or are triticale (X T*riticosecale*) or maize (*Zea mays*), and for the same reason. Artificial hybridization and selection produced triticale and maize, and they can, conceivably, generate productive perennial grains.

Even if there is a negative correlation between perenniality and grain yield, it does not preclude selection. Consider two sexually com-

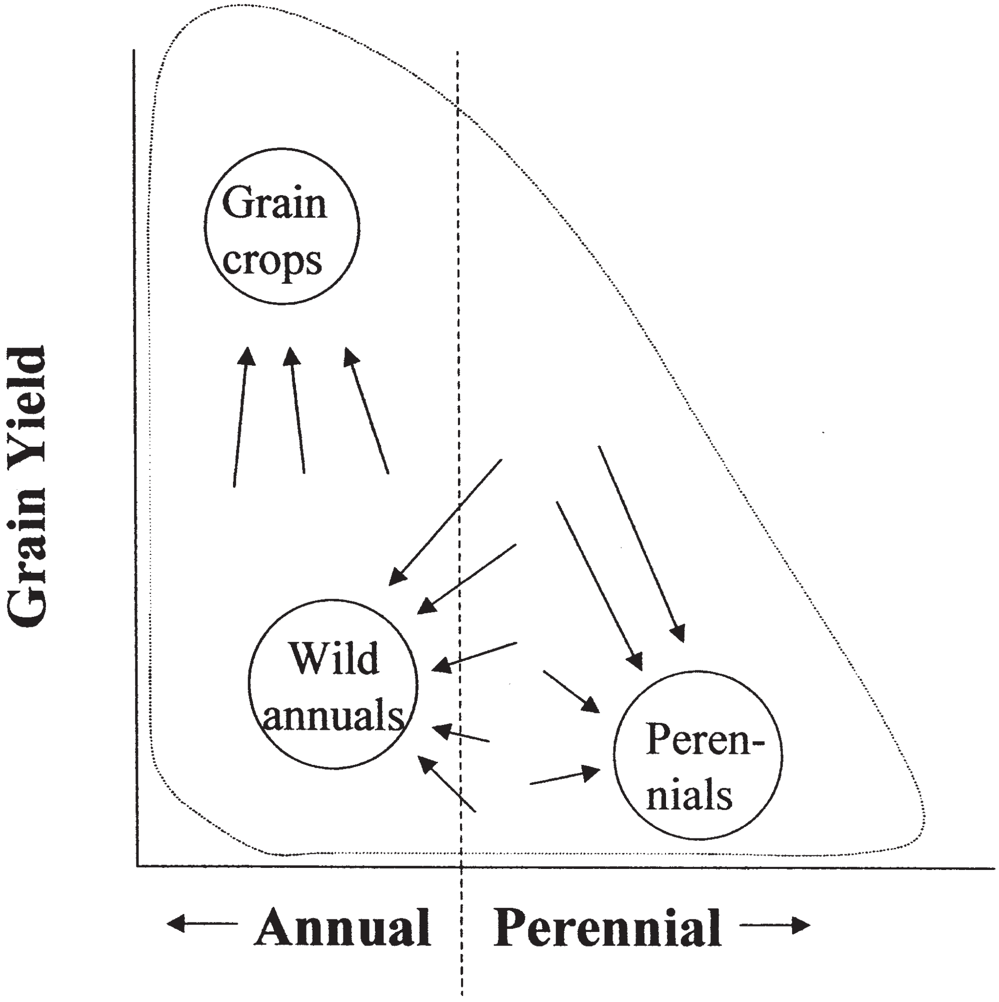

FIGURE 1. Divergent selection pressures restricting the variability of perennial plants, wild annual plants, and annual grain crops. The horizontal axis represents a gradient ranging from strong annuality to strong perenniality, with a threshold (dashed line) separating the growth habits. The vertical axis is grain yield per season. The dotted curve represents hypothetical genetic limits of the two-way distribution.

patible gene pools (Figure 2): an annual population with high grain yield (P_1) and a perennial one with low grain yield (P_2). If P_1 and P_2 are crossed, the hybrid population H_0 will tend to lie in an elongated distribution between them — a "recombination spindle" (Anderson, 1949). The long axis is oriented between the parents because of genetic linkages and pleiotropic trait associations. The latter includes any negative correlation between grain yield and perenniality that might result from a carbon tradeoff.

Selection in the hybrid population along the long axis of its distribution (i.e., toward P_1 or P_2) would result in a larger response per generation than selection perpindicular to the long axis. However, even when selection is perpendicular to the long axis — in the direction of higher grain yield and stronger perenniality — it has the potential to approach the ancestral genetic limits (Figure 1) or even exceed them via new introgression or mutation (Figures 2 and 3). Direct selection within a perennial population for grain yield (Figure 3) does not take advantage of genes from the annual crop and may be a longer-term project.

In any plant breeding program, negative correlations are a daily challenge. As Figures 2 and 3 illustrate, simultaneous selection for negatively correlated traits can succeed if compromises in gains for individual traits are accepted. For example, selection for seed protein or oil concentration often has a negative effect on grain yield (Loffler et al., 1983; Brim and Burton, 1978; Burton and Brim, 1981); nevertheless, yield and grain quality have been improved simultaneously

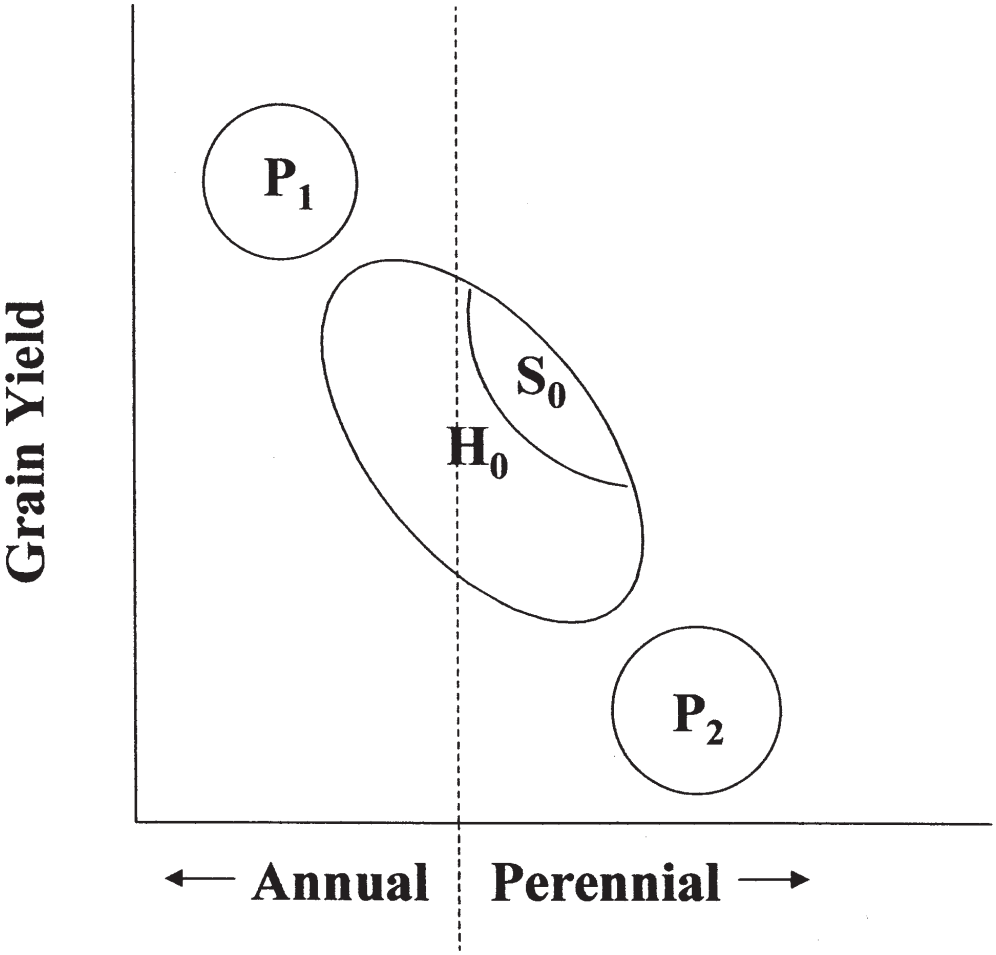

FIGURE 2. Distributions of an annual grain-crop population P_1, a perennial population P_2, a population H_0 derived by hybridizing P_1 with P_2, and a segment of H_0 (S_0) selected for both perenniality and grain yield.

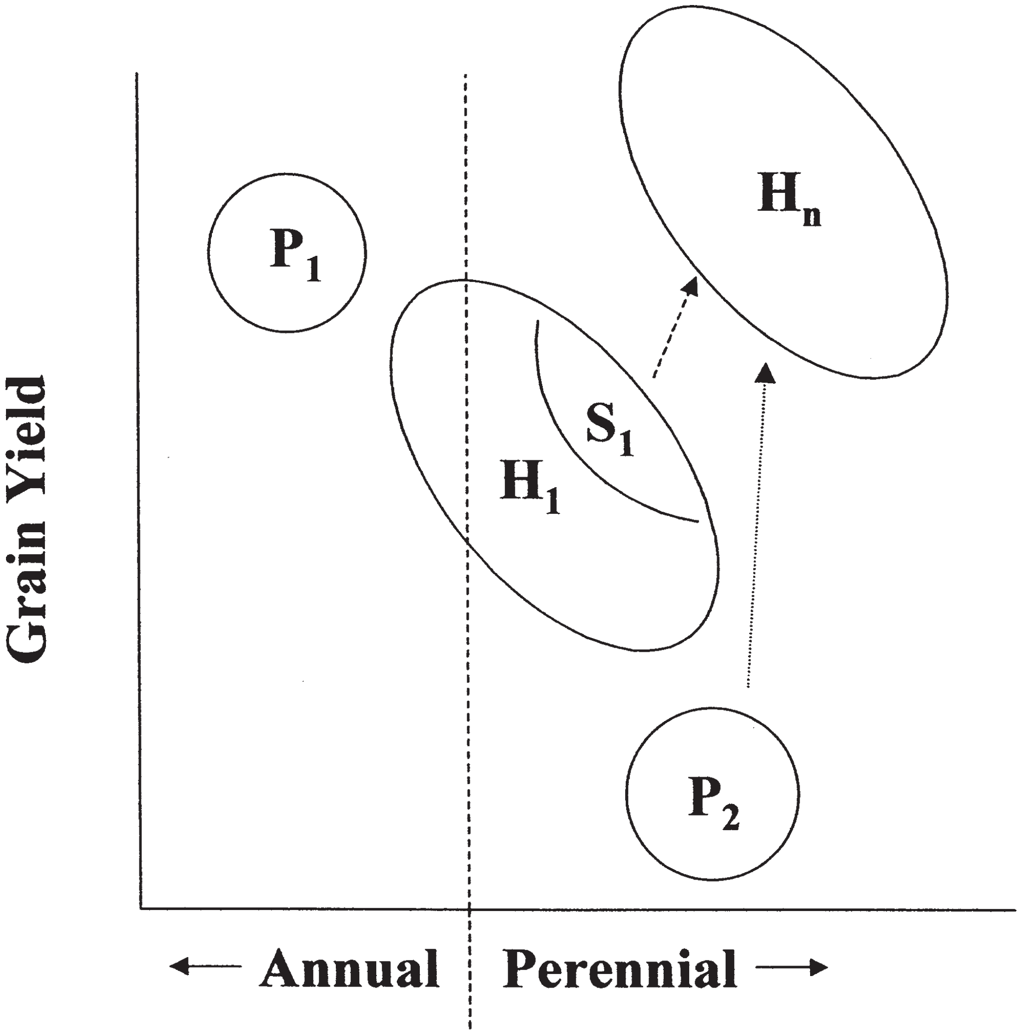

FIGURE 3. Distributions of two parental populations (P_1 and P_2), a population H_1 derived by interpollinating selected individuals (S_0 from Figure 1), a selected segment of H_1 (S_1), and a population H_n resulting from n cycles of selection for grain yield among selected individuals (dashed arrow). Direct selection within P_2 for grain yield (dotted arrow) could also produce a population such as H_n.

by breeding programs (Cox et al., 1989). Plant breeders routinely make some sacrifice in grain yield to improve pest resistance, and the cost in resources and effort is real, regardless of whether the resistance is genetically linked to lower yielding ability. Breeders of legumes could obtain almost immediate yield increases by eliminating symbiotic fixation of atmospheric nitrogen, which has a higher energetic cost to the plant than does absorption of nitrate from the soil (Finke et al., 1982; Salsac et al. 1984). However, they forgo that yield increment because biological nitrogen fixation is highly valued.

