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Prospects for Developing Perennial Grain Crops

THOMAS S. COX, JERRY D. GLOVER, DAVID L. VAN TASSEL, CINDY M. COX, AND LEE R. DEHAAN

Perennial plants, growing in mixtures, make up most of the world's natural terrestrial biomes. In contrast, monocultures of annual crops are sown on more than two-thirds of global cropland. Grain and oilseed crops are the foundation of the human diet, but to date there are no perennial species that produce adequate grain harvests. Yet perennial plant communities store more carbon, maintain better soil and water quality, and manage nutrients more conservatively than do annual plant communities, and they have greater biomass and resource management capacity. These advantages provide a base from which to begin hybridization and selection for increased resource allocation to developing seeds, a decades-long process that must overcome or circumvent genetic complications. Breeding programs aimed at developing perennial grain crops have been initiated in wheat, sorghum, sunflower, intermediate wheatgrass, and other species.

Keywords: crop domestication, interspecific hybridization, perennial grain, plant breeding, sustainable agriculture

The world's farms are generating more food than ever before. At the same time, many researchers agree that agriculture is the "largest threat to biodiversity and ecosystem functions of any single human activity" (Clay 2004, p. vii). To quote from the 2005 synthesis report of the United Nations' Millennium Ecosystem Assessment program, "Cultivation often has a negative impact on provision of [ecosystem] services. For example, cultivated systems tend to use more water, increase water pollution and soil erosion, store less carbon, emit more greenhouse gases, and support significantly less habitat and biodiversity than the ecosystems they replace" (Cassman and Wood 2005, p. 749).

Jackson (1980) argued that agriculture's two antithetical roles—producer and depleter—find their common root not in the day-to-day decisions of farmers, government officials, agricultural scientists, corporate leaders, or consumers, but in humanity's 10,000-year-long reliance on the cropping of annual plants. In this article, we examine the ecological impact of annual cropping and prospects for the development of perennial grain crops, which will help resolve agriculture's central dilemma.

The need for diverse, perennial grain cropping systems

Since the advent of agriculture, more than one-fourth of Earth's land surface has been converted for agricultural purposes, with more land converted since 1950 than in the previous 150 years. This recent expansion of cropland has been accompanied by an accelerated application of chemical fertilizers and pesticides, which can significantly alter natural nutrient cycles and decrease biodiversity at many scales (Tilman et al. 2001, Cassman and Wood 2005).

The world's natural terrestrial biomes comprise primarily perennial plants in mixtures (Chiras and Reganold 2004), whereas more than two-thirds of global cropland is sown to monocultures of annual crops. Conversion from natural to agricultural landscapes dramatically changes the plant communities that are integral to ecosystem processes.

Perennial plants are highly efficient and responsive micro-managers of soil, nutrients, and water. In contrast, annual crops require seedbed preparation, precisely timed inputs and management, and good weather during narrow time windows. With shorter growing seasons and less extensive root systems (figure 1), annual crops provide less protection against soil erosion, manage water and nutrients less effectively, store less carbon below ground, and are less resilient to pests and abiotic stresses than are perennial plant communities (Glover 2005).

The type of vegetation covering a landscape—annual versus perennial—is the most important factor governing soil loss; in a Missouri field experiment monitored for over 100 years, perennial crop cover was more than 50 times more effective than annual crops in maintaining topsoil (Gantzer et al. 1990). Conservation tillage (which leaves crop residue on the soil surface) and no-till methods (in which crops are

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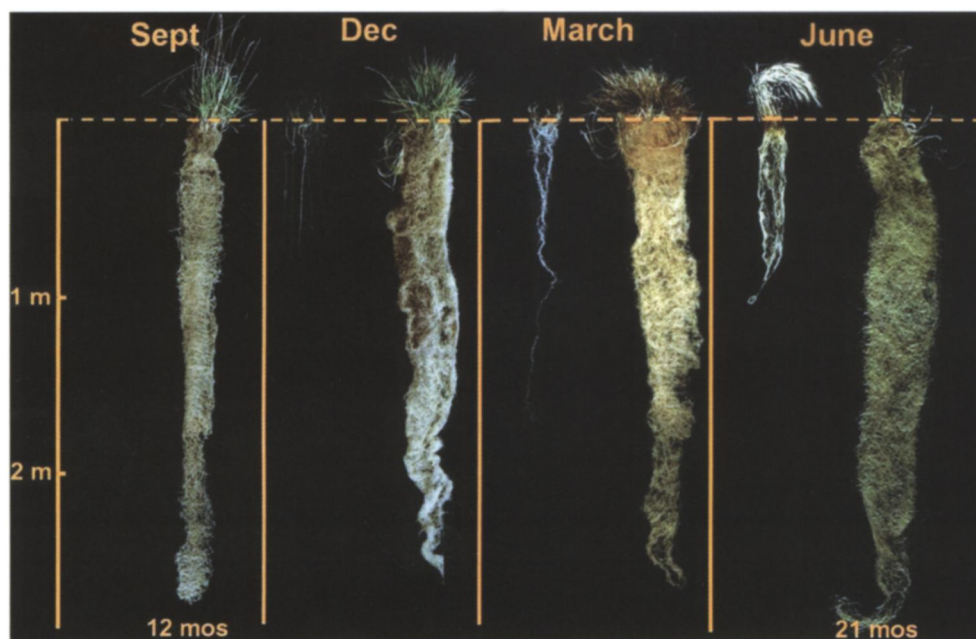


Figure 1. Root systems of annual wheat (on the left in each panel) and intermediate wheatgrass, a perennial, at four times of the year. Although roughly 25% to 40% of the wheatgrass root system dies off and must grow back each year, its longer growing season, and consequently greater access to resources, results in greater above- and belowground productivity than its annual counterpart.

farmed with no tillage at all) reduce soil loss but do not reduce nutrient and water losses from annual crop fields (Randall and Mulla 2001). Global data for maize, rice, and wheat indicate that only 18% to 49% of nitrogen applied as fertilizer is taken up by crops; the remainder is lost to runoff, leaching, or volatilization (Cassman et al. 2002). Nitrogen losses from annual crops may be 30 to 50 times higher than those from perennial crops (Randall and Mulla 2001).

