

Breeding for the perennial cropping systems of the future

Stan Cox

The Land Institute, Salina, KS, USA, www.landinstitute.org Email cox@landinstitute.org

Abstract

Agriculture's impact on the Earth has been amplified by industrial farming, but the fundamental problem has its origins 10,000 years ago, in the domestication of those annual crops that are still the staples of the global food supply. Annual crops, with ephemeral, often low-density root systems, have a lower capacity than do perennials to foster microbial ecosystems in the soil or micro-manage nutrients and water. Some of the more striking results of annual cropping have been the emergence of marine hypoxic zones at the mouths of major rivers and soil salinisation in parts of Australia. The means that modern agriculture relies upon to overcome the weaknesses of annual crops cannot simultaneously resolve all of the key problems. For example, no-till methods curtail erosion in the top layer of soil but, done consistently on a large scale, they require heavier use of chemical inputs and leave the lower soil profile unimproved. Conversely, organic methods eliminate toxic pesticides but not the soil erosion and water deterioration that occur as consequences of tillage. In an effort to resolve the dilemma, plant breeders in the US, Australia, and other countries are now breeding perennial counterparts of annual grain and legume crops, including wheat, wheatgrasses, sorghum, sunflower, and others. With their longer growing seasons and the greater opportunity for carbon fixation that results, diverse systems of such crops are aimed for both grazing and grain production. Perennial grains, combined with established and novel sustainable-agriculture practices, could help end the 10,000-year-old conflict between food production and ecological health.

Key Words

Perennial grains, sustainable agriculture, plant breeding, wheat, sorghum, sunflower

Introduction

Before the introduction of agriculture, almost all of the world's landscapes were covered mostly by perennial plants growing in mixed stands (Chiras and Reganold, 2004); today, the bulk of global cropland is sown to monocultures of annual crops. The conversion is accelerating, with more land having been converted from perennial to annual cover since 1950 than in the previous 150 years. This recent expansion of cropland has made it more and more necessary to apply chemical fertilisers and pesticides, which disrupt natural nutrient cycles and erode biodiversity (Jackson, 1980; Tilman et al. 2001; Cassman and Wood 2005).

The roots of perennial plants – including plant communities used for pasture, hay, rangeland, and tree crops – have been shown to be efficient micromanagers of soil, nutrients, and water. In contrast, annual crops such as cereals, grain legumes, and oilseeds typically provide less protection against soil erosion, waste water and nutrients, store less carbon below ground, and are less tolerant of pests than are perennial plant communities (Glover et al., 2007).

Three-fourths of the world's food-producing land is under grains and oilseed crops, and those species make up a similar portion of the human diet (directly in much of the world, via grain-fed animals in other regions). With a few very small-scale exceptions, no perennial cereal, pulse, or oilseed crops currently exist. By developing perennial grain crops, plant breeders could help enlarge that portion of the agricultural landscape under perennial vegetation (Cox et al., 2002, 2006).

DeHaan et al. (2005) predicted that artificial selection in a properly managed agricultural environment could increase seed yield while maintaining perenniality. Applied to agronomic traits and perennial growth habit simultaneously, artificial selection has the potential to generate perennial grain crops with acceptable yields. Four characteristics of perennial plants differentiate them from annual plants and provide them with extra resources that, through selection, can be re-allocated to grain production:

- Better access to resources and a longer growing season (Scheaffer et al., 2000),
- More conservative use of nutrients (Cox et al., 2006),
- Generally higher biomass production (Piper and Kulakow, 1994), and
- Sustainable production on marginal lands (Cassman et al., 2003)

Past and current efforts in the field

Even when vegetation covers the soil during the growing season, management of water and nutrients is less efficient with annual crops than with perennials. The replacement of native perennial root systems with the annual roots of crops has subtracted or reduced many of the elements (e.g. carbon pools, micro-organism populations, and root channels) that make soils healthy. Annual crops also require frequent soil disturbance, precisely timed inputs and management, and favourable weather in critical, often narrow, time windows. In one field experiment encompassing 100 years of data collection, perennial crops were more than 50 times more effective than annual crops in maintaining topsoil (Gantzer et al. 1990).