The relatively low yield of perennial grains recorded to date should not be attributed entirely to the carbon tradeoff. Perennial grains currently undergoing domestication are still essentially wild. In perennial grains being developed from interspecific hybridization, different genetic problems, each with its own array of possible solutions, have hampered breeding for yield. Among such obstacles are partial sterility caused by chromosomal differences between parental species; instability of chromosomal constitution; failure to eliminate genes for poor adaptation (unassociated with perenniality) from breeding populations; and lack of genetic diversity.

If breeding perennial grains is a difficult but attainable goal, it is important for research institutions to initiate cereal-, legume-, and oilseedbreeding programs aimed exclusively at developing perennials. Today, while 33% of the world's cereal crop is fed to animals in the developed countries (Evans, 1998), we have some latitude to begin breeding crops that preserve the land while, initially at least, producing fewer total bushels than our current crops with their heavy subsidy of energy and chemicals. If we wait several decades to begin a breeding program, it may very well be too late.

We now review recent results and prospects for perennial counterparts of major annual crop species and some perennial species that have not yet been domesticated. A realistic consideration of prospects, crop by crop, may give some insight into how research resources and efforts should be allocated among and within species in coming decades.

III. BREEDING PERENNIAL GRAINS: COOL-SEASON GRASSES

A. Wheat

1. Development of Perennials up to 1990

Hexaploid wheat [*Triticum aestivum*, 2n=42, genomes AABBDD] arose approximately 5000 years ago when the genomes of tetraploid wheat (*T. turgidum* or *T. carthlicum*, both 2n=28, AABB) and an Asian goatgrass (*Aegilops tauschii*, 2n=14, DD) were combined via amphiploidization (i.e., natural hybridization followed by spontaneous production of 2n gametes in the hybid.) Tetraploid wheat itself is a much older natural amphiploid, incorporating the genomes of two diploid grasses. Both wheats are part of the large and diverse Triticeae tribe of the grass family (Gramineae), which also includes scores of perennial species, many of which can be hybridized with wheat (Dewey, 1984.)

Wagoner (1990a) examined in detail the early history of efforts in the United States, Canada, Germany, and, most importantly, the USSR to transfer genes for perenniality from alien grass species into bread wheat, citing more than 65 publications on the subject. None of these efforts produced a truly perennial grain cultivar, but they did spin off much valuable annual germplasm with genes for disease resistances and other traits. In the end, most of the effort in the perennial-wheat programs was diverted into producing improved annual cultivars, where progress was more easily achieved.

Of the few perennial, grain-producing genotypes developed from wide hybrids at the time of Wagoner's review, none was agronomically successful. Soviet-developed 'perennial' cultivars (Tsitsin, 1965) produced good grain harvests only in the year in which they were established from seed; in the end, they were used mainly as forage cultivars that provided no more than one grain harvest. The U.S. germplasm 'MT-2', derived from a hybrid between *T. turgidum* and *Thinopyrum intermedium* (2n=42), released by Schulz-Schaeffer and Haller (1987) in Montana, had very low kernel weight and unreliable persistence. In Sweden, Fatih (1983) found that yields of perennial *T. aestivum*/*Th. intermedium* partial amphiploids (2n=56) were, on average, only 48% of the yields of 42-chromosome, annual, backcross-derived lines of similar parentage.

2. Production of New Hybrids

In the decade since Wagoner's review, no perennial wheat cultivars have been released for production. However, basic research on hybridization and cytogenetics has opened up new possibilities for geneticists and breeders interested in the problem.

Species of the genus *Thinopyrum* have been hybridized with wheat more often than have any other perennial species (Dewey, 1984) because of the ease of producing partially fertile hybrids, often without embryo rescue (Jauhar, 1995). *Thinopyrum intermedium* (2n=42) is rhizomatous, and two other commonly utilized species, *Th. ponticum* (2n=70) and *Th. elongatum* (2n=14) are caespitose. Researchers at Washington State University have launched a new program to develop perennial wheat from *Thinopyrum* crosses, with promising preliminary results (Scheinost et al., 2001; Cai et al., 2001). As we shall see (Section III.A.3.), recent cytological and molecular studies have explained why *Thinopyrum* crosses have often led to frustration, and in doing so have suggested new approaches.

Other species in the genera *Thinopyrum*, *Elymus*, and *Leymus* have long been investigated as sources of perenniality (Wagoner, 1990a), and the perennial gene pool available to wheat geneticists is growing rapidly. In a review, Sharma and Gill (1983) listed only 16 perennial species that had been hybridized with hexaploid or tetraploid wheat, including only one species — *Elymus giganteus* — outside the *Agropyron-Thinopyrum* complex. A decade later, Jiang et al. (1994) added 38 additional species, including 17 in *Elymus* and 6 in *Leymus*, to the list of hybrids. Sharma (1995) reviewed the production of hybrids between wheat and more than 50 perennial species.

Our ability to make crosses and backcrosses between distantly related species has grown along with advances in embryo rescue, hormone treatments, intraovarian fertilization, bridge crosses, and protoplast fusion (Sharma, 1995). The effects of these techniques are magnified when they are used to exploit intraspecific variation for crossability, combining ability, or variation among species carrying the same or similar genomes. Especially important are reciprocal crosses followed by embryo rescue when the traditional method of using the species with higher chromosome number fails (Sharma, 1995).

Within each perennial species, accessions can vary in crossability, and choice of the annual wheat parent can also have a strong effect. For example, homozygosity for *kr* crossability alleles often makes hybridization possible, and may even improve early seed development; however, it may not affect results in extremely wide crosses (Sharma, 1995). Choice of the wheat parent may depend on other considerations. Hybrids of *Thinopyrum* and *Leymus* with Chinese Spring (*krkr*) could not survive winter temperatures, whereas hybrids with two Japanese spring wheats were winterhardy (Comeau et al., 1985). Fertility in the F_1 through production of unreduced gametes can be induced by crossing the perennial species with the tetraploid wheat *T. carthlicum* and maintaining low temperatures during pollination and embryo development (Anamthawat-Jonsson et al., 1997).

Many wheat/*Elymus* hybrids have been made in recent years (see Jiang et al., 1994; Sharma, 1995), and addition, substitution, and translocation lines have been developed (Jiang et al., 1993; Gill et al., 1988; Morris et al., 1990). However, to our knowledge, no explicit effort to transfer perenniality from *Elymus* to wheat is underway. Lu and von Bothmer (1991) produced hybrids between 12 *Elymus* species (2n=28 or 42) and wheat (2n=42). Hybridization was made possible by using *Elymus* as the female parent and rescuing hybrid embryos, as first demonstrated by Sharma and Gill (1983). All hybrids were perennial, but chromosome pairing was very low, as expected. The hybrids were not treated with colchicine to produce amphiploids.

Hybridization between wheat and the genus *Leymus* has a long history, but has not led to perennial cultivars (Wagoner, 1990a). Hybrids are most easily obtained with the larger-seeded, self-pollinated species of the genus: *L. arenarius* (2n=56), *L. racemosus* (2n=28), and *L. mollis* (2n=28) (Dewey, 1984), and these species also have the greatest agricultural potential (Anamthawat-Jonsson, 1996). Wheat has been crossed with eight *Leymus* species in all (see Jiang et al., 1994; Sharma, 1995). Most crosses require embryo rescue (e.g., Mujeeb-Kazi and Rodriguez, 1981; Plourde et al., 1989a and b; Anamthawat-Jonsson et al., 1997). Hormonal treatment has been used in producing F_1 (Anamthawat-Jonsson et al., 1997) and BC_1 (Mujeeb-Kazi and Rodriguez, 1981) seed.

Wheat/*Leymus* hybrids produced by the Soviet perennial-wheat breeding program were perennial (Bodrov, 1960; Petrova, 1960) but less winterhardy than wheat-*Thinopyrum* hybrids (Bodrov, 1960). In recent studies, hybrids produced by pollinating two wheat species (*T. aestivum* and the tetraploid *T. carthlicum*) with *L. arenarius* and *L. mollis* were perennial, producing short rhizomes (Anamthawat-Jonsson et al., 1997) and exhibiting some intergenomic pairing and a high enough level of fertility to permit backcrossing (Anamthawat-Jonsson and Bodvarsdottir, 1998). Hybrids between *T. aestivum* and two other species, *L. innovatus* and *L. multicaulis*, were nonrhizomatous (Plourde et al., 1989a and b).

3. Advances in Chromosome Identification

A revolution in cytogenetic techniques has led to a better understanding of the problems faced by perennial wheat breeders. MT-2 provides a good example. It was derived by selfing a 70-chromosome amphiploid containing the genomes of durum wheat (*T. turgidum*, 2n=28, genomes AABB) and *Th. intermedium*, (2n=42, genomes StStEEEStESt). Schulz-Schaeffer and Haller (1987) predicted that MT-2 would stabilize at 2n=56 through elimination of *Thinopyrum* chromosomes. In fact, according to Jones et al. (1999) individual plants of MT-2 vary in chromosome number, with most having 2n=56. However, genomic *in situ* hybridization (GISH) showed that 56-chromosome MT-2 plants contained numbers of wheat chromosomes varying between 24 and 28. Therefore, there had been a loss of wheat chromosomes in some plants, and *Thinopyrum* chromosomes had been eliminated at random. Plants contained up to four St-E or St-Est translocated chromosomes but no wheat-*Thinopyrum* translocations.