Perennial crops also store more carbon in the soil (320 to 440 kilograms [kg] per hectare [ha] per year) than do annual crops (0 to 300 kg per ha per year) (Robertson et al. 2000). Through greater carbon storage and lower needs for applied chemicals, perennial crops could help restrain climate change. Their net values for global warming potential are negative, having been estimated at –200 to –1050 kg of carbon dioxide (CO₂) equivalents per ha per year, as compared with positive potentials of 410 to 1140 kg per ha per year for annual crops (Robertson et al. 2000).

Because annual crops are more sensitive than perennials to conditions in the soil's topmost layer and have a shorter growing season in which to adapt to stresses, they are more detrimentally affected by temperature increases of the magnitude predicted by most climate-change models. Increases of 3 to 8 degrees Celsius are predicted to increase yields of switchgrass (*Panicum virgatum*), a perennial forage and energy crop, by 5000 kg per ha, whereas yields are predicted to decline for the annual species maize (–1500 kg per ha), soybean (–800 kg per ha), sorghum (–1000 kg per ha), and wheat (–500 kg per ha) (Brown et al. 2000).

Some perennial crops are currently available for use by farmers around the world. Perennial hay, forage, and pasture crops are attracting greater attention in the United States as researchers and farmers look for alternative crops to improve soil and water quality and farm profitability. Federal policies such as those promoted in the the Conservation Reserve Program have also encouraged the use of perennial vegetation on millions of hectares across the United States. In tropical regions, agroforestry, alley cropping, and perennial forages offer opportunities to replace erosion-prone annual crops with perennials and are also important for maintaining the productivity of marginal lands that cannot support annual grain crops for long periods (Cassman et al. 2003).

However, the dietary requirements and preferences of a growing human population set a limit on the degree of ecological restoration that can be achieved with currently available perennial species. Approximately 69% of the planet's cropland is sown to cereal grains, food legumes, and oilseeds. Those three broad groups of crops—all annuals—yield food products that contain energy and protein in concentrated form and are easily stored and transported. They form the foundation of the human diet in most of the world, whether they are eaten directly or fed to livestock. In contrast, hay and pasture occupy only 15%, and perennial fruit, berry, and nut species less than 4%, of global agricultural land. By developing perennial grain crops, plant breeders could help dramatically enlarge that portion of the agricultural landscape that is kept intact by perennial roots. To do so will require a massive, long-term effort, because, with a few negligible exceptions, no perennial cereal, pulse, or oilseed crops currently exist (Cox TS et al. 2002).

Can perennials produce sufficient yields of grain?

Traditionally, the two traits of greatest interest in a grain crop are yield of edible seed per unit of land area, which is the basic measure of productivity, and size of individual seeds, which affects ease of utilization and food quality. Seed yields and seed sizes of wild herbaceous plants, annual or perennial, are far smaller than those of annual grain crops, and, on average, wild perennials produce smaller seeds than do wild annuals. Perennial grain breeders are in a sense aiming to replicate the achievements of the Neolithic peoples who domesticated and improved the grain crops on which agriculture

depends today. Therefore, one yield comparison of interest is that between the wild ancestors of annual grain crops and those of perennial species that are currently or potentially the subjects of domestication and breeding.

Experimental data on seed yields for wild progenitor species are rare in the literature, because the wild plants' small seeds, asynchronous ripening, and shattering (spontaneous shedding of seed before harvest) make full recovery of seed difficult. Among yields that have been reported for wild annuals, the highest by far are those produced by the ancestors of barley, durum wheat, and oat (table 1). The productivity of barley and durum wheat helps explain why these were the first grain species to be domesticated by humans, more than 10,000 years ago. The progenitors of sorghum, pearl millet, and sunflower have more modest yields (table 1). Yields of wild perennial species (table 1), including those that are the subject of domestication efforts, have been lower than those of wild barley, wheat, and oat, but within the range of other annual crop progenitors. Individual seeds of perennials are also much smaller than those of wild barley and wheat, but they are comparable to those of other annual progenitors (see the references in table 1; data are not shown).

The high yields of modern crops are the result of long-term, intense selection for increased allocation of photosynthate to the seed and decreased intraspecific competition. Conversely, as argued by DeHaan and colleagues (2005), the relatively low seed yields of wild perennial species result from natural selection in highly competitive environments. The evolutionary fitness of a wild annual plant is heavily dependent on seed production and dispersal, but the fitness of a wild perennial

depends more on the survival of vegetative structures than on seed traits.

DeHaan and colleagues (2005) predicted that artificial selection in a properly managed agricultural environment could increase seed yield while maintaining perenniality. Artificial selection has the potential to generate perennial grain crops with acceptable yields, if it is applied to agronomic traits and perennial growth habit simultaneously. This is suggested by four characteristics of perennial plants that differentiate them from annual plants, as discussed below.

