12

FROM GENETICS AND BREEDING TO AGRONOMY TO ECOLOGY

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ABSTRACT

With annual grain monocultures, there is frequent clear-cutting of crop root systems; as a result, ecosystem processes below the soil surface cannot sustain themselves in a healthy state. Each year, we disrupt this rich ecological resource, which otherwise could have been contributing to high, stable grain yields. The science of agronomy arose out of the necessity to cope with such a compromised landscape and make up for lost ecological processes. But we are severely limited in what we can accomplish with the "software" we call agronomy as long as we are saddled with the deficiencies of the annual crop species that have always served as the "hardware". Once perennial grain-producing species become available, however, soil ecosystems can contribute much more to food production, while much of the landscape-repair work that we now call upon agronomy to provide will not be necessary. Perennial hardware will open up innumerable possibilities for bringing new ecological software into agriculture. An example is provided by the potential development of perennial sorghum for tropical regions. To date, breeding of winterhardy grain sorghum has occurred solely in North America. When those breeding populations begin to be evaluated in diverse tropical environments, selection for proper adaptation will be essential. Once that is accomplished, an interim objective may be to develop a “super-ratooning” sorghum. But in the longer term, a true perennial growth habit will make possible whole new farming systems that combine sorghum with perennial food legumes and other crops. We can make such systems productive and ecologically sound without resorting to many of the agronomic interventions that annual grain crops require.

Keywords: crop root system, soil ecosystem, grain sorghum, perennial food legumes, agriculture and ecology

INTRODUCTION

In recent years, the potential benefits of perenniality for agriculture have come to be widely recognized. For example, in 2009, a group of researchers assembled by the Royal Society in the United Kingdom endorsed the idea of perennial grains. They noted, “Perennial crops would store more carbon, maintain better soil and water quality and would be consistent with minimum till practice. These crops would also manage nutrients more conservatively than conventional annual crops, and they would have greater biomass and resource management capacity” (Royal Society, 2009).

In a further discussion of perennial grains’ potential, the National Research Council of the National Academy of Science in the United States went into more detail with the following statements (National Research Council, 2010):

- Perennial plants reduce erosion risks, sequester more carbon, and require less fuel, fertilizer, and pesticides to grow than their annual counterparts.
- Perennials have greater access to resources over a longer growing season.
- Perennials have greater ability to maintain the health and fertility of a landscape over longer periods of time.
- Recent advances in plant breeding... provide new opportunities for plant breeders to select for desired characteristics.

In a policy paper in the journal *Science*, twenty-eight United States and international scientists called on plant breeders and geneticists worldwide to launch an all-out effort to develop perennial grain crops. (Glover *et al.* 2010). Then in August 2013, perennial grain researchers from around the world met in Rome for their first global meeting: the FAO Expert Workshop on Perennial Crops for Food Security (this volume).

These and other recent events have been prompted by the recognition that substituting perennial cereals, grain legumes, and oilseeds for their annual counterparts would constitute a major change of crop “hardware”, enabling agriculture to support a vast new range of cropping-system "software." The transformation will make possible food-producing ecosystems that function as well as healthy, fully intact natural ecosystems. Previous efforts to create such systems have been limited by our dependence on the problematic software of annual crops. Perennial grains will provide a solid foundation on which necessarily complex food-producing ecosystems can be built.

In doing this work, it will be essential to draw upon the extensive research that has been carried out by ecologists over more than a century. Embedded within wild ecosystems are answers needed in the design of current and future agricultural ecosystems. Processes that have run for many millions of years, some known and some yet to be discovered, are of paramount interest if we are to develop a sustainable, resilient agriculture. Moreover, successful use of the ecosystem as a conceptual tool can be expected to provide a bonus: greater social and economic justice for farmers, their communities, and the wider society.

Were we to stop with the development of perennial monocultures, we would miss the opportunity to realize the robust potential that biological diversity has to offer. To achieve sustainable nutrient management, stabilize or prevent insect and disease damage, optimize water use, take advantage of complementary growth periods, and ensure other important features of low-input farming will require information drawn from diverse natural ecosystems. Fortunately, the principles of ecosystem function derived from studies of grasslands, forests, and other non-cultivated landscapes are available for adoption (Jackson and Piper, 1989).