A wheat/*Thinopyrum* hybrid known as AT 3425, which has resistance to Cephalosporium stripe disease and perennial growth habit (Mathre et al., 1985), has 2n=56; fluorescent genomic in situ hybridization (FGISH) and C-banding showed that AT 3425 has 36 wheat chromosomes, 14 *Thinopyrum* chromosomes, and 6 chromosomes resulting from translocations between the two species (Cai et al., 1998). The *Thinopyrum* chromatin in AT 3425 and another line with the same chromosome configuration, PI 550713, probably originated from *Th. ponticum*, and both lines are cytologically stable (Cai et al., 2001). Another perennial, 56-chromosome line, AgCs, carries the combined genomes of hexaploid wheat and the diploid species *Th. elongatum* (Cai et al., 2001).

Banks et al. (1993) examined meiotic pairing in crosses among eight 56-chromosome partial amphiploids derived from crosses between hexaploid wheat (*T. aestivum*) and *Th. intermedium*. As is often found (Dvorak, 1976), the lines had all 42 wheat chromosomes as well as 14 from *Thinopyrum*. The sets of chromosomes originating from *Th. intermedium* differed in all but two lines. Unfortunately, all eight amphiploids studied meiotically by Banks et al. (1993) were annual; two Soviet-developed perennial wheats were examined only phenotypically.

Recently, partial amphiploids that had originated in the Soviet progam (Bodrov, 1960; Petrova, 1960) have been found to be hexaploid, containing 30 chromosomes from tetraploid wheat and 12 from *L. mollis* (Anamthawat-Jonsson, 1999). Thus, as in wheat-*Thinopyrum* amphiploids, elimination of the perennial parent's chromosomes had occurred. In addition, one pair of wheat chromosomes had been substituted for a pair from *L. mollis*. The partial amphiploids were annual.

Thinopyrum elongatum (2n=14) is a diploid that is more difficult to hybridize with wheat than are *Th. intermedium* or *Th. ponticum*; however, the resulting amphiploids are vigorous, stable, and perennial. Because *Th. elongatum* contributes only a single genome, all plants should have the same 56-chromosome complement. For example, the wheat/*Th. elongatum* amphiploid AgCs is cytologically stable and perennial (Cai et al., 2001). Jauhar (1992) produced trigeneric hybrids between a *Th. bessarabicum* – *Th. elongatum* amphiploid and tetraploid wheat (*T. turgidum*). The hybrids (2n=28, ABJE) were vigorous and perennial.

The maximum number of chromosomes that can be tolerated in amphiploids between wheat and *Thinopyrum* spp. appears to be 56 (Dvorak, 1976; Dewey, 1984), although 42-chromosome genotypes are more meiotically stable. Usually, partial amphiploids resulting from crosses with tetraploid wheat will contain approximately 28 chromosomes from the wheat parent and approximately 28 from *Thinopyrum,* whereas partial amphiploids with hexaploid wheat will have approximately 42 from wheat and 14 from *Thinopyrum*. Cauderon (1979) pointed out that partial amphiploids are automatically selected for "good balance" between wheat and perennial chromosomes through the elimination process; however, as we have seen, the same chromosomal complements are not consistently selected. Breeding populations based on collections of such lines would be plagued with sterility and lack of chromosome pairing unless a diploid perennial parent such as *Th. elongatum* is used.

The goal of a breeding program cannot be to develop a single perennial wheat cultivar. One partial amphiploid carefully selected to be cultivated as a perennial would have a unique chromosomal constitution. It would be a gene pool of one individual — a dead end in a breeding program. To launch a perennial wheat breeding program based on partial amphiploids would be an ambitious undertaking, involving the following steps for any polyploid perennial species targeted:

- Hybridize tetraploid and hexaploid wheats with the polyploid perennial species, making many parental combinations and sampling diversity of all parental species.
- Produce amphiploids and self-pollinate with mild selection for enough generations to achieve stable chromosome numbers.
- Use *in situ* hybridization, chromosome banding, genetic markers, and other techniques to identify chromosomes in a large population of selected plants representing many parental combinations.
- Assign partial amphiploids to groups of homogeneous chromosomal constitution.
- Compare groups for all phenotypic traits of interest and select one or a few on which to base further breeding. Develop foundation breeding pools from those groups. Experiment with intercrosses between groups, selecting for potentially superior chromosomal combinations.
- In creating new partial amphiploids to introduce into breeding pools, select strictly for appropriate chromosomal complements.

Such a plan would require a mammoth investment of resources, but the initial production of stable partial amphiploids is feasible on a large scale. Selfing and stabilization will occupy several years; by the time genotypes requiring chromosome identification can be produced, vastly more efficient cytological and molecular techniques are almost certain to be available, bringing the breeding program into the realm of the practical. However, technological improvements do not guarantee the development of truly perennial grains, and parallel strategies are needed.

4. New Strategies for Perennial Wheat

The perennial grasses of the tribe Triticae have long been used in wheat improvement, primarily as sources of individual resistance genes. A traditional strategy for transferring genes is to produce F_1 hybrids between wheat and the donor species; either double the chromosome number of the hybrid to produce an amphiploid or pollinate the F_1 directly; backcross to wheat genetic stocks to produce lines carrying the normal wheat complement of 42 chromosomes plus one or a pair of chromosomes from the donor parent; and — at some point in the process — attempt to induce a translocation that transfers a segment carrying the target gene to a wheat chromosome. There are many variations on this strategy, but the usual goal is to transfer a single gene, eliminating as much of the rest of the donor genome as possible.

Perenniality in wheat's relatives is more genetically complex than the single-gene traits transferred to date and may require a different approach. Amphiploids are not always perennial, and as we have seen they are usually genetically unstable and agronomically undesirable. Backcrossing to wheat usually results in a return to the annual habit. Therefore, Anamthawat-Jonsson (1996) proposed backcrossing instead to the perennial parent — in their research, either *Leymus arenarius* or *L. mollis*. The objective then becomes to improve traits such as grain yield and kernel weight in the perennial species.

Anamthawat-Jonsson (1996) listed the traits to be improved by incorporating wheat germplasm into *Leymus* species: perenniality, grain quality, harvestability, threshability, kernel weight, synchronization of maturity, lodging and shattering resistance, meiotic stability, and, of course, grain yield. She has backcrossed partial amphiploids to *L. mollis*, and the progeny were vigorous with long rhizomes.

In light of the many problems that have been encountered in transferring perenniality to wheat, the converse approach — using wheat to improve the perennial species — may have considerable merit. Backcrossing to the perennial will almost certainly produce breeding populations with low average grain yields and a high frequency of shattering, requiring the screening of large numbers of genotypes. Logic suggests that perennial allopolyploid species will be more tolerant of added or substituted wheat chromosomes. As we have seen, *L. arenarius* has been used as a grain crop in the past, and efforts to improve it using wheat as a donor parent are underway (Anamthawat-Jonsson et al., 1997). *Th. ponticum* is easily crossed with wheat, but its high ploidy level and lack of diploidization (Jauhar, 1995) probably would prevent its use in grain production. Wheat might be used as a donor parent for improving *Th. intermedium* or some hexaploid species of *Elymus* with which it can be crossed (Jiang et al., 1993, 1994).

B. Rye

1. Diploids

Rye (*Secale cereale*) appears to be at least as promising a candidate for perennialization as is wheat. Its chromosomes are homologous with those of its direct perennial ancestor, *S. montanum*. Both species are diploid and cross-pollinated. Rye is very winterhardy, well adapted for grazing, and useful in weed control because of its allelopathic properties (Anaya, 1999). The Soviet perennial-grains program included a large effort in rye (Derzhavin, 1960a), and they produced some weakly perennial genotypes that were used in limited production (Wagoner, 1990a). Later, a decades-long effort to breed perennial rye in Germany met with only partial success (Reimann-Philipp, 1995). Recently, a perennial rye cultivar, 'Perenne', was released in Hungary for grain and forage production (Hodosne-Kotvics et al., 1999).

Despite initial expectations, no perennial rye cultivar has been used in full-scale grain production. Breeders have been stymied by the tendency of plants in *S. cereale*/*S. montanum* populations to be either fertile and annual or highly sterile and perennial (Reimann-Philipp, 1995). A chain of translocations involving three of rye's seven pairs of chromosomes separates the two species (Stutz, 1957; Devos et al., 1993), and gene(s) from *S. montanum* governing perenniality are located on one or more of the translocated chromosomes. Because meiosis in plants heterozygous for one or more translocations produces many inviable gametes with duplications or deficiencies of chromosomal segments, plants in interspecific rye populations fall into one of three categories: homozygous for the *S. cereale* chromosomal arrangement (fertile, annual); heterozygous for one or more of the translocations (highly sterile); or homozygous for the *S. montanum* arrangement (perennial, fertile).

Plants in this last category would seem to answer the breeder's need; however, they are rare, and the large portion of their genomic content derived from *S. montanum* reduces their agronomic desirability and spike fertility. According to Reimann-Philipp (1995), seed-set in *S. montanum* itself is low — approximately 80%. Reimann-Philipp (1995) selected intensely for the *S. cereale* phenotype within an interspecific, perennial population. This population was presumed to be homozygous for the three *S. montanum*–derived chromosomes involved in the translocations, identified as $4R^{mon}$, $6R^{mon}$, and $7R^{mon}$ by Koller and Zeller (1976) but referred to as $2R^{mon}$, $6R^{mon}$, and $7R^{mon}$ by Reimann-Philipp (1995). He was attempting to keep these chromosomes fixed while restoring completely the other four chromosome pairs from *S. cereale* through recombination and selection. He could not achieve a kernel weight greater than 15 mg (compared with typical values of 40 mg for annual rye under those conditions).

As an alternative, Reimann-Philipp (1995) proposed selection for perennial plants carrying chromosomes 2R, 6R, and 7R of *S. cereale*. Presumably, such plants would arise from recombination within the ring of six translocated chromosomes. Dierks and Reimann-Philipp (1966) had postulated that perenniality was governed by a single gene that lay approximately 10 crossover units from one of the breakpoints. Selection for perenniality would be routine, but selection for the *S. cereale* chromosomal constitution would require either a laborious testcross procedure or a cytological test. A morphological difference between chromosomes 6R and $6R^{mon}$ (Reimann-Philipp and Rohde, 1968) did not prove satisfactory for this purpose. Today, the extensive genetic map of rye (Melz et al., 1992) could allow marker-assisted selection for the *S. cereale* arrangement. A large initial experiment could provide much more detailed information on the genetic control of perenniality; as noted by Reimann-Philipp (1995), the trait is probably affected by more than one gene.

Yet another strategy was followed by L.F. Myers and R.J. Kirchner in the breeding of 'Black Mountain' perennial rye in Australia (Freer et al., 1997; Oram, 1996): backcrossing the interspecific hybrid twice to the *S. montanum* parent. Perennialism (and, presumably, the *S. montanum*-type chromosomal arrangement) was quickly restored by backcrossing. However, this cultivar was intended primarily as a forage grass, with *S. cereale* donating genes for nonshattering rachis and improved seed production. Oram (1996) practiced six cycles of half-sib family selection for grain and forage yield in Black Mountain, achieving gains in both traits while maintaining a low level of shattering. With grazing, stands of 'Black Mountain' decline after 3 years; however, if shattering is permitted, stands can be continually replenished by volunteer seedlings (Oram, 1996). Without selection to develop a cultivar strictly for grain production, we cannot know whether backcrossing to perennial rye while selecting for alleles from annual rye can achieve sufficient yield improvement.