Better access to resources and a longer growing season.

Perennial plants grow over a longer season than do annuals, so they can intercept sunlight, utilize rainwater, and absorb nutrients during parts of the year when cropland devoted to annuals lies completely bare or is sparsely covered by small seedlings with shallow roots. In the Land Institute's breeding nurseries in Kansas, shoots emerge from the rhizomes (underground stems) of perennial sorghum in the spring at least one month before shoots emerge from seeds of annual sorghum sown on the standard date of approximately 15 May, and the rhizome-derived shoots grow more rapidly. In Kansas, intermediate wheatgrass (a perennial cool-season grass) maintains a large, photosynthetically active leaf area between July and September, a period during which annual wheat plants are not growing at all. In Minnesota, the first cutting of alfalfa, a perennial legume crop, is typically done in the second week of June (Sheaffer et al. 2000). In contrast, the emergence of annual soybean seedlings from the soil does not reach 85% completion, on average, until 12 June in Minnesota, accord-

Table 1. Grain yields of six annual wild progenitors of grain crops and their corresponding domesticates, and of four perennial species and a group of perennial species that are candidates for domestication as grain crops.

Growth habit	Common name	Progenitor Botanical name	Progenitor grain yield (kilograms per hectare)	Domesticated grain crop	Domesticated grain yield (kilograms per hectare)	Reference
Annual	Wild emmer	<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	2100 ^a	Durum wheat	4600	Beharav and Nevo 2004
	Wild barley	<i>Hordeum spontaneum</i>	1860 ^a	Barley	2690 ^a	Vega and Frey 1980
	Wild oat	<i>Avena sterilis</i>	1480 ^a	Oat	3720 ^a	Lawrence and Frey 1976
	Wild sorghum	<i>Sorghum bicolor</i> ssp. <i>arundinaceum</i>	710	Sorghum	4310	Cox TS and Frey 1984, Cox TS et al. 1985
	Wild millet	<i>Pennisetum glaucum</i> ssp. <i>monodii</i>	470	Pearl millet	2820	Bramel-Cox et al. 1986
	Wild sunflower	<i>Helianthus annuus</i>	200	Sunflower	— ^b	Cummings and Alexander 2002
Perennial	Intermediate wheatgrass	<i>Thinopyrum intermedium</i>	600 ^a	—	—	Wagoner 1990a
	Mean of 25 forage grasses		490 ^a	—	—	Wagoner 1990a
	Illinois bundleflower	<i>Desmanthus illinoensis</i>	890	—	—	DeHaan et al. 2003
	Alfalfa	<i>Medicago sativa</i>	820	—	—	Bolanos-Aguilar et al. 2002
	Maximilian sunflower	<i>Helianthus maximiliani</i>	410	—	—	Jackson and Jackson 1999

Note: Each crop species was compared with its progenitor in a common experiment; different crops, progenitors, or prospective domesticates were evaluated in different studies. However, all evaluations were done in environments to which the species involved were well adapted, under experimental small-plot conditions. All values are means across genotypes and environments, not values for unusually high-yielding genotypes.

a. Includes weight of hulls (adhering lemma and palea).

b. Data for seed yields of wild and domesticated annual sunflowers from a common experiment were unavailable.

Articles

ing to US Department of Agriculture statistics. Therefore, by the time a soybean crop has just begun to photosynthesize, a field of alfalfa has already produced about 40% of the season's production (Sheaffer et al. 2000).

More conservative use of nutrients. Perennial plants use nutrients more efficiently, resulting in a greater potential for long-term sustainable harvests. Some native tallgrass prairie meadows in Kansas have been harvested annually for 75 to 100 years with no substantial fertility inputs other than nutrients from atmospheric deposition, weathering of parent material, and biological nitrogen fixation. Comparisons of soil nutrient contents maintained by five continuously cropped wheat fields with those maintained by adjacent native hay meadows on level bottomlands in north-central Kansas illustrate the point. The wheat fields and native hay meadows, all harvested for approximately 75 years, currently yield similar amounts of nitrogen in the form of grain or hay. The wheat fields, however, have received approximately 70 kg of fertilizer nitrogen per ha per year for more than a decade, while no fertilizer has been applied to the hay meadows. Despite similar levels of nitrogen export and substantially different levels of nitrogen inputs, the hay meadows maintain significantly greater amounts of total soil nitrogen and carbon to a depth of 1 meter than do the fields producing annual crops (table 2). Soil phosphorus and potassium are at similar levels for the two production systems, even though fertilizer is added to the wheat fields each year.

Table 2. Soil nutrient contents, to a depth of 1 meter, of adjacent wheat fields and native hay meadows in north-central Kansas.

Nutrient	Wheat fields (kilograms per hectare)	Hay meadows (kilograms per hectare)
Total nitrogen	9630a	12,520b
Total carbon	126,700a	179,300b
Total phosphorus	4677a	4280a
Exchangeable potassium	3499a	3317a

Note: Values within a row followed by different letters are significantly different at the 0.05 level of probability.