“No-till” methods (in which annual crops are farmed without tillage) reduce soil loss but require heavy chemical inputs for control of weeds and sometimes other pests. With its improved soil permeability, no-till farming decreases nutrient runoff but does not address the increasingly serious problem of nutrients and water leaching from annual crop fields into groundwater and eventually into rivers and seas (Randall and Mulla 2001).

With annual cereals such as maize, rice, and wheat, only 18% to 49% of nitrogen applied as fertiliser is taken up by crops; the remainder is lost to runoff, leaching, or volatilisation (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). Organic farming with annual crops addresses the problem of pesticide contamination but, except in rare circumstances, requires as much or more tillage than conventional agriculture. And the inadequate root systems of annual species handle water and nutrients inefficiently even when grown organically.

One of the globe’s most striking results of annual cropping has been the emergence of soil salinisation in parts of Australia. An economic analysis by Bell et al. (2007) concluded that “perennial wheat used for the dual purposes of grain and forage production could be developed as a profitable option for mixed crop/livestock producers.” Citing a survey of lucerne research by Ward (2006), they projected that escape of rainwater below the root zone (which can lead to rising water tables and salinisation) could be reduced 90 percent by replacing annual wheat with perennial wheat. Perennial wheat might be used in rotation in drier areas or in long-term stands in higher-rainfall zones.

Researchers in traditional sustainable agriculture are making the most of currently available perennial plants, by attempting to increase coverage of landscapes by perennial hay and pasture crops; grow perennial biofuel crops; plant more trees and grass along rivers and streams to take up nutrients and other contaminants that escape cropland; and take more erodible lands out of grain production altogether. (Jordan et al., 2007). Such defensive measures are necessary because agriculture is still dependent on annual crop plants.

Approaches to breeding perennial grains

Several groups, including The Land Institute in the US, the Future Farm Industries Cooperative Research Centre in Australia, the Yunnan Academy of Agricultural Sciences in China, and other research groups in a half-dozen US states and the Canadian province of Manitoba are conducting or initiating breeding programs for perennial grains. Programs follow two types of approaches that can often be followed in parallel: direct domestication of wild perennial species, and hybridisation between annual crops and related perennial species followed by selection.

Direct domestication

The first approach begins with identification of perennial species that have high and consistent seed production relative to other wild species and perhaps other beneficial traits. That is followed by cyclic 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 area. Very large populations allow high selection intensity with avoidance of serious genetic drift. Selection can be based on evaluation of replicated, clonally propagated individuals or on progeny testing.

In breeding perennial grains in this way, the experience of forage breeders in improving seed production (Sleper, 1987) provides many lessons on strategies and techniques; however, by not selecting for forage yield or quality, breeders can accelerate progress in grain production.

With the advantages of genetic knowledge and technology, today's perennial grain breeders can expect to make more rapid progress than did ancient domesticators of annual plants; however, the gap to be traversed between current and desired yields is formidable. Fortunately, although the mean productivity of an unselected population of perennial plants is invariably low, the available genetic variation is often very large, and selection progress can be rapid. In obligate outcrossing species, controlled sib-mating or forcing of rare self-pollination may be needed to expose variation influenced by beneficial recessive genes.

Wide hybridisation

This second approach to perennial grain breeding is a way of shortening the domestication process by taking advantage of useful genetic variation already fixed in high-yielding crop cultivars. Of the world's 13 most widely grown grain or oilseed crops, 10 can be hybridised with perennial relatives (Cox et al., 2006).

Annual crops are an obvious source of genes that promote domestication. Mutant plants with characters such as free threshing or nonshattering are rare in the wild ancestors of existing annual grain crops as well as in potential perennial grains. Managed gene flow from cultivated species is a potentially 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 hybridisation do not come without a genetic cost. When most crops – including wheat, rice, barley, rye, maize, sorghum, pearl millet, soybean, and 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 et al., 2002). The plant breeder working with such crosses must struggle with genomic disruptions while selecting to improve multiple traits simultaneously.