Reimann-Philipp (1995) warned of a hazard when growing diploid perennial rye with the *S. montanum* chromosomal arrangement on a field scale. If pollen from the perennial drifted into seed production fields or breeding nurseries of annual rye, the resulting translocation heterozygosity would seriously and irreversibly degrade fertility in subsequent generations.

2. Tetraploids

In an effort to improve kernel weight, Reimann-Philipp (1995) used colchicine to double the chromosome number of a perennial *S. cereale*/*S. montanum* population homozygous for the $4R^{mon}$, $6R^{mon}$, and $7R^{mon}$ chromosomes. The resulting tetraploid, named 'Permontra', had a kernel weight of approximately 30 mg (double that of the diploid), and first-year grain yields over 2000 kg/ha when grown in Germany. Yields declined in subsequent years (Reimann-Philipp, 1986). 'Permontra' achieved a similar grain yield in the Land Institute's plots in Kansas, but only 15 to 20% of the plants regrew in the next season (Piper, 1993). After a first-year harvest in the hot, dry summer of 2001, a stand of Permontra at The Land Institute died out completely by September.

Another problem with 'Permontra' — poor seed set — is also common in annual tetraploid rye, because the formation of multivalent chromosomal associations leads to production of gametes with extra or missing chromosomes (Bremer and Bremer-Reinders, 1954). Selection can improve seed-set in tetraploid rye (Bremer and Bremer-Reinders, 1954), and Reimann-Philipp (1995) pointed out that selection for seed set or meiotic stability can be practiced much more effectively in a perennial, by screening phenotypically or cytologically in one flowering cycle and intercrossing selected plants in the next. He found that phenotypic selection greatly improved seed-set in the perennial spring rye 'Soperta', which was derived from seven 'Permontra' plants that did not require vernalization in order to flower. Another approach would be to introduce the *Ph1* gene from wheat into a tetraploid hybrid between *S. cereale* and *S. montanum* to enforce diploid pairing and improve fertility. The *Ph1* gene was shown to operate when the chromosome carrying it was added to rye (Schlegel et al., 1991).

Tetraploid perennials may provide advantages beyond increased kernel weight. They are reproductively isolated from diploid annual seed production fields (Reimann-Philipp, 1995). In one study, 'Permontra' had greater heat and drought tolerance, and a much more extensive root system, than did diploid or tetraploid annuals (Gordon-Werner and Dorffling, 1988). However, perennial rye, whether tetraploid or diploid, will not be grown widely as a grain crop until the problems of sterility, persistence, and maintenance of yield over seasons are solved.

C. Triticale

To date, the only species to be synthesized by artificial hybridization for use as a cereal crop is triticale (X *Triticosecale*), an amphiploid of durum wheat (*T. turgidum*) and *S. cereale*. (Octoploid triticale cultivars — *T. aestivum*/*S. cereale* — have also been produced but not widely used commercially.) Triticale has not become one of the world's leading cereals, but its modest success suggests the possibility of developing perennial *T. turgidum*/*S. montanum* triticales. Derzhavin (1960b) produced and intercrossed many amphiploids derived from crosses between durum wheat and perennial rye accessions. He augmented the gene pool by allowing the amphiploids to pollinate a large number of different wheat/rye F_1 hybrids. However, the resulting populations were only weakly perennial. Three-way hybrids — from crosses between wheat/*Th. intermedium* hybrids and perennial rye — were more strongly perennial but had sterility, low yields, and small seeds (Derzhavin, 1960b; Lapchenko, 1960).

Robert Metzger (USDA-ARS retired, Corvallis, OR, personal communication) reports that a *S. montanum*-derived triticale that he has developed is not sufficiently perennial, but he recommends producing and screening more new amphiploids involving a wider range of *S. montanum* germplasm. It could be that no triticale will be fully perennial, having only one of three genomes derived from a perennial species. Intercrossing of diverse lines followed by selection could improve persistence over years. If improved hexaploid or tetraploid perennial wheats can be developed, they could be crossed with *S. montanum* to produce more strongly perennial triticales.

In attempting to develop perennial triticales, breeders can take lessons from development of the annual crop (Skovmand et al., 1984; Horlein and Valentine, 1995). Primary triticales, that is, newly doubled wheat/rye hybrids, inevitably suffer from sterility, seed shrivelling, lodging, and low yield potential. Decades of intense selection and introgression have resulted in triticales that are cytologically stable and improved for all of these traits, but they stand on a narrow germplasm base. Improving the performance and genetic variability of the triticale gene pool can be accomplished by several means: production of new primary triticales; triticale/wheat crosses; triticale/rye crosses; and crosses between hexaploid and tetraploid triticales (Skovmand et al., 1984).

Primary triticales derived from the wild *S. montanum* are even more agronomically primitive than *S. cereale*-based primary triticales and will require even greater breeding effort with a wide range of parents. “Substituted” triticales in which one or more wheat chromosomes replace those of rye are often agronomically superior; chromosomes 2D and 6D appear to be selectively propagated by breeders in populations segregating for R- and D-genome chromosomes (Gustafson et al., 1989). However, it must be kept in mind that until genes conditioning perenniality can be mapped, random substitution of wheat for *S. montanum* chromosomes will reduce the chances of selecting a strongly perennial triticale.

D. Direct Domestication of the Perennial Triticeae

1. Intermediate Wheatgrass

From domestication of perennial grasses with wheat or rye as a donor parent (Anamthawat-Jonsson, 1996; Oram, 1996), it is a relatively short leap to domestication without any interspecific crossing. Three large-seeded perennial species that have been hybridized with wheat also have attracted attention as candidates for direct domestication. By far, the most work in this area has been done with *Th. intermedium* by Wagoner (1990a, 1995) at the Rodale Institute in Pennsylvania and her colleagues at the USDA-NRCS Big Flats Plant Materials Center in New York. Wagoner (1990a) described in detail the characteristics that make intermediate wheatgrass a good candidate for domestication as a perennial grain, while noting shortcomings that must be addressed. Becker et al. (1991) concluded that its grain has protein quality “superior to the cereal grains now commonly grown”, with no significant amounts of antinutrients.

Recurrent selection is a logical breeding method for improving an only slightly domesticated, cross-pollinated species like *Th. intermedium*. Using mass selection without controlled pollination, Knowles (1977) increased seed yield in an intermediate wheatgrass population by 10% per cycle. In each cycle, 1000 plants were evaluated for spike fertility over 3 years, and the best 50 were selected. When selected plants were removed to the greenhouse over the winter to exclude pollination by nonselected plants, thereby doubling parental control, gain per cycle increased to 20% — a result perfectly consistent with selection theory (Fehr, 1987).

Gridded mass selection is used to exercise control over microenvironmental effects and increase selection response (Gardner, 1961). Wagoner (1990a, 1995) evaluated 300 accessions of intermediate wheatgrass, for grain yield, yield components, and end-use quality, selecting the 20 best accessions in 1989. The selections were transplanted into a polycross nursery, and 380 progeny resulting from pollination among the selections were evaluated, in a field divided into blocks of 25 plants each, between 1991 and 1994 (Wagoner, 1995; Wagoner et al., 1996). The best 11 plants resulting from within- and among-block selection, plus three selections resulting from further evaluation of other accessions, were put into a second-cycle polycross, and 400 individual progenies were evaluated in a second blocked nursery (Wagoner, 1995). Yield per plant in the 14 selections was approximately 25% higher than the population mean. Evaluation of the second-cycle population is underway, and selected plants will be intermated in 2002 to complete another breeding cycle (M. van der Grinten, USDA-NRCS, Big Flats, NY, personal communication) Better environmental control through selection within blocks may have produced the 5%-point improvement in selection response over that of Knowles (1977), but it remains to be seen if the small effective population size in the second cycle (14 plants) will restrict genetic gain in the future.

2. Wildrye

The Land Institute in Kansas has studied perennial cool-season grasses as potential grain crops for over 20 years (Jackson and Jackson, 1999). They evaluated almost 1500 accessions representing 85 species of *Agropyron*, *Thinopyrum*, *Elymus*, and *Leymus*, along with 2630 accessions of other species, between 1979 and 1987. The species selected as having the greatest potential for domestication was *L. racemosus*, known commonly as giant or mammoth wildrye. However, prospects for utilization of this species in the near future are unclear. Among 16 accessions evaluated over 2 years, yields did not exceed 830 kg/ha (Piper, 1993), and yield declined rapidly in the second and third years. Wildrye's great vigor, accompanied by large spikes but sparse seed-set, resulting in low harvest index (Wagoner, 1990a), may provide considerable scope for breeders to select for diversion of photosynthate toward grain production. However, there is no current breeding program for grain yield in *L. racemosus*; until selection is undertaken, no conclusions can be drawn regarding its potential. *L. racemosus* is self-pollinated and would require a breeding approach different from that taken with *Th. intermedium*.

3. Lyme Grass

Lyme grass or beach wildrye (*Leymus arenarius*) has been used as a food grain since the time of the Vikings (Griffin and Rowlett, 1981), and, as we have seen, is being studied as a potential grain crop in Iceland (Anamthawat-Jonsson , 1996). There is significant genetic variation among accessions of *L. arenarius* and *L. mollis* (Anamthawat-Jonsson et al., 1999), and it would be interesting to know which approach would result in more rapid genetic progress: direct selection within the species or an interspecific backcross program using wheat as a donor parent (Anamthawat-Jonsson, 1996). The latter strategy takes advantage of genes selected through millenia of wheat domestication and breeding, but introduces chromosomal instability.

4. Prospects for Direct Domestication

Is there sufficient genetic variation within these three, or other, cool-season grasses to support large improvements in yield, kernel weight, and other traits? The very existence of annual grain crops proves that selection over thousands of years can move the mean of a species far beyond its original phenotypic range. Gains of 20 to 25% per cycle (Wagoner, 1995; Knowles, 1977) are much more rapid than typical gains in major annual crops, even considering the longer selection cycle of perennials, but to effect sufficient changes in a matter of decades rather than centuries — while possibly working "uphill" against the problem of resource allocation in perennials

— will require much larger breeding efforts than have been undertaken to date. Relatively small efforts at domestication, which are within the capabilities of nonprofit organizations such as the Rodale Institute or Land Institute (or small-scale breeding programs within larger organizations such as USDA or universities), must be expanded to a much larger scale by university, government, or corporate breeding programs if wholly new perennial grain crops are to be developed.

The yield increases of 25% per cycle achieved by Wagoner et al. (1996) are remarkable, especially considering that they selected for other traits in addition to yield. However, because response to recurrent selection tends either to follow a linear path or decelerate (Hallauer and Miranda, 1988), future gains per cycle will probably be no greater than a constant percentage of the *base* population's yield. If a hypothetical perennial grass population yielding 500 kg/ha of grain undergoes selection, with a yield increase of 125 kg/ha/cycle (25% of the base yield), 20 cycles will be required to reach 2500 kg/ha. Because selection in perennials must be based on evaluation over two or more seasons, a single cycle can occupy 4 or 5 years. Obviously, if it is going to take almost a century to develop a high-yielding perennial crop through direct selection, a long-term commitment is required; however, such a rate of progress is much greater than the rate at which our annual crops were domesticated and improved. Marker-assisted selection and/or some genetic input from wheat could speed up the process.