High biomass production. Perennials generally yield more aboveground biomass than do annuals, and some of the carbon that goes into the biomass might be reallocated to grain production through breeding. Although those species currently being domesticated as perennial grain crops have low seed yields, their total aboveground productivity is often higher than that of annual crops with long breeding histories (DeHaan et al. 2005). Piper and Kulakow (1994), for example, reported a mean aboveground biomass for self-pollinated progeny of annual \times perennial sorghum hybrids that was 62% higher than that of their annual parent. However, the hybrids' mean harvest index (ratio of seed yield to total aboveground biomass) was much lower than that of the annual parent. The carbon allocated for excess vegetative

production (from a human point of view) in perennials is available for reallocation through plant breeding. This kind of increase in harvest index was largely responsible for yield increases achieved in annual crops by the Green Revolution (Evans 1998).

Sustainable production on marginal lands. Because of growing population pressure in many parts of the world, landscapes especially vulnerable to damage from annual cropping, such as those with steep slopes or thin topsoil, are becoming increasingly important sources of food and income. Cassman and colleagues (2003) wrote that for large areas in poor regions of the world, "annual cereal cropping...is not likely to be sustainable over the longer term because of severe erosion risk. Perennial crops and agroforestry systems are better suited to these environments" (p. 319). Some perennial crops, such as perennial forages, are available now for these landscapes, but increased global demands for grain will most likely pressure farmers to plant grains (all of which are currently annual crops), not forages. Perennial grain crops, once developed, will have the potential to satisfy demand for grains while protecting soil, even when grown on erosion-prone land.

Two complementary approaches to breeding perennial grains

Although impediments to the development of perennial grains are not insurmountable, they will not be overcome quickly or easily. There are two possible approaches to breeding perennial grains, each of which involves serious challenges (Cox TS et al. 2002). When both approaches are possible in a given group of species or genera, it may be advisable to pursue them in parallel because of their complementary strengths and weaknesses.

Direct domestication. The first approach, direct domestication, starts with identification of perennial species that have high and consistent seed production (in comparison with wild species in general) and other traits that might add to their utility as grain crops. That is followed by selection within those species to increase the frequency of genes for traits of domestication such as synchronous flowering and maturity, large seeds that do not shatter but can be threshed mechanically, and high yield of seed per unit of land.

Domestication of annual grains occurred under many and varied genetic conditions. Doebley and Stec (1993) showed that the dramatic morphological difference between maize and its wild ancestor teosinte can be accounted for by changes in as few as five relatively small genomic regions. They argued that such large-effect mutations may facilitate adaptation to drastically new environments, including those encountered during domestication. But when Burke and colleagues (2002) found a large number of small-effect genes governing domestication in sunflower, they concluded that "domestication may have occurred much more readily than if it had required the fortuitous occurrence of multiple major mutations."

Centuries of experience have shown that once any seed-bearing species has been domesticated, its seed yield and other traits can be improved through phenotypic selection. Furthermore, because the direct domesticator is working within a species in which plants are, for the most part, sexually compatible, the entire range of genetic diversity in that species is available at any time for incorporation into the breeder's gene pool.

With the advantages of genetic knowledge and technology, today's perennial grain breeders can make more rapid progress than did ancient domesticators of annual plants; however, the gap to be traversed between current and desired yields is formidable. For example, suppose we were to improve the yield of intermediate wheatgrass—a perennial relative of wheat currently targeted for domestication and breeding as a grain crop—from its current 600 kg per ha (table 1) to 2300 kg per ha, which would be a modest but typical yield for annual wheat in Kansas. If we could increase yield at either an exponential rate of 10% per generation of selection or a linear rate of 110 kg per ha per generation (either of which would be an impressive achievement relative to typical estimates of selection progress in established crop species), it would require 16 generations, or 48 years, at the fastest possible turnover rate of three years per generation, to reach a yield of 2300 kg per ha.

Wide hybridization. The second approach to perennial grain breeding, wide hybridization, is a way of short-cutting the domestication process by taking advantage of useful genetic variation already established in high-yielding crop cultivars. Proponents of this approach hope that artificial selection in populations derived from interspecific or intergeneric hybrids will be able to produce a widely grown and consumed crop more quickly than could be accomplished by direct domestication. Of the world's 13 most widely grown grain or oilseed crops, 10 are capable of being hybridized with perennial relatives (table 3). Currently, such interspecific and intergeneric hybrids are being used by a handful of breeding programs as a base from which to develop perennial grain-producing crops (Cox TS et al. 2002).

Annual crops can supply genes that promote domestication as well as genes for high grain yield. In the ancestors of annual crops, mutant plants with characters such as reduction of the hard fruitcase in teosinte plants or nonshattering in the wild cereals of the Middle East were usually rare, as they are likely to be in wild perennials as well. Identifying and increasing the frequency of such genes in a species undergoing direct domestication would most likely require substantial time and resources. Managed gene flow from cultivated species could be a faster way of obtaining genes important for domestication, along with the complex genetic systems underlying high grain yield and large seeds (DeHaan et al. 2005).

The useful genes acquired through hybridization come at a cost, however. When most crops—including wheat, rice, barley, rye, maize, sorghum, pearl millet, soybean, and

Table 3. The world's 13 most commonly grown grain crops and examples of perennial species with which 10 of them have been hybridized.