In the taxa studied to date, plants derived from interspecific hybrids tend to be perennial only when the expected proportion of their total genome derived from a perennial parent is at least 50 percent (Cox et al., 2002). That is, one backcross to the annual species tends to produce populations consisting of almost 100 percent annual plants; however, intense selection can identify perennials. Perenniality in sorghum, rice, and probably other species is under complex genetic control (Paterson et al., 1995; Hu et al., 2003) and interact strongly with the environment. Therefore, it will not be achieved through manipulation of individual genes. There is little chance that transgenic technology can dramatically speed up the development of perennial grains from annual x perennial hybrid populations.

On the other hand, analytical techniques such as genome mapping hold considerable promise. A cross between cultivated sorghum and the perennial grass *Sorghum propinquum* has been used to map the genes coding for rhizome development (Paterson et al. 1995). Rhizomes are essential to 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.

Using genetic stocks of wheat to which individual chromosomes of the perennial grass *Thinopyrum elongatum* have been added, Lammer et al. (2004) determined that *T. elongatum* chromosome 4E confers post-sexual-cycle regrowth. Selection for that chromosome can ensure that selected plants have the capacity to remain alive after maturity and harvest, but further selection is required to obtain plants 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.

Progress to date in perennial grain breeding

Breeders are directly domesticating the perennial species intermediate wheatgrass, Illinois bundleflower, and Maximilian sunflower for eventual use as perennial grains. They are following the interspecific hybridisation/selection strategy to develop perennial wheat, triticale, sorghum, sunflower, and rice.

Intermediate wheatgrass

Intermediate wheatgrass (*Thinopyrum intermedium*) is a perennial relative of wheat (*Triticum aestivum*). Carrying forward and expanding a Rodale Institute / US Dept. of Agriculture breeding program from the

1980s and 90s, The Land Institute is domesticating this species by breeding for increased seed size, seed yield, and ability to thresh freely. The main approach is to evaluate thousands of individual plants over two years, followed by a third year to intermate the 5 percent of best-performing plants. The second cycle will soon be completed. Experiments have shown that the first round of selection increased mean yield by about 18% and mean seed size by about 10%. Some individual families are much larger. In a separate population, four fast cycles have increased the fraction of free-threshing seed from about 8% to around 30%. The most dramatic development has been an increasing frequency of short, stiff-strawed genotypes with erect leaves and large spikes (Figure 1). In following the route to higher yields that breeders of annual plants have followed (Evans, 1998), intermediate wheatgrass breeders can utilise such variation to improve harvest index.



Figure 1. Left: A conventional forage-type intermediate wheatgrass plant. Right: A stiff-strawed, dwarf intermediate wheatgrass plant from a second cycle of selection for grain production. Plants of the latter type have increased to approximately one percent frequency in the population. Both plants photographed in their second year of growth.

Wheat and triticale

These cool-season cereals can be hybridised with a wide range of perennial species. For decades, wheat geneticists have crossed many genotypes of these annuals with many genotypes of perennial relatives, usually with the goal of introgressing genes for disease or insect resistance. Researchers at The Land Institute, Washington State University (WSU), and with the Future Farming CRC are now making such crosses, primarily using *Thinopyrum* species, with the explicit objective of developing perennial wheat and triticale. Chromosome doubling in the high-ploidy hybrids is extremely difficult, so few amphiploids have been made. Backcrossing to the annual has produced thousands of plants with good seed yields. In the greenhouse, a large proportion of these plants continue to live after their mature seed has been harvested, but in the field in Kansas, we have only identified about 10 plants out of thousands that were able to re-grow after harvest.

A cooperative trial of lines and bulks from The Land Institute and WSU was sown in September, 2007 in Washington, Kansas, Texas, Oklahoma, and Michigan to evaluate for yield, postharvest regrowth, and perenniality in diverse environments.