E. Oat

Perennial oats for grain production might be developed from crosses between the cultivated hexaploid oat (*Avena sativa*, 2n=42, genomes AACCDD) and a wild, perennial, autotetraploid relative, *A. macrostachya* (2n=28, CCCC). Such crosses require embryo rescue. The F_1 is highly sterile, but backcrosses to *A. sativa* have been made, and limited pairing between chromosomes from different parents does occur (Leggett, 1985). J. P. Murphy (North Carolina State Univ., personal communication) has produced a 70-chromosome amphiploid between the species. The objective of this cross is to improve winterhardiness in the annual crop; perenniality has not been evaluated. Because of the partial homology that exists between chromosomes of the parental species, the amphiploid is likely to suffer from the same chromosomal instability found in wheat amphiploids. However, the amphiploid, like the hybrid, can be backcrossed to *A. sativa* (Murphy, personal communication). Ladizinsky (1995) domesticated accessions of two wild annual oat species by using the cultivated oat *A. sativa* as the donor of genes for nonshattering and other traits. Perhaps this approach could be tried with *A. macrostachya.*

More hybrid combinations and larger populations will be needed if genetic studies and selection for perenniality are to succeed in the backcross generations. A more diverse sample of *A. macrostachya* parents would be desirable, but the species is restricted to two mountain ranges in Algeria, limited germplasm collections exist in the United States, and there are very few accessions held in other countries (Guarino et al., 1991). Selection for perenniality in colder climates could be thwarted by the lack of winterhardiness in oats; winter annual oats are not generally sown above 35 degrees latitude in North America. At sites where *A. macrostachya* was collected by Guarino et al. (1991), the mean minimum temperature of the coldest month ranged from –0.6 to –3.6°C.

F. Rice

Although tropically adapted, rice (*Oryza sativa*) has the C_3 carbon fixation pathway and is included here with the cool-season grasses. The perennial ancestor of *O. sativa* is *O. rufipogon*. Both species are diploid (2n=24) with homologous chromosomes and they can be hybridized easily. Indeed, natural hybridization and introgression occur in the field (Majumder et al., 1997).

From 1995 to 2001, the International Rice Research Institute (IRRI) had a program for development of perennial rice cultivars to reduce erosion on the steep slopes where upland rice is often grown (Bennett et al., 1998; Schmit et al., 1996). Populations from IRRI's breeding program, which was discontinued in 2001, have been distributed to cooperators in China, where perennial rice breeding efforts continue.

Sacks et al. (2001) found wide variation in second-year survival among 51 *O. sativa*/*O. rufipogon* F_1 hybrids. Sixteen percent of the hybrid combinations had greater than 50% survival, and 19% of all hybrid plants survived. In a cross between a rice cultivar with a regeneration score of 1.0 and an accession of *O. rufipogon* with a score of 3.8, the F_1 had a regeneration score of 4.0, and the scores of F_2 clones ranged from 0 to 5 (Xiong et al., 1999). Paradoxically, in three of the four chromosomal segments that affected regeneration ability, it was the annual parent's allele that had a positive effect. In contrast to mapped regrowth loci in *Sorghum bicolor*/*S. propinquum* populations (Paterson et al., 1995), none of the regeneration loci were associated with effects on tiller number.

Selection in interspecific populations may be aided by rice's detailed molecular map and the known locations of chromosomal segments affecting traits of domestication (Xiong et al., 1999; Kohm et al., 1997; Cai and Morishima, 2000). Many of the traits separating the annual and perennial species show polygenic inheritance. Surprisingly, *O. rufipogon* was the source of four chromosomal segments with positive effects on testcross grain yield in one set of backcrosses (Xiao et al., 1998); however, three of the four segments were adjacent to segments that either increased plant height or delayed maturity. With positive alleles affecting perenniality *and* productivity apparently being contributed by *both* parental species, prospects for breeding high-yielding perennial rice genotypes may be bright.

Oryza sativa can also be hybridized with *O. longistaminata*, the perennial ancestor of West African rice, *O. glaberrima*. The perenniality of *O. rufipogon* lies in its ability to regrow repeatedly through production of new tillers, whereas *O. longistaminata* regrows from rhizomes (Maekawa et al., 1998). In crosses between *O. sativa* and *O. longistaminata*, genes affecting rhizome production appear to be linked to genes for hybrid embryo abortion. Consequently, IRRI scientists backcrossed rare hybrids to both parental species and intercrossing the progeny in an effort to develop a rhizomatous, agronomically acceptable genotype (Bennett et al., 1998). Tao et al. (2001) recovered a single rhizomatous individual from among 162 plants produced by backcrossing an *O. sativa*/*O. longistaminata* hybrid to *O. sativa*.

A long-lived, three-species hybrid (*O. sativa*/*O. rufipogon*/*O. longistaminata*) has persisted through winters in China with monthly mean temperatures as low as 5°C (Li, 1998). Crossing the hybrid with *O. sativa* and intermating perennial progenies has eliminated shattering (Li, 2000). One possibility for breeding an even more cold-tolerant perennial rice exists. An ecotype of *O. rufipogon* known as 'Dongxiang' has the ability to regrow in regions of China where temperatures below –10°C are common (He et al., 1996).

IV. BREEDING PERENNIAL GRAINS: WARM-SEASON GRASSES

A. Sorghum

1. Hybridization with Sorghum propinquum

In tropical environments, grain sorghum (*S. bicolor*, 2n=20) is able to regrow from basal nodes to produce a rattoon crop. However, breeding a sorghum that is winterhardy in temperate regions will require transfer of genes from related species.

A perennial native of southeast Asia, *S. propinquum* is rhizomatous and diploid, with chromosomes largely homologous to those of grain sorghum. Paterson et al. (1995) evaluated rhizome-related traits of 370 F_2 and 378 BC_1 plants from a cross between the two species. Surviving a mild winter in southern Texas, USA, with only three nights reaching temperatures of –3°C to –4°C, 92% of F_2 plants and 46% of BC_1 regrew in the spring. Plants regrew either from tillers or from rhizomes. Forty-eight F_2 plants representing the range of the population were selected for progeny testing.

From all F_2 plants and F_3 lines, Paterson et al. (1995) collected data on number of rhizomes producing above-ground shoots, distance between the center of the crown and the most distal shoot, a subterranean rhizome score, tillering, and regrowth. They mapped chromosomal segments affecting these traits in the F_2 plants and F_3 lines, using 78 RFLP loci.

Rhizomatousness was a complex trait, with nine different chromosomal regions on seven of sorghum's ten chromosomes having detectable effects on at least one of the rhizome traits. Individual segments accounted for between 5 and 13% of the total variation. All but one of the seven segments associated with regrowth was also associated with one or more rhizome traits, and all four segments associated with tillering were also associated with regrowth or rhizomatousness.

Because *S. propinquum* is a tropical species, rhizomatous progeny of crosses between S. bicolor and *S. propinquum* would probably not be winterhardy at middle or northern latitudes, without successful selection for deeper rhizome growth. However, there is great potential for developing a perennial grain sorghum for the tropics or subtropics from such populations.

2. Hybridization with Johnsongrass

Johnsongrass (*S. halapense*, 2n=40) is a tetraploid, probably an amphiploid that combines the genomes of *S. bicolor* and *S. propinquum* (Paterson et al., 1995). It is a very strong and aggressive perennial, and a notorious weed. Like *S. propinquum*, johnsongrass stores starch in its rhizomes. As a consequence, its rhizomes have no cold hardiness, unlike those of temperate grasses, which store fructosans (Monaghan, 1979). Natural selection for deeper-growing rhizomes has allowed johnsongrass to spread as a weed as far north as Ontario (Warwick et al., 1986). Although the most northerly biotype reproduces mainly by seed, regrowth from rhizomes occurs throughout the range of the species.

Early research on hybrids between diploid sorghum and johnsongrass (Hadley, 1953, 1958; Hadley and Mahan, 1956) produced two types of hybrids: 30-chromosome plants that were male-sterile but could be backcrossed to the diploid parent and 40-chromosome plants derived from unreduced female gametes in the diploid parent. The 30-chromosome plants were more strongly rhizomatous. Hadley and Mahan (1956) identified seven 20-chromosome backcross plants that were rhizomatous, but most were chlorophyll mutants. Three years of selection failed to produce a single diploid line that was rhizomatous.

Hybrids between *S. halapense* and induced tetraploid lines of *S. bicolor* are easily made (Casaday and Anderson, 1952; Sanguden and Hanna, 1984; Piper and Kulakow, 1994). In an effort to produce a perennial grain sorghum at The Land Institute, Piper and Kulakow (1994) crossed *S. halapense* with tetraploid grain sorghum lines. In an interspecific F_3 population, approximately 40% of plants were rhizomatous. There was no significant negative correlation between rhizome production and grain yield in the F_3 generation, but a negative association arose with backcrossing. Yield was strongly related to plant biomass and root biomass, both with pheontypic correlations of 0.70. The F_3 population — selected for winterhardiness but not for yield — had a grain yield 62% as high as the mean nonirrigated sorghum yield in Saline County, Kansas, where the experiments were conducted. However, rhizome production dropped to near zero in other populations derived by backcrossing to tetraploid *S. bicolor* in an effort to increase grain yield.

Land Institute breeders have selected for winter survival among the rare rhizomatous BC_2 plants and their selfed progeny. The phenotypes of winterhardy selections remain very distant from that of the cultivated parent, despite the latter's expected 87.5% genetic contribution to the BC_2. The selections are taller and later maturing than either parent, have open panicles and small seed, and produce many tillers, although not as many as johnsongrass. Rhizome mass is less than 10% that of johnsongrass — sufficient for overwintering, but not enough to allow interspecific progenies to become aggressive weeds.

Both rhizomes and tillers originate from meristems at the base of the plant, and there appears to be considerable overlap in their genetic control (Paterson et al., 1995). It may not be possible, or even desirable, to select a low-tillering, sufficiently rhizomatous genotype. Indeed, selection for yield improvement may be more effective in highly tillering populations. If a grass plant is regarded as a population of largely autotrophic tillers (Jackson and Jackson, 1999), and each tiller supports both seeds and rhizomes, then the most direct route to increased yield is via additional tillers. Of course, this implies increased biomass.

Piper and Kulakow (1994) concluded that development of a winterhardy sorghum (i.e., one that produces 80 g of rhizomes per plant) with a grain yield of over 4000 kg/ha is feasible, through selection for greater biomass and reallocation of photosynthate to seed production. The foundation germplasm for breeding a perennial sorghum may necessarily consist of high-biomass plants that produce more tillers than annual sorghum. With a sufficiently large genetic base, subsequent selection for improved harvest index and seed size could be successful.