Annual crop		Perennial relatives
Common name	Species	
Barley	<i>Hordeum vulgare</i>	<i>Hordeum jubatum</i>
Chickpea	<i>Cicer arietinum</i>	<i>Cicer anatolicum</i> <i>Cicer songaricum</i>
Common bean	<i>Phaseolus vulgaris</i>	—
Maize	<i>Zea mays</i>	<i>Zea mays</i> ssp. <i>diploperennis</i> <i>Tripsacum dactyloides</i>
Oat	<i>Avena sativa</i>	<i>Avena macrostachya</i>
Peanut	<i>Arachis hypogaea</i>	—
Pearl millet	<i>Pennisetum glaucum</i>	<i>Pennisetum purpureum</i>
Rape	<i>Brassica campestris</i>	—
Rice	<i>Oryza sativa</i>	<i>Oryza rufipogon</i> <i>Oryza longistaminata</i>
Sorghum	<i>Sorghum bicolor</i>	<i>Sorghum propinquum</i> <i>Sorghum halepense</i>
Soybean	<i>Glycine max</i>	<i>Glycine tomentella</i>
Sunflower	<i>Helianthus annuus</i>	<i>Helianthus maximiliani</i> <i>Helianthus rigidus</i> <i>Helianthus tuberosus</i>
Wheat	<i>Triticum</i> spp.	<i>Thinopyrum</i> spp. <i>Elymus</i> spp. <i>Leymus</i> spp. <i>Agropyron</i> spp.

Source: Data on global grain production are adapted from an FAO database (FAO 2005).

sunflower—are crossed with perennial relatives, differences in chromosome number, lack of chromosome homology, or other factors can cause moderate to complete sterility and restrict genetic recombination in the progeny (Cox TS et al. 2002). The plant breeder working with such crosses must struggle with genomic disruptions while selecting to improve multiple traits simultaneously. The history of plant breeding shows that progress in such situations is often achieved slowly and only through extraordinary efforts.

To reduce the number of traits that must be improved simultaneously, breeders could use annual parents that have perennial "tendencies." For example, some tropical cultivars of annual sorghum and rice are well adapted to ratoon cropping; that is, they are able after harvest to produce new tillers that, given favorable conditions, can produce a second crop. Crosses with such parents might produce a higher frequency of perennial progeny than would crosses with more strictly annual parents.

In the taxa studied to date, plants derived from interspecific hybrids tend to be perennial only when 50% or more of their total genome is derived from a perennial parent (Cox TS et al. 2002). Traits like perenniality that involve complex genetic control and interact with the environment are not susceptible to improvement through manipulation of individual genes. Therefore, there is little chance that transgenic technology can dramatically speed up the development of perennial grains from annual × perennial hybrid populations.

On the other hand, analytical techniques such as genome mapping hold considerable promise. To date, the rice genome

is the most thoroughly mapped and sequenced of any grain-crop genome, and a national effort to sequence the sorghum genome is under way. As part of this effort, a cross between cultivated sorghum and the perennial grass *Sorghum propinquum* has been used to map the genes coding for rhizome (underground stem) development (Paterson et al. 1995). Rhizomes are an essential basis of perenniality in some species. Molecular-marker-assisted selection could help accelerate the simultaneous improvement of perenniality, fertility, and grain production in rice, sorghum, and other species.

A pair of unlinked genes for rhizome formation in *Oryza longistaminata*, a perennial relative of rice, have been mapped to the same chromosomal regions as two markers associated with rhizomatousness in the sorghum relative *S. propinquum*. However, the two rice genes appeared also to interact with other genes as yet to be identified, and the corresponding genomic regions in sorghum together account for only 12% of the total variation for rhizomatousness and less than 4% of the variation for regrowth from rhizomes (Paterson et al. 1995). Chromosomal segments affecting rhizome presence, abundance, and growth were found on 8 of rice's 12 chromosome pairs and on 9 of 10 pairs in sorghum (Hu et al. 2003). Furthermore, genetically complex as it is, rhizome production in rice or sorghum is only one piece of the perenniality puzzle—a necessary but not sufficient condition for long-term persistence of the perennial growth habit.

Other genetic technologies of relatively recent origin offer valuable analytical tools, permitting breeders to identify, for example, the genomic origin of each of the chromosomes in progeny of hybrids between wheat and its perennial relatives. Using genetic stocks of wheat to which individual chromosomes of the perennial grass *Thinopyrum elongatum* have been added, Lammer and colleagues (2004) determined that *T. elongatum* chromosome 4E confers post-sexual-cycle regrowth. Current studies are locating the gene or genes on 4E that govern the trait.

However, regrowth in wheat, like rhizome development in rice or sorghum, indicates the capacity to remain alive after maturity and harvest but does not in itself guarantee perenniality. For example, the tissues of a perennial wheat plant that survives after summer harvest must also be able to remain in or return to a vegetative state (to avoid flowering out of season, which could be fatal), maintain a robust root system, stay alive through hot or dry conditions during late summer, survive freezing temperatures (if in the temperate zone), and then initiate reproductive growth at the appropriate time the following spring (Lammer et al. 2004). These complex environmental responses are affected by many genes.

Perennial grains, like annual crops, cannot succeed if they are highly susceptible to diseases, insects, or other pests. Whereas genetic erosion has reduced genetic variation for disease resistance in many annual crops, their wild perennial relatives are important sources of resistances. For many decades, interspecific and intergeneric hybrids have been used to transfer pest-resistance genes from perennial species into crops such as wheat. Now, similar hybrids derived from

crosses with the wheatgrass genus *Thinopyrum* have demonstrated resistance to a multitude of economically important wheat pests and diseases such as leaf and stem rust (caused by *Puccinia triticina* and *Puccinia graminis*, respectively), wheat streak mosaic (caused by wheat streak mosaic virus), the wheat curl mite (*Aceria tosichella*), barley yellow dwarf (caused by barley yellow dwarf virus), Cephalosporium stripe (caused by *Cephalosporium gramineum*), eyespot (caused by *Tapesia yallundae* and anamorph *Pseudocercospora herpotrichoides* var. *herpotrichoides*), and tan spot (caused by *Pyrenophora tritici-repentis*) (Friebe et al. 1996, Cox CM et al. 2002, 2005a).