To obtain larger numbers of perennial plants, breeders at The Land Institute have crossed hundreds of interspecific hybrid plants to the perennial parent. Out of hundreds of hybrids, many were sterile, as expected. Crossing the few plants that produced viable pollen with pollen-sterile plants has helped restore fertility. A few resulting plants have exhibited good fertility, large seed, and vigorous regrowth.

Grain sorghum

This drought-hardy feed grain in America and Australia, and a staple food in Africa and Asia, can be hybridised with the tetraploid perennial species *Sorghum halepense*. The Land Institute is currently the only organisation working on perennial sorghum, having produced large plant populations from hundreds of diploid x tetraploid hybrids. (Such crosses are possible because male sterile grain sorghum plants, when pollinated with tetraploid perennials, produce a low frequency of doubled female gametes.) In replicated trials of more than 400 lines derived from crosses originally made in 2002, approximately 1.5% of the total number of individual plants tested in summer 2005 survived to re-emerge in spring 2006. The 40 least “wild” of those surviving plants produced some selfed progenies with 40 percent the grain yield of their annual grain sorghum parents, and seed is about half the size of grain sorghum’s – a fourfold improvement over *S. halepense* and some of the largest seed of any perennial grain-in-development.

Over the winter of 2007-08, several of those progenies had almost 100 percent survival in one location, and very low survival in another. A tropical plant, sorghum overwinters in temperate regions through survival of rhizomes. The genetic basis of winter survival is even more complex than that of rhizome production, and harder to achieve through breeding. However, mean grain yields of families with and without winter-hardiness have not been significantly different; indeed, families segregating for winter-hardiness have exceeded non-hardy families in yield by as much as 20% in some trials. Meiotic analyses have provided evidence that there are no serious obstacles to pairing between chromosomes derived from *S. bicolor* and *S. halepense*, which improves the chances of breaking possible linkages between genes affecting perenniality and low grain productivity.

Illinois bundleflower

This native prairie species, *Desmanthus illinoensis*, produces unusually large seed for a perennial, and the seed is high in protein (Kulakow, 1999). The Land Institute has assembled a large collection of seed from a wide geographical area and initiated a breeding program. Making controlled hybrids is extremely difficult technically, but methods have been developed to foster natural hybridisation and identify hybrids using morphological or molecular markers. Non-shattering families – crucial to domestication – have been selected and used as initial parents. The species is a strong, widely adapted perennial, and selection criteria will include shattering resistance, synchronous maturity, seed yield, and seed size and quality.

Sunflower relatives

Maximilian sunflower (*Helianthus maximiliani*) and Kansas rosinseed (*Silphium integrifolium*) are native perennials related to sunflower. The Land Institute is in the process of domesticating these species as perennial oilseed crops, via methods similar to that described above for intermediate wheatgrass. There is a parallel program for inbreeding to expose rare, valuable recessives. Seed production is low, but phenotypic variation is extensive in these species, and heritability estimates in the chief breeding population have been reasonably high (Table 1). In addition to the usual traits, selection pressure is being applied to fuse the numerous small seed-heads into larger, more compact heads and eliminate seed dormancy. In the case of the large-seeded Kansas rosinseed, selection to increase seed fertility of the head is in progress.

Sunflower

The highly productive annual oilseed crop *Helianthus annuus* can be hybridised with several perennial species in its genus, including the diploid Maximilian sunflower and two hexaploids: rigid-leaf sunflower (*H. rigidus*) and Jerusalem artichoke (*H. tuberosus*). Hybrids between annual and Maximilian sunflower are highly sterile, unless their chromosome numbers are doubled to produce tetraploids. The best strategy to produce perennial, partially fertile plants is to cross both annual and Maximilian sunflower to the hexaploid species to produce tetraploid plants and then inter-cross the different tetraploids. Large perennial populations have been produced in this way, and they are being subjected to selection for greater seed fertility.