Because there is some homology between the chromosomes of grain sorghum and johnsongrass, multivalent chromosome associations are common at meiosis in interspecific tetraploids. Multivalents, in turn, cause poor seed set because of nondisjunction of chromosomes. Luo et al. (1992) demonstrated that selection for fertility can be effective in autotetraploid grain sorghum, which is generally plagued by low seed set. Breeders could cross perennials with the highly fertile tetraploid germplasm that Luo et al. (1992) have produced.

Broadening and improving the genetic base of tetraploid perennial sorghum will require introduction of more agronomically elite germplasm. One rapid method of incorporation would be to pollinate both diploid and induced-tetraploid strains of elite, large-seeded inbred lines with the best tetraploid perennials. From the diploid/tetraploid crosses, breeders can select 40-chromosome hybrids that arise from unreduced gametes (Hadley, 1953). The Land Institute is now taking this approach to develop genetically diverse breeding populations.

B. Pearl Millet

Pearl millet (*Pennisetum glaucum*, 2n=14), like sorghum, is a tropical, annual diploid with a perennial, tetraploid relative. Napiergrass, *P. purpureum* (2n=28) has one genome homologous and one nonhomologous to that of pearl millet (Jauhar, 1981). Amphiploids resulting from colchicine treatment of hybrids between the species are male and female fertile (Gonzalez and Hanna, 1984). Hanna (1990) backcrossed these hexaploids to diploid and tetraploid pearl millet lines and produced perennial progeny; however, both types of backcross plants (tetraploid and pentaploid) were highly sterile and unable to survive the mild winters of south Georgia, USA. Napiergrass, the only known species in pearl millet's secondary gene pool, is not rhizomatous, so selection for winterhardiness would probably not be successful. A perennial millet for grain production in the tropics is a reasonable prospect.

Dujardin and Hanna (1990) interpollinated hybrids and their derivatives from crosses between tetraploid pearl millet and *P. squamulatum* (2n=54), a more distant, perennial, apomictic relative. Some progenies (2n=48) were both perennial and apomictic. Apomixis can be used to ensure grain production and genetic stability in highly heterozygous progenies of interspecific crosses (Hanna and Bashaw, 1987). *Pennisetum squamulatum* is also nonrhizomatous, and its progeny are not likely to be perennial outside of the tropics.

C. Maize

1. Hybridization with Tetraploid Perennial Teosinte

Efforts to develop perennial maize (*Zea mays* ssp. *mays*, 2n=20) have been sporadic at best; as in other crops, hybridization between maize and perennial relatives has led primarily to improvement of the annual crop (Wagoner, 1990a). Shaver (1964) first attempted development of maize-like perennials from crosses between colchicine-induced tetraploids of maize and a wild, perennial, tetraploid relative, *Z. mays* ssp. *perennis* (2n=40). Selection within the resulting tetraploid populations and backcrosses to tetraploid maize effectively increased the frequency of perennial progeny. Crosses to diploid maize produced perennial triploids, but all diploid selections were annual.

Shaver (1967) combined a postulated gene (*pe*) for perenniality with recessive genes for indeterminacy (*id*) and grassy tillers (*gt*) in a diploid background to produce perennial plants; however, the *idid* genotype prevented production of ears. Because Shaver (1967) had developed a separate *idid* population in a different genetic background that did produce ears, he suggested that perennial diploids could also be made fertile if the genetic background were manipulated.

2. Hybridization with Diploid Perennial Teosinte

Little further attention was paid to perennial maize until the dramatic discovery of a diploid species of perennial teosinte, *Z. mays* ssp. *diploperennis* (Iltis et al., 1979). Initial studies showed that inheritance of perenniality was relatively simple in maize/*diploperennis* crosses, but perenniality was inferred from tillering habit, a potentially misleading technique (Shaver,1964). In subsequent, larger-scale experiments, inheritance of tillering in progeny of similar intersubspecific crosses was more complex, and perennial maize types were not recovered even in large segregating populations (Srinivasan and Brewbaker, 1999).

Genetic mapping in maize/annual teosinte crosses show that most traits of domestication separating the species are oligogenic, and the loci tend to be clustered on the map, through either linkage or pleiotropy (Doebley and Stec, 1993). A similar study of these traits, plus perenniality, in crosses between maize and diploid perennial teosinte would be of great value to any breeding program attempting to combine perenniality with the agronomic phenotype of maize. This would require a substantial effort to evaluate large segregating populations for tillering, rhizome production, and capacity to produce seed over multiple seasons. Once the genomic regions of interest are identified, marker-assisted selection can be used to incorporate them into a maize background and eliminate unwanted alleles such as those conditioning hard glumes and shattering.

One serious obstacle to adoption of any teosinte-derived perennial grains is the lack of winterhardiness of these tropical species. There are no winterhardy species of *Zea*. Because the bulk of maize production and breeding occurs in temperate areas, there has been little incentive to develop perennials from crosses with *Z. mays* ssp. *diploperennis*. One possible approach has not been suggested to date: selection for rhizome depth. As we have seen, johnsongrass rhizomes also are not winterhardy if near the soil surface, but dispersal of the species into higher latitudes has been made possible by selection for deeper rhizomes. Superimposing selection for this undoubtedly complex trait on selection for perenniality and traits of domestication, not to mention yield, may entail a much larger effort than any breeding program is willing to undertake.

3. Hybridization with Eastern Gamagrass

The closest winterhardy relatives of maize are in the genus *Tripsacum*. Eastern gamagrass (*T. dactyloides*), for example, is currently grown as a perennial forage grass as far north in the western hemisphere as Kansas and Massachusetts, and can be grown in the Corn Belt (Voigt et al., 1995). *T. dactyloides* has been hybridized many times with maize, beginning with the work of Manglesdorf and Reeves (1931). Plants of the diploid (2n=36) or tetraploid (2n=72) races may be crossed with maize. If *Tripsacum* is used to pollinate maize, embryo rescue is necessary (deWet et al., 1973; James, 1979), but if maize is used as the male, some hybrid seed may be obtained without rescue (deWet et al, 1973). In addition, several strains of popcorn, when pollinated with tetraploid *T. dactyloides*, produce large amounts of hybrid seed that does not require embryo rescue (Kindiger and Beckett, 1992). Some have good crossability with diploid *T. dactyloides* as well. Contrary to typical results, Eubanks (1995, 1997) reported that a putative 20-chromosome hybrid between *T. dactyloides* and *Z. diploperennis* showed 93 to 98% pollen fertility.

Natural introgression between *Tripsacum* and maize has not been observed, but morphological (deWet et al., 1983) and molecular (Talbert et al., 1990; Dewald and Kindiger, 1998) evidence supports the hypothesis that the species *T. andersonni* is an intergeneric hybrid containing three genomes (54 chromosomes) from *Tripsacum* and 10 chromosomes from *Zea* in *Tripsacum* cytoplasm. The uniformity of this ancient natural hybrid indicates that *T. andersonii* arose from a single hybridization. It has been able to spread across tropical Latin America because of its vigorous perenniality (deWet et al., 1983; Dewald and Kindiger, 1998).

In addition to being perennial, tetraploid *T. dactyloides* is a facultative apomict. Perennial hybrids result from artificial crosses between tetraploid *Tripsacum* and maize (Farquharson 1957), and some seed-set can result from apomixis. The hybrids, derived from parents with different basic chromosome numbers and chromosomes of different sizes (those of maize being larger), are male sterile, with cytological behavior that is anything but regular. Harlan and deWet (1977) summarized methods for utilizing such hybrids in maize improvement. Either 28-chromosome or 46-chromosome hybrids — derived from diploid and tetraploid *T. dactyloides* parents, respectively — can be backcrossed to maize. In either case, *Tripsacum* chromosomes are eliminated with backcrossing. Elimination occurs more gradually in progeny of 46-chromosome hybrids, and the 20 chromosomes of the resulting backcross plants can contain significant genetic material from *Tripsacum* (Harlan and deWet, 1977; Stalker et al., 1977a and b). All 20-chromosome backcross plants derived to date have been annual and nonapomictic. Kindiger et al. (1996) derived an annual, 39-chromosome line that carried 9 *Tripsacum* chromosomes and displayed an intermediate level of apomixis.

Most hybridization with *Tripsacum* has been for the purpose of either elucidating the evolution of maize or transferring resistance or other genes to annual maize. The latter purpose implies backcrossing to maize. However, development of perennial populations may require interpollinating plants in early backcross generations that still carry many *Tripsacum* chromosomes (Harlan and deWet, 1977), or even backcrossing to *Tripsacum*. As Harlan and deWet (1977) commented, “Apparently, if one wishes to contaminate maize with *Tripsacum* one should first contaminate *Tripsacum* with maize.”

New approaches to perennial maize are being explored. An anomalous fertile hybrid between diploid *T. dactyloides* and maize was discovered by one of the authors (BEZ) in 1997 near the mouth of the Big Nemaha river in Richardson County, Nebraska, USA. This derivative of natural introgression between *T. dactyloides* and a putative commercial hybrid is being hybridized with gynomonoecious *Tripsacum* — both diploid (Dewald and Dayton, 1985; see below) and tetraploid (Salon and Earle, 1998) — and with tasselseed popcorn to develop a 56-chromosome perennial cultivar for production of grain, forage, fiber, and fuel.

The difficulties encountered in introgressing apomixis from *Tripsacum* into maize (Kindiger et al., 1996) should temper hopes for a rapid synthesis of perenniality with high grain yield. Whatever the initial population, and even with marker-assisted selection, the process of recovering perennial, winterhardy segregants with maize-like ears, and then breeding for yield and other agronomic traits will be long and arduous.

D. Direct Domestication of Warm-Season Grasses

1. Eastern Gamagrass

Could *T. dactyloides* be domesticated directly, without introgression of genes from maize? To do so would be an accomplishment parallel to that of domesticating maize from annual teosinte — a feat requiring thousands of years and producing genetic and physiological changes much greater than those involved in domestication of Asian cereals such as wheat and rice (Iltis, 2000; Beadle, 1980). To develop a crop from Eastern gamagrass using the knowledge and techniques provided by 21st-century genetics, while leaving aside the important genes of domestication available in maize, would be an ambitious project.

Wagoner (1990a) described in detail the status of Eastern gamagrass as a potential grain crop, and the species’ most discouraging characteristic: very low seed yield. Interest had been stimulated by the discovery of a gynomonoecious, or pistillate, mutant (DeWald and Dayton, 1985) in which pistillate and perfect spikelets replace the staminate spikelets of the normal inflorescence. The result is an increase of up to 20-fold in the number of seeds produced per plant; however, the seeds are small, so that the weight of seed produced per plant is increased by only a factor of 3 (Jackson and Jackson, 1999).

Plants of Eastern gamagrass are large, vigorous, and widely adapted. The increase in sink size made possible by the pistillate mutant may provide an opportunity to increase seed yield dramatically through increased harvest index — the yield component usually found to have had the greatest effect on yield improvement in traditional grain crops (Evans, 1998). Furthermore, Jackson and Dewald (1994) found that the increased seed yield of pistillate plants did not come at the expense of plant vigor or longevity. Carbohydrate reserves were significantly higher in pistillate than in normal genotypes. For breeders, there is a huge pool of genetic variability available in the species (Newell and deWet, 1974; Wright et al., 1983). Although tetraploid *T. dactyloides* reproduces apomictically, parental combinations can be produced via B_{III} hybrids, in which an unreduced egg is fertilized by a haploid sperm (Kindiger and Dewald, 1994). Alternatively, obligately sexual tetraploid plants can be produced via colchcine treatment of diploid *T. dactyloides* plants, all of which are sexual. The genus *Tripsacum* contains many species that lack winterhardiness but have desirable traits that, potentially, could be transferred to eastern gamagrass: synchronous flowering, large spikelet number, higher seed yield, and other variations in plant morphology.