FROM AGRONOMY TO ECOLOGY

Starting with the invention of agriculture, annual grain monocultures have by definition required removal or disturbance of entire vegetative structures and communities. Ecosystem processes below the soil surface, opaque to the farmer, were crippled. This annual "clear-cutting" of the soil, which rendered a vast array of ecological processes unavailable to the food producer, has come at a heavy cost in degraded and eroded soil, water, and biodiversity.

The science of agronomy arose out of the necessity to mitigate and substitute for disrupted ecological processes in order to ensure a consistent food supply. Agronomy is a discipline forced to cope with a compromised landscape and make up for lost ecological processes through management. It can be viewed as a ten-thousand-year-old success story accomplished first by farmers alone, and in more recent times, by highly trained experts working with technologically astute farmers, backed up by fossil fuel subsidies and an industrialized, growth-oriented economy. But it is an unsustainable success story. With perennial cereals, grain legumes, and oilseeds, however, diverse ecological processes formerly denied to agricultural landscapes will have a chance to be reactivated and sustained over the long term.

The notion that native perennial ecosystems constitute the best model for agriculture is an acknowledgement and appreciation of the complexities and efficiencies in ecological relationships that have come about through community succession and natural selection operating on individual organisms over very long periods of time. As Jackson and Piper (1989) noted, "Nature is ill-defined, and natural ecosystems are dynamic. But the patterns and processes discernible in natural ecosystems still remain the most appropriate standard available to sustainable agriculture."

Deciding which aspects of non-agricultural ecosystems should inform the design of food-producing systems remains an open question. Denison *et al.* (2003) asked to what extent the outcomes of natural selection in native systems are congruent with the goals of agriculture:

> *We present two main hypotheses. Our first hypothesis is that natural selection had ample opportunity, before the wild ancestors of our crops were domesticated, to test alternative solutions to problems that limited individual fitness under preagricultural conditions... further improvement of these traits is likely to be difficult. Instead, opportunities for further genetic improvement of crop yield will mainly involve tradeoffs between plant adaptation to agricultural versus natural conditions, or between the competitiveness of individual plants and the collective performance of plant communities. Our second main hypothesis is that natural selection is the only reliable source of improvement (by any definition relevant to agriculture) in natural ecosystems that operate on a time scale longer than the lifetime of individual plants. Natural selection acts at the level of genes, individuals, and family groups, not communities and ecosystems. Therefore, our second main hypothesis is inconsistent with the suggestion that agricultural ecosystems whose structure is based on natural ecosystems will be consistently more efficient, sustainable and productive. Although this hypothesis rejects mindless mimicry, natural ecosystems, properly understood, are nonetheless a valuable source of ideas for agriculture.*

The perspective of Denison and colleagues has been valuable in motivating a deeper analysis and greater clarity in describing the value of natural ecosystems as conceptual tools for grain-producing agriculture. One crucial realization that has become clearer than ever is the extent to which their arguments rest implicitly on the assumptions that 1) progress in crop development equates to increased yield alone, and 2) the continued protection and facilitation of high yields with purchased inputs is both possible and desirable. An agriculture that requires minimal inputs and is resilient to changing environmental conditions is very different from the agriculture underlying Denison and colleagues' critique.

Natural selection acting on genes, individuals, and family groups can result in consistent properties that are manifest at the community and ecosystem level. This is different from selection happening at the community and ecosystem level. Consider, for example, the ability of members of the legume family to host nitrogen fixing bacteria in their roots. This mutualism is clearly the outcome of natural selection acting on legume plants and rhizobia bacteria; however, the entire ecosystem benefits from this mutualism as the N fixed by it is released for other organisms to appropriate upon legume senescence (Hooper and Dukes, 2004, DeHaan *et al.*

2010). The same is true for other nutrient acquisition strategies (e.g. Vance *et al.* 2003). In an agricultural system in which all nutrients are not provided in the form of mineral fertilizers, this type of community-level interaction becomes not only relevant but essential.

The life history strategy of perennials and their near-universal dominance of land ecosystems is another example of natural selection acting on the level of genes, individuals, and family groups and in turn predictably influencing community and ecosystem-level functions. While perenniality confers numerous advantages to individual plants existing in communities, it also prevents nutrient loss, soil erosion, weed invasion, and other ecological outcomes that benefit the ecosystem as a whole, whether native or agricultural (Picasso *et al.* 2008, Glover