Table 1. Heritability estimates based on variation among half-sib families from a population of Maximilian sunflower evaluated in Salina, Kansas in 2005, the second year of growth.

Trait	Heritability
Yield per square meter	0.32
Lodging score	0.39
Yield per stalk	0.51
Weight per seed	0.46
Percent shattering	0.56
Plant height	0.61
Yield per head	0.65
Maturity	0.65
Head diameter	0.78

In 2007, 185 of The Land Institute's strongly perennial plants from interspecific crosses yielded at least 10 seeds each, which is relatively high for such plants; of those, 102 had more than 100 seeds, and 26 yielded more than 500 seeds each. This breeding strategy had been based on reports that certain sunflower species could be crossed without completely losing sexual fertility. The 2007 results support the decision to proceed without attempting complex methods for restoring fertility such as protoplast fusion and chromosome doubling.

Rice

In the 1990s, the International Rice Research Institute achieved significant progress toward breeding a perennial upland rice by crossing the domesticate *Oryza sativa* with a wild progenitor *Oryza rufipogon* (Sacks et al. 2003) and the more distantly related species *O. longistaminata*. The project was terminated in 2001, but the breeding and genetic populations were transferred to the Yunnan Academy of Agricultural Sciences, where work has been continued. The focus is on the more difficult work with *O. longistaminata* crosses, which produce rhizomatous progeny with relatively poor fertility. However, plants with strong rhizome production and as much as 37% pollen fertility have been obtained.

Conclusions

The germplasm and strategies are in place to develop perennial cereals, oilseeds, and grain legumes. The time scale needed to bring such crops to the farm varies across species. Intermediate wheatgrass, for example, is ready for small-scale on-farm testing to work out agronomic practices, handling, and processing. Its use in test kitchens has shown that the grain can be used to make a wide variety of foods that wheat is used for, and chemical analyses have shown large potential nutritional benefits.

Although some perennial grain species could be available many years before others, and some could have dual uses – for grazing and grain production – the ultimate goal is to grow perennial grains in cropping systems that contain more than one species. The simplest would include simply a perennial cereal and a legume that grows only vegetatively, for nitrogen fixation. But eventually, two and more species both grown for seed harvests in as-yet undetermined sowing arrangements will provide more resilience, closer to the highly diverse perennial systems that covered what are now agricultural lands. In the central plains of the U.S., the ultimate goal is a system that serves the ecological functions that the original prairie did. In Western Australia, alternating strips of trees and yet-to-be-developed perennial wheat could serve to obtain good production while preventing the rise in water tables that causes salinity problems. In Asia, systems involving perennial upland rice and food-producing trees could prevent erosion on lands that are highly susceptible.

The agroecological work to design those and many other systems for other regions can be started with prototype perennial grains such as intermediate wheatgrass, but decades of breeding work are required to produce the perennial grains that are central to long-term agricultural sustainability.