The maximum seed yield of eastern gamagrass in plots at The Land Institute has been 240 kg/ha, in the third year after sowing (Piper, 1999). It remains to be seen how rapidly yield can be improved through selection within pistillate populations, and there is another question: would the 10-, 20-, or 30-fold yield improvements required to make Eastern gamagrass a viable grain crop have larger negative effects on plant vigor and persistence than did the threefold yield boost brought about by the pistillate mutation? That increase was large relative to the grain yield of a normal plant but required diversion of only a small amount of photosynthate, relative to the plant's large biomass.

The food quality of Eastern gamagrass is excellent (Bargman et al., 1989). However, even if yield can be improved, other problems must be solved. One problem is disease. Infection by maize dwarf mosaic virus B has been very serious in plots at The Land Institute (Seifers et al., 1993). Also, the hard fruitcase of *Tripsacum* weighs almost three times as much as the seed itself and makes processing difficult. It was an extremely rare mutation in annual teosinte that freed the kernel from the fruitcase and allowed its use as a grain and the development of maize (Iltis, 2000). This may be a gene that breeders will be forced to transfer from maize.

2. Indian Ricegrass

Grain is currently being harvested from a perennial grass for human food in northeastern Montana, USA. Indian ricegrass (*Oryzopsis hymenoides*), cultivar Rimrock (Jones et al., 1998), has reduced seed-shattering (Jones and Nielson, 1991) and produces gluten-free grain. The grain is being produced, milled, and marketed under the tradename Montina. Yields vary between 250 and 500 kg/ha, but improvement through breeding may be feasible. Germplasm collections exhibit great phenotypic diversity, and very large-seeded genotypes are known (T.A. Jones, USDA-ARS, Logan Utah, personal communication). Certainly, other perennial grasses native to the Western USA could be considered for domestication as grain producers, but no attempts have been made.

V. BREEDING PERENNIAL GRAIN LEGUMES: PROSPECTS

A. Soybean

The genus *Glycine* is divided into two subgenera, *Glycine* and *Soja*. The cultivated soybean, *Glycine max*, and its close relative and ancestor *Glycine soja*, both annual diploids (2n=40; genome GG), make up the subgenus *Soja*. The subgenus *Glycine* contains 16 perennial species (Singh and Hymowitz, 1999). Numerous attempts have been made to cross perennials with *G. max*, but hybrids have been produced only with *G. tomentella* (2n=80; genomes DDEE; Bodanese-Zanettini et al., 1996; Hymowitz and Singh, 1987; Hymowitz et al., 1998; Newell and Hymowitz, 1982; Shoemaker et al., 1990; Singh and Hymowitz, 1999). In most cases, successful hybridization has required the use of ovule culture (Newell and Hymowitz, 1982). All hybrids have been sterile, but when their chromosome number has been doubled with colchicine to produce amphiploids with the genome constitution DDEEGG, some fertility has been restored (Shoemaker et al., 1990; Singh et al., 1993).

Recently, Singh et al. (1998) produced 22 monosomic addition lines of soybean, each carrying a single chromosome from *G. tomentella*. During development of the lines, a slight tendency toward perenniality persisted up to the BC_2, but all monosomic lines had an annual growth habit (R. Singh, Univ. of Illinois, personal communication). Little or no pairing occurs between chromosomes of the two species (Singh et al., 1998), so even if genes governing perenniality can be identified, their transfer to soybean will be difficult. Perhaps even more difficult would be the incorporation of winterhardiness, which does not exist in any species of *Glycine*. Winterhardiness would need to derive from another legume species such as alfalfa, via transgenesis.

B. Illinois Bundleflower

To dispel doubts that herbaceous perennials can produce large amounts of seed, one need only point to a legume species of the North American prairie. Illinois bundleflower (*Desmanthus illinoensis*) has a wide geographic range, stretching well beyond the prairie, from Colorado to Minnesota to Florida to Texas (Latting, 1961). It is a good nitrogen-fixer, a preferred forage for livestock, and produces relatively high yields of large seeds with favorable nutritional profiles (Kulakow, 1999).

In evaluating a germplasm nursery of 141 highly diverse *D. illinoensis* accessions, Kulakow (1999) identified 15 in which seed shattering was reduced or eliminated, a prerequisite for grain crop. The highest-yielding 20 accessions in the first sowing (1988) produced a mean of 1500 kg/ha in their first year and 1180 kg/ha in their second year of growth. These accessions significantly exceeded the nursery's mean yield in a second experiment sown in 1990, averaging 1090 kg/ha. Severe drought occurred in their second year of growth, and their yields fell below 500 kg/ha. In related studies, yields have approached 2000 kg/ha (Piper, 1993).

The germplasm collection studied by Kulakow (1999), along with more extensive plant collection of *D. illinoensis* and its southern relative *D. leptobolus*, can provide the foundation for breeding Illinois bundleflower as a grain crop. The chief hurdle to be overcome is the palatability of the seed. Although the seed contains no toxic levels of oxalates, cyanides, nitrates, or alkaloids, and cooked seed has digestibility and a protein efficiency ratio similar to that of cooked oats (Kulakow et al., 1990), unprocessed bundleflower seeds have a foul odor and taste. Nothing is known about the compound(s) involved. The Land Institute is investigating induced mutagenesis, but some method of processing, as is necessary for utilization of soybeans as human food, for example, may solve the problem. Our results (DLV) indicate that roasting whole seeds may eliminate the undesirable taste.

C. Other Legumes

Wild senna, *Cassia marilandica*, has one of the highest seed yields of any perennial species yet evaluated by The Land Institute (Piper, 1992, 1993), but yields decline after the first year. Perhaps most importantly, the species is not known to establish associations with *Rhizobium* for symbiotic nitrogen fixation; therefore, its usefulness would be limited in cropping systems that include little or no application of inorganic nitrogen fertilizers.

The chickpea (*Cicer arietinum*) is one of nine annual species in the genus *Cicer*, which also contains 34 perennial species (van der Maesen, 1987). The perennial species are little studied;

accessions representing 12 species are maintained at the Western Region Plant Introduction Station in Pullman, Washington. Two species, *C. anatolicum* and *C. songaricum*, have survived for 10 years in the field and continue to produce seed. One accession of *C. songaricum* is white-flowered, has some degree of shattering resistance, and produces seed similar to the commercial 'desi' type (F.J. Muehlbauer, WRPIS, personal communication). The presence of these traits suggests that *C. songaricum* was once cultivated in Asia.

Many species of the Leguminosae may be grown as perennials for seed production in the tropics. For example, second-crop seed yields of pigeonpea (*Cajanus cajan*) were higher than first-crop yields in two studies in India (Newaj et al., 1996; Nimbole, 1997).

VI. BREEDING PERENNIAL COMPOSITES: PROSPECTS

A. Sunflower

The relatives of the annual cultivated sunflower (*Helianthus annuus*, a diploid with 2n=34) are genetically diverse, consisting of 14 annual and 36 perennial species (Seiler and Riesenberg, 1997). If attempts to develop a perennial sunflower fail, it will not be because the available gene pool is too small. According to data compiled by Jan (1997), along with a recent study by Sukno et al. (1999), 20 perennial species have been hybridized with *H. annuus*. In approximately half of the crosses, F_1 plants were perennial; sometimes one accession of a species produced perennial hybrids, while another produced annuals. The majority of hybrids have enough fertility to be backcrossed.

Some hybrids were produced before the development of the first effective embryo-rescue technique for sunflower by Chandler and Beard (1983). Heiser and Smith (1964) crossed wild *H. annuus* with the *H. decapetalus, H. hirsutus*, and *H. strumosus* (all 2n=68), and Jerusalem artichoke (*H. tuberosus*, 2n=102). They found, as have subsequent researchers, that crosses were far more successful when the polyploid species was used as the female. Only the hybrids with *H. strumosus* and *H. tuberosus* were winterhardy. Whelan (1978) failed to produce interspecific crosses with cultivated sunflower, but his hybrids between wild *H. annuus* (as the male) and two diploid perennial species, *H. maximiliani* and *H. giganteus,* were fertile enough to backcross to a cultivar. Neither the hybrids nor the backcrosses were perennial. Whelan (1978) found that the perennials differed cytologically from the annual in three translocations and a paracentric inversion. Hybrids were highly sterile, but backcrossing to *H. annuus* rapidly restored male and female fertility (Whelan and Dorrell, 1980).

More recently, many crosses with perennial diploids, tetraploids, and hexaploids have been made — usually, but not always, via embryo rescue (Georgieva-Todorova, 1984; Krauter et al., 1991; Atlagic et al., 1995; Espinasse et al., 1995; Sukno et al., 1999). However, few backcrosses have been attempted. Seiler (1991, 1993) released BC_1-derived germplasms from crosses between cultivated sunflower and three perennial species: *H. hirsutus*, *H. resinosus* (2n=102), and *H. tuberosus*. All germplasms were annual, but hybridizing them with perennial parents could increase the probability of recovering perenniality in another round of backcrossing.

Protoplast fusion is an efficient method of producing interspecific amphiploids in *Helianthus.* Krasnyanski and Menczel (1995) produced *H. annuus* + *H. giganteus* hybrids that had good fertility but were not perennial. Henn et al. (1998) produced large numbers of *H. annuus* + *H. giganteus* and *H. annuus* + *H. maximiliani* hybrids that developed rhizomes from which shoots emerged. Colchicine-induced or protoplast fusion-derived amphiploids of different parentage could be intercrossed to develop populations for breeding perennial, grain-producing plants.

Little is known about the genetics of perenniality in sunflower, and there have been no efforts to develop a perennial crop. When cultivated *H. annuus* is used as the female parent, the F_1 is usually a weak, short-lived perennial, and perenniality is quickly lost upon backcrossing to the annual. When the wild perennial is used as the female, some hybrids are more strongly perennial and bear a closer resemblance to the wild parent. Recovery of full perenniality and winterhardiness may require backcrossing to the wild parent (G. Seiler, personal communication). As in sorghum, a "wilder" plant type, with a greater number of heads per plant, may not be incompatible with good grain yield, if maturation is relatively synchronous.

Breeders aiming to develop a perennial sunflower should select perennial parents based on past success in hybridization and occurrence of perennial progeny, as well as regions of adaptation. The Land Institute is investigating *H. maximiliani* as a parent because of its wide adaptation across much of the North American prairie, its vigorous growth and seed production, and its crossability with *H. annuus*.