Genetic resistance to all pests is not usually present in a single cultivar, and genetic monocultures often exert selection pressure that increases the frequency of insect, fungus, or other pest genotypes that are unaffected by the genetic resistance of crops. Some cultural practices that manage pests in annual crops, such as annual tillage and short-term crop rotation, will not be suitable for stationary, long-lived perennial grain crops. To manage pests in perennial systems, it will be necessary to deploy greater genetic diversity both among and within crop species, improve our understanding of host and microbial diversity effects on pests over different landscapes and timescales, and employ cultural practices such as field burning and long-term rotations (Cox CM et al. 2005b).

Examples of current research

Current work on intermediate wheatgrass exemplifies direct domestication, and breeding programs in perennial wheat, sorghum, and sunflower illustrate the wide hybridization approach.

Intermediate wheatgrass. Among the many perennial members of the grass family's Triticeae tribe—which also includes the annual crops wheat, barley, and rye—intermediate wheatgrass has received the most attention from both breeders of annual wheat and breeders interested in developing a new perennial grain crop.

Intermediate wheatgrass propagates via production of tillers (aboveground stems), rhizomes, and seed. Its seed yield is close to the typical seed yield of other forage grasses (table 1). Forage crops represent a precedent, albeit a limited one, for breeders attempting to increase the grain yield of perennial species. The traits of greatest interest in perennial forages are biomass yield and quality, but economic considerations have prompted breeders to select for seed yield as well (Wilkins and Humphreys 2003).

Moore and colleagues (1995) concluded that existing forage cultivars of intermediate wheatgrass have not been genetically narrowed; each contains enough genetic variation to fuel continued breeding progress. Knowles (1977) used mass selection to double the seed yield of an intermediate wheatgrass population. Significantly, he also found that breeding exclusively for seed yield did not lead to a reduction in forage yield. In another study, identification of higher-yielding

strains, followed by intermating and two cycles of mass selection, improved seed yield at a rate of approximately 20% per cycle (Wagoner et al. 1996).

After evaluating 100 species, Wagoner (1990a) identified intermediate wheatgrass as the most promising perennial cool-season grass for development as a grain crop. It came the closest to meeting the following criteria for a perennial, mechanically harvested grain: hardy persistence; stiff, erect culm; synchronous seedset; resistance to shattering; rapid dry-down at maturity; easy threshing; relatively large seed; and good seed flavor. Although it cannot be used alone to make leavened bread, intermediate wheatgrass has a nutritional value similar to or better than that of wheat (Becker et al. 1991).

Since 2002, the Land Institute has established several breeding populations of intermediate wheatgrass for direct domestication (DeHaan et al. 2005), employing bulk breeding and mass selection. In a wheatgrass population serving as the base for mass selection, there was high variability for all traits evaluated. Estimates of broad-sense heritability (the proportion of variation attributable to genetic causes) were moderate to high for almost all traits, including 0.59 for seed yield per spike, 0.64 for 100-seed weight, and 0.62 for proportion of free-threshing seed. Such heritability levels indicate that selection will be capable of increasing the frequency of genes conferring desirable traits in the population.

Wheat. As discussed earlier, breeding of high-grain-yielding intermediate wheatgrass cultivars could require half a century. However, it and other perennial species can also be hybridized with either durum or common wheat, and such hybrids have long been looked to as possible gateways to development of a perennial wheat. The chromosomes of wheat and wheatgrass do not pair during meiosis in hybrids. The sterile hybrids sometimes undergo spontaneous doubling of their chromosome number (producing a plant known as an amphiploid), but more often are backcrossed to one or the other parent; both routes have the potential to produce fertile plants.

To date, most plants referred to as “perennial wheat” have been partial amphiploids; that is, their genomes contain the complete or near-complete genome of durum or common wheat plus a substantial portion of the genome of one or another perennial species of the genus *Thinopyrum*. Wagoner (1990b) gave a thorough account of early programs to breed perennial wheat, including a decades-long effort in the Soviet Union that was finally abandoned in the 1960s because of persistent problems with sterility, inconsistent perenniality, and undesirable agronomic characteristics. Little or no germplasm survives from the Soviet program.

Efforts in the United States have made better but still modest progress. Suneson and colleagues (1963) reported that 25 years of work with perennial wheat in California had produced lines whose first-year grain yields fell “within the range of the lowest yielding commercial wheat varieties” of the time, with a rapid yield decline in the second and third years, when

plants regrew as perennials. The perennial, weakly rhizomatous strain MT-2, derived from a hybrid of durum wheat and intermediate wheatgrass, was released as a germplasm line by the Montana Agricultural Experiment Station. Eight lines derived from complex wheat × *Thinopyrum* hybrids and selected for regrowth ability in eastern Washington State produced between 1600 and 5800 kg per ha in field trials that also included a popular wheat cultivar yielding almost 9000 kg per ha (Scheinost et al. 2001).

In North America’s hard winter wheat belt, centered on the state of Kansas, no researchers have ever reported survival of perennial wheat beyond the first year of growth. In six years of testing at the Land Institute in central Kansas, perennial wheat strains developed by programs in other states have invariably died at some point between the first-year harvest in early July and the arrival of cool weather in September. No research has been done to explain why currently available perennial wheat strains always die while intermediate wheatgrass plants easily survive the summer in Kansas. It is clear that perennial wheat development in Kansas will require the exploration of new gene pools.