References

- Bell, LW, Byrne (nee Flugge), F, Ewing, MA, and Wade, LJ. 2008. A preliminary whole-farm economic analysis of perennial wheat in an Australian dryland farming system. *Agricultural Systems* 96,166-174.
- Cassman KG, Dobermann A, and Walters D (2002) Agroecosystems, nitrogen-use efficiency, and nitrogen management. *Ambio* 31, 132-140.
- Cassman KG and Wood S (2005) Cultivated systems. In *Millenium Ecosystem Assessment*, pp. 741-876. Island Press, Washington, DC.
- Cassman KG, Dobermann A, Walters DT, and Yang H (2003) Meeting cereal demand while protecting natural resources and improving environmental quality. *Annual Review of Environment and Resources* 28, 315–358.
- Chiras DD, Reganold JP. 2004. *Natural Resource Conservation:Management for a Sustainable Future*, 9th ed. Prentice Hall, Upper Saddle River, NJ.
- Cox, TS, Bender, M, Picone, C, Van Tassel, DL, Holland, JB, Brummer, CE, Zoeller, BE, Paterson, AH, and Jackson, W. 2002. Breeding perennial grain crops. *Critical Reviews in Plant Sciences* 21: 59-91.
- Cox, TS, Glover, JG, Van Tassel, DL, Cox, CM, and DeHaan, LR. 2006. Prospects for developing perennial grain crops. *BioScience* 56: 649-659.
- DeHaan, LR, Van Tassel, DL, and Cox, TS. 2005. Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems* 20: 5-14.
- Evans, LT. 1998. *Feeding the Ten Billion: Plants and Population Growth*. Cambridge: Cambridge University Press.
- Gantzer, CJ, Anderson, SH, Thompson, AL, and Brown, JR. 1990. Estimating soil erosion after 100 years of cropping on Sanborn Field. *Journal of Soil and Water Conservation* 45: 641-644.
- Glover, JD, Cox, CM, and Reganold, JP. 2007. Future of farming: A return to roots? *Scientific American*, August, 2007: 66-73.
- Hu FY, et al. 2003. Convergent evolution of perenniality in rice and sorghum. *Proceedings of the National Academy of Sciences* 100: 4050–4054
- Jackson W. 1980. *New Roots for Agriculture*. San Francisco: Friends of the Earth.
- Jordan, N, Boody, G, Broussard, W, Glover, JD, Keeney, D, McCown, BH, McIsaac, G, Muller, M, Murray, H, Neal, J, Pansing, C, Turner, RE, Warner, K, and Wyse, D. 2007. Sustainable development of the agricultural bio-economy. *Science* 316: 1570-1571.
- Kulakow, PA. 1999. Variation in Illinois bundleflower (*Desmanthus illinoensis* (Michaux) MacMillan): a potential perennial grain legume. *Euphytica* 110: 7-20.
- Lammer D, Cai XW, Arterburn M, Chatelain J, Murray T, Jones S. 2004. A single chromosome addition from *Thinopyrum elongatum* confers a polycarpic, perennial habit to annual wheat. *Journal of Experimental Botany* 55: 1715–1720.
- Paterson, AH, Schertz, KF, Lin, YR, Liu, SC, and Chang, YL. 1995. The weediness of wild plants: molecular analysis of genes influencing dispersal and persistence of johnsongrass, *Sorghum halepense* (L.) Pers. *Proceedings of the National Academy of Sciences* 92: 6127-6131.
- Piper JK, Kulakow PA. 1994. Seed yield and biomass allocation in *Sorghum bicolor* and F₁ and backcross generations of *S. bicolor* X *S. halepense* hybrids. *Canadian Journal of Botany* 72: 468–474.
- Randall, GW, and Mulla, D. 2001. Nitrate nitrogen in surface waters as influenced by climatic conditions and agricultural practices. *Journal of Environmental Quality* 30: 337-344.
- Tilman, D, Fargione, J, Wolff, B, D'Antonio, C, Dobson, A, Howarth, R, Schindler, D, Schlesinger, WH, Simberloff, D, and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* 292: 281-284.
- Sacks EJ, Roxas JP, Sta. Cruz MT. 2003. Developing perennial upland rice I: Field performance of *Oryza sativa*/O. *rufipogon* F₁, F₄ and BC₁F₄ progeny. *Crop Science* 43: 120–128.
- Sheaffer CC, Martin NP, Lamb JAFS, Cuomo GR, Jewett JG, Quering SR. 2000. Leaf and stem properties of alfalfa entries. *Agronomy Journal* 92: 733–739.
- Sleper, D. A. 1987. Forage grasses. In *Principles of Cultivar Development, Volume 2: Crop Species*. pp. 161-208. Fehr, W. R., Ed., Macmillan Publishing Co., New York.
- Ward PR, Micin SF, Dunin FX (2006) Using soil, climate, and agronomy to predict soil water use by lucerne compared with soil water use by annual crops or pastures. *Australian Journal of Agricultural Research* 57, 347–354.