B. Direct Domestication of Perennial *Helianthus*

Annual sunflower is the only species of *Helianthus* that has been domesticated as a seed crop. However, *Helianthus* contains a wide diversity of perennial species (Seiler and Riesenberg, 1997), many of which are potential domesticates. The Land Institute has studied the common prairie species *H. maximiliani* as a candidate for direct domestication (Jackson and Jackson, 1999). It is a vigorous prairie plant with small but edible seed. Seed yield estimates have varied widely (Jackson and Jackson, 1999; Piper, 1999), and yields tend to decline after the first year of propagation in monoculture. Maximilian sunflower has strong allelopathic properties, making it potentially useful in suppressing annual weeds during the establishment of perennial polycultures (Piper, 1999). It spreads so aggressively that thinning or partial tilling to reduce stands can actually increase grain yield (Jackson and Jackson, 1999).

VII. ESTABLISHING GENE POOLS

A. Widening Genetic Bottlenecks

Developing the first perennial grain genotype with acceptable yield will be a demanding process in itself, but that will be only the beginning; no new agricultural system can be based on only a handful of genotypes per species. Sown over large regions, even polycultures will be genetically vulnerable if they do not incorporate intraspecific as well as interspecific variation. Furthermore, breeding of perennial grains will quickly reach a dead end without sufficient genetic diversity. During the domestication process, most crop species suffered a similar "founder effect" that restricted the gene pool on which early cultivators drew (Ladizinsky, 1985). In probably the most extreme example, all modern bread wheat may have descended from one or a few natural interspecific hybrids that occurred around 5000 years ago (Cox, 1998). If new perennial crops are to be developed on a shorter time scale, a founder effect must be avoided.

To ensure intraspecific diversity in the field and foster further genetic improvement, breeders will need to develop deep gene pools for each crop. In rye, rice, sorghum, intermediate wheatgrass, wildrye, lymegrass, eastern gamagrass, Indian ricegrass, Illinois bundleflower, or Maximilian sunflower, this will be a straightforward matter of incorporating new annual or perennial parents, manipulating ploidy or ensuring homozygosity of translocations, and alternate rounds of selection and recombination. It will involve considerable effort, but large gene pools exist to be drawn on.

Where the perennial crop has resulted from hybridization between species with nonhomologous chromosomes — as has been accomplished in a limited way in wheat and maize and remains to be done in oat, soybean, and sunflower — introducing sufficient diversity will be a more daunting task. In such a situation, new germplasm can be brought into the breeding pool only by repeated interspecific hybridization. The human-made species triticale is an example of an annual crop developed through interspecific hybridization that has always been hampered by a restricted gene pool (Skovmand et al., 1984).

Because of their more readily available gene pools, we may expect perennial versions of rye, rice, or sorghum to be the first to move beyond the experimental stage. Creating a gene pool of interspecific hybrids in wheat, oat, maize, or sunflower may take as long as or longer than domesticating wild species such as Illinois bundleflower, Maximilian sunflower, or those of the perennial Triticeae "from scratch".

B. Biotechnology

We have seen that sophisticated chromosomal manipulation will be necessary in developing perennial versions of some crops from interspecific hybrids. We have not discussed genetic engineering in its narrower sense: asexual insertion of individual genes. We can speculate on the potential for transforming annual into perennial plants by gene insertion, but with the state of knowledge today, we can go no further.

No research to date suggests that perenniality is governed by a single gene, or even two or three genes, in any crop or crop relative. Although some wheat amphiploids with as little as 25 to 30% of their genome derived from the perennial parent are themselves perennial (Cai et al., 2001), we have seen that in rye, triticale, sorghum, maize, soybean, and sunflower, dilution of the perennial-derived genome to below approximately 50% often eliminates perenniality. This, along with the lack of success by breeders of any crop to backcross a gene or chromosome conditioning perenniality into any annual genotype attests to, but does not prove, the complexity of the trait.

In a few taxa — for example, *Sorghum*, *Secale*, and *Oryza* — segregation of mostly homologous chromosomes can be observed in crosses between annual and perennial species. As we have seen in sorghum and rice, molecular-marker studies do not show that perenniality is simply inherited (Paterson, 1995; Kohm et al., 1997). The postulation of a single gene for perenniality on one of the three *S. montanum* chromosomes $4R^{mon}$, $6R^{mon}$, or $7R^{mon}$ (Dierks and Reimann-Philipp, 1966) has not been confirmed, and the relatively weak perenniality of the cultivar Permontra, which carries all three chromosomes, indicates that the trait is more complex.

Of course, it is not impossible that a gene could be isolated that conditions the perennial growth habit when transferred to an annual plant, but if a “perenniality gene” is identified in a particular species and cloned, its effect when transferred to any but very closely related species is entirely unpredictable. Anamthawat-Jonsson (1996) lists other obstacles to employing gene-transfer technology to improve physiologically complex traits in genetically complex species such as the polyploid Triticeae. Transgenic technology may be useful, once perennial grain crops have been developed, in improving their pest resistance, food quality, or other more simply inherited traits; however, other breeding and cultural methods will also be available in most cases.

VIII. BREEDING PERENNIAL VS. ANNUAL GRAINS

A. General Considerations

Almost all crop breeding involves direct selection for plant productivity — grain yield in the present context — whether the plants are annual or perennial. The discussion of differences between breeding strategies for annuals and perennials has usually concentrated on allocation of photosynthetic resources between seeds and vegetative structures (Gardner, 1989), but perennials will also require arrays of adaptive traits very different from those usually addressed by breeders of annuals.

Breeders developing perennial grains for existing monoculture systems will be faced with finding genetic solutions to problems that are exacerbated when individual plants must survive and produce over a period of years rather than months in the same patch of soil. Breeding for resistance to diseases, insects, and adverse soil conditions will probably be even more important in developing perennial grains for monoculture than they are for annuals, but the majority of perennial grain breeders will not be selecting for adaptation to monoculture. Most efforts to breed perennial grains have environmental protection as an explicit goal. This leads breeders to select genotypes adapted to systems like organic farming (Wagoner, 1990b; Scheinost, 2001) or natural systems agriculture (Jackson and Jackson, 1999) that receive lower subsidies of nonrenewable energy and synthetic chemicals. Such systems usually incorporate inter- and intraspecific diversity. The greater biodiversity and better soil conditions inherent in these systems is designed to reduce pressures on the breeder to select for resistance to pests and soil problems.

B. Differences in Selection Criteria Between Perennial and Annual Grains

Obviously, persistence and maintenance of grain yield over seasons has been difficult to achieve in the past and will occupy much of the attention of perennial-grain breeders. We will need to consider adopting some of the methodologies used by breeders of forages (Sleper, 1987) or tree crops (Libby, 1992). Breeding of perennials obviously entails longer selection cycles, but perenniality can also have a positive effect on genetic gain, through greater control over pollination (Knowles, 1977; Reimann-Philipp, 1995), the capacity for asexual propagation in breeding nurseries, and a longer time scale for evaluating traits and genetic markers.

Avoidance of tillage will leave crop debris on the soil surface, favoring pathogens that overwinter on plant parts. The potential for damage to a perennial crop rooted in place for several years in the midst of its own debris is obvious. Breeders may need to incorporate a higher level of genetic resistance to saprophytic pathogens in perennial grains, just as they must in some annual crops intended for no-till production (Bockus and Shroyer, 1998).

Unless they are grown in more ecologically sound farming systems than are most annual grains, perennial grains may need increased resistance or tolerance to soil-borne fungi, nematodes, and viruses. Annual crops are often vulnerable to these organisms, but an infection that is late or slow to develop may not cause serious damage, and a new, initially healthy crop can be sown the next year. Crop rotation can suppress such problems in annual systems. In contrast, perennial crop plants, once infected, could be subject to damage over a period of years or killed outright. Without ecological or genetic protection, replanting and rotation cycles would have to be shortened.

Breeding for perenniality through interspecific hybridization may bring some genetic protection against pests. The majority of disease-resistance genes in wheat, to take one important species, have been transferred from other species (Cox, 1998). The extensive hybridization with wheat's perennial relatives envisioned herein would bring in a bonus of new resistance genes. The same may occur in sunflower (Seiler, 1992) and other species.

The need for rapid stand establishment from seed, especially under cooler conditions, has become even more important for breeders of annual crops with the widespread adoption of no-till agriculture (Crosson, 1981). Breeders of perennials will have to devote some attention to seedling establishment, but they can divert much of that effort into selection for persistence over seasons. Because sowing would be necessary only once every few years, much more effort could be put into using cultural methods to ensure good establishment.

C. Problems Rendered Less Severe by Growing Perennials in Biologically Diverse Systems

Plant breeders continually face the effects of genotype-environment interactions with "environment", meant to include everything except the crop populations under selection. Breeding methodology traditionally attempts to control all environmental factors except the one or few under study. In more genetically diverse systems with lower external subsidies, genotype-environment and genotype-genotype interactions cannot be controlled or eliminated but must be relied on to drive the system.

Biodiversity, which can be manifested at many different levels in agricultural systems (Cox and Wood, 1999), is the plant breeder's friend when it provides relief from problems that would otherwise be handled genetically. Breeders of annual crops for monoculture are being asked more and more to find genetic remedies for problems that do not exist in natural ecosystems. Natural systems agriculture seeks to mimic those ecosystems and eliminate many problems from the breeder's checklist: soil compaction, phosphorus deficiency, low-pH and/or aluminum toxicity, and other potential consequences of annual monoculture.

Breeding programs across the globe probably spend a larger proportion of their time and effort on incorporating genes for resistance to diseases and insects than on any other activity. However, lower levels of genetic resistance to diseases should be acceptable in breeding perennials to be grown in mixtures. Species diversity can provide protection against pathogens (Browning, 1974) and insects (Altieri and Nicholls, 1999). To take a simple example, a bacterial leaf spot causes severe attacks in monocultures of Illinois bundleflower, but it is insignificant in polyculture because a grassy understory cushions raindrops and reduces splashing (Jackson and Jackson, 1999). Perennial crop cultivars should also be designed as populations of genotypes rather than inbred lines or F_1 hybrids. Intraspecific diversity can retard development of virulent insect biotypes (Cox and Hatchett, 1986; Gould, 1986) and reduce infection by aerial, splash-borne, or insect-vectored pathogens (Garrett and Mundt, 1999, 2000; Zhu et al., 2000). On the other hand, diversity may not compensate for the increased vulnerability of perennial grains to soil-borne pathogens.

Perennial mixtures will require new breeding methodologies, as do annual intercropping systems (Francis, 1990). Other crop species, weeds, mycorrhizal fungi, nitrogen fixers, other soil microorganisms, dead organic material, and a wide variety of herbivores and their own predators or parasites will affect the growth and productivity of the crops under selection.

IX. CONCLUSION

We have described parental germplasm and possible methodologies for breeding at least 20 species of perennial grains. Prospects for success vary among species, but we can be certain that highly productive perennial grains will not be developed quickly or without immense effort. For any one of these species, the debate over feasibility of breeding a perennial grain crop could be the subject of an entire book or symposium; however, the only way to answer the question of feasibility is to carry out breeding programs with adequate resources and appropriate methodologies on a sufficient time scale. A massive program for breeding perennial grains could be funded by diversion of a relatively small fraction of the world’s agricultural research budget.

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