Until recently, perennial wheat breeding rested on a narrow genetic base. To improve the chances of identifying plants that are perennial in a wider range of environments, hybridization among a much more diverse range of parents is necessary. Since 2000, perennial wheat researchers at Washington State University and the Land Institute have been hybridizing plants belonging to several *Thinopyrum* species with annual crop species, including durum wheat, common wheat, and triticale (an amphiploid of durum wheat and rye). More than 1500 such hybrids have been produced at the Land Institute (DeHaan et al. 2005), and thousands of fertile backcross progenies are currently being screened for perenniality.

Backcrossing produces plants that vary widely in chromosome number and genomic composition. This results in a gene pool that is difficult for a perennial wheat breeder to manage, because crossing two plants with different chromosomal complements often produces sterile progenies. Therefore, when fertile, perennial plants are identified, it will be important to determine the genomic origin of each of their chromosomes. The perennial parent’s chromosomes can be distinguished from those of wheat through genomic *in situ* hybridization, which separates them by color fluorescence (figure 2), and allows detection of chromosomal abnormalities such as translocations. Two other cytogenetic techniques, fluorescent *in situ* hybridization and C-banding, facilitate differentiation of chromosomes from the same parent.

Sorghum. *Sorghum bicolor* is a staple food crop in many parts of Africa and Asia and a major feed grain in the United States. An annual species domesticated in the tropics of Africa, sorghum is a diploid with 10 pairs of chromosomes. The perennial species *Sorghum halepense* is a tetraploid with 20 pairs of chromosomes, 10 of them similar to those of *S. bicolor* and 10 similar to those of the diploid perennial *S.*

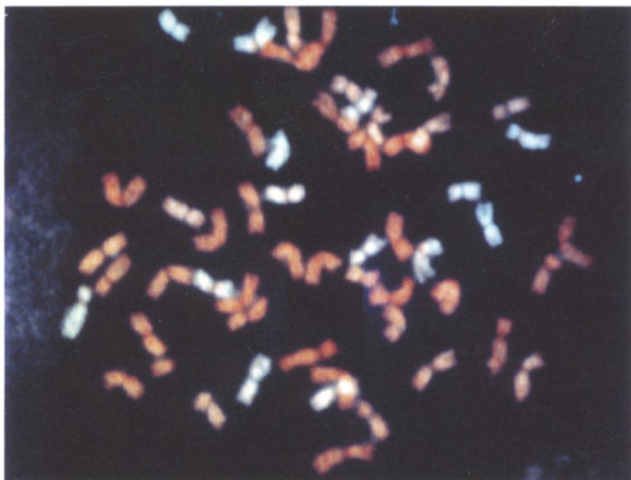


Figure 2. A single mitotic cell of a 56-chromosome perennial wheat plant (*Triticum aestivum* × *Thinopyrum* spp.). Chromosomes from wheatgrass and common wheat have been made to glow green and red, respectively, by genomic in situ hybridization (GISH). GISH technology allows the identification of genomic affinity to whole or partial chromosomes within a single plant using fluorescent-labeled total genomic DNA as a probe from the donor species.

propinquum (Paterson et al. 1995). *Sorghum halepense* has migrated throughout much of the United States and into Canada as a highly successful, rhizomatous weed known as johnsongrass.

There appear to have been no attempts to domesticate *S. halepense* directly, and the only known program to develop perennial grain sorghum through *S. bicolor* × *S. halepense* hybridization was initiated by the Land Institute in the 1980s (Piper and Kulakow 1994). Because the two species differ in chromosome number, those early hybrids were produced using artificially chromosome-doubled (tetraploid) *S. bicolor* plants as female parents. The tetraploid F_1 hybrids were fertile, and 50 F_2 plants derived by self-pollination of the hybrids varied widely in rhizome production. A majority of those plants were perennial; that is, after harvest, their rhizomes survived through the winter to produce new shoots the following spring.

The mean seed yield of the F_2 plants was 1720 kg per ha (Piper and Kulakow 1994), which compares favorably with wild progenitors of annual crops and perennial domesticates (table 1). However, no plants had short stature, stiff stalks, synchronous maturity, relatively compact panicles, large seeds, or other characteristics of domesticated sorghum. When hybrids were backcrossed to the *S. bicolor* parent to recover genes governing those traits, perenniality was largely lost (Piper and Kulakow 1994).

Perennial sorghum seed from the hybrids produced by Piper and Kulakow (1994) was maintained and regenerated through the 1990s. In 2001, the Land Institute initiated a new effort to introgress genetic variability into the perennial gene pool from diploid, male-sterile *S. bicolor* plants, rather

than from tetraploid plants. Male sterility in sorghum can be caused by any of a series of recessive nuclear genes or by interaction between cytoplasmic and nuclear genes. Through rare meiotic errors, male sterile plants produce a small number of unreduced female gametes that, when they unite with male gametes from tetraploid sorghum plants, produce tetraploid progeny (Hadley 1958).

In 2001, 2003, and 2004, Land Institute researchers hybridized improved male-sterile grain sorghum plants with perennial sorghum plants descended from Piper and Kulakow's tetraploid *S. bicolor* × *S. halepense* populations. Almost 300 tetraploid F_1 hybrid plants representing more than 90 parental combinations were produced. Thousands of families derived by self-pollinating those hybrids are currently undergoing field evaluation for rhizome production, perenniality, seed yield, seed size, and other agronomic characters. In the Land Institute's perennial sorghum populations, there appear to be no serious obstacles to the recovery of new trait combinations from segregating progenies. For example, short, relatively croplike plants with long rhizomes (figure 3) arise rarely but consistently in tetraploid F_3 populations from crosses between male-sterile *S. bicolor* and tetraploid perennials.

In a temperate climate, production of rhizomes does not guarantee that a sorghum plant will regrow the following spring; rhizomes buried in the soil through the winter must have the capacity either to survive periods of exposure to freezing temperatures or to grow deeply enough to escape freezing. Although the rhizomatous sorghum plants evaluated at the Land Institute have exhibited a high degree of diversity for aboveground traits, from johnsongrass-like to croplike, none of the winter-hardy rhizomatous plants identified to date have had short stature, thick culms, compact panicles, or large seeds.

In April and May, 2006, researchers at the Land Institute selected more than 300 perennial F_4 plants that emerged from overwintering rhizomes. The F_3 -derived families to which those plants belonged had significantly higher grain yields than did families with no perennial members. The newly selected F_4 plants, given further self- and cross-pollination and adequate genetic recombination, can be expected to give rise to some perennial progeny with improved agronomic characteristics.

Sunflower. Maximilian sunflower, a perennial native to North America, has potential as an oilseed or food-grain crop (Jackson and Jackson 1999). The Land Institute has initiated a domestication program to develop nonshattering populations of this species with high yield and larger seed. A wide range of perennial species, including Maximilian sunflower, can be hybridized directly with domesticated sunflower if embryo rescue is used. The fertility of hybrids is very low, but backcrossing to the annual parent is done routinely (Jan 1997). Fertility of similar interspecific hybrids has been increased using chromosome doubling to create amphiploids (Jan and Chandler 1989).

The hexaploid perennial sunflower *Helianthus tuberosus*, commonly known as Jerusalem artichoke, crosses readily with many diploid annual and perennial species (Rogers et al. 1982), enabling it to serve as a genetic bridge. Tetraploid hybrids resulting from crosses between annual sunflower and Jerusalem artichoke have acceptable fertility (Jan 1997). More than 40 F_1 plants from crosses between cultivated sunflower (as male) and hexaploid plants belonging to several strains of Jerusalem artichoke and *Helianthus rigidus* survived the winter of 2005–2006 in Land Institute field plots. F_1 plants from crosses among Jan and Chandler's crop \times wild perennial amphiploids (Jan and Chandler 1986) survived that winter as well. Complex hybrids among all of these tetraploids will constitute a gene pool for the development of a perennial sunflower at the Land Institute.

Other possible perennial grain crops. Illinois bundleflower, a perennial legume with a vast native range across North America, is among the highest seed-yielding herbaceous perennial species known (table 1; DeHaan et al. 2003). As with intermediate wheatgrass and Maximilian sunflower, the Land Institute is domesticating Illinois bundleflower for grain production. This effort will require development of new food uses. Whereas the species has been studied and used as a forage, its seed has never been utilized for food or livestock feed.

Another legume with potential for high seed production is alfalfa (table 1). There are no current efforts to breed alfalfa as a grain crop, but as a domesticated forage, it has enjoyed a long history of extraordinary success under a wide range of conditions (Russelle 2001). Alfalfa might well be considered a candidate for domestication as a grain.

The International Rice Research Institute achieved significant progress toward breeding a perennial upland rice from crosses between the domesticate *Oryza sativa* and a wild progenitor, *Oryza rufipogon* (Sacks et al. 2003). However, the project was terminated in 2001 because of budgetary cutbacks.

T. S. Cox and colleagues (2002) reviewed a wide range of taxa with potential for the development of perennial grains, but for which no breeding programs currently exist. The taxa included pearl millet, oat, maize, soybean, and chickpea, as well as the wild perennial species *Leymus arenarius*, *Leymus racemosus*, *Tripsacum dactyloides*, *Oryzopsis hymenoides*, and *Senna marilandica*.

The future

The superior capacity of perennial plants to store carbon, manage resources, and stop soil erosion is widely recognized among ecologists and soil scientists, yet in 2006 only a handful of plant breeders are working to develop perennial grain crops.

Even with expanded efforts, the road leading to perennial grains will be long, and it may often be rough; however, the time required should be put in context. Had large programs to breed perennial grains been initiated alongside the Green Revolution programs a half-century ago, farmers might well have had seed of perennial varieties in their hands today. As



Figure 3. A relatively short sorghum plant with a relatively compact panicle (seed head) showing emergence of shoots from underground rhizomes in October 2005. This plant was excavated from a field experiment designed to evaluate families derived by self-pollination from hybrids between male-sterile grain sorghum and perennial sorghum. A meter stick is shown in the photograph. Fall emergence of rhizome shoots is not a desirable trait in itself, because such shoots will die with the first freeze. The ability to produce rhizomes is necessary for sorghum perenniality, however, and plants in which fall rhizome emergence is observed are more likely also to produce winter-hardy rhizomes that emerge the following spring. More than 300 plants in the population to which this plant belongs did emerge in spring 2006.

it is, the burden of feeding humanity into the second half of this century will fall on conventional agriculture, enhanced by improved conservation practices. Meanwhile, a growing body of evidence is demonstrating that the breeding of perennial grains is both necessary and feasible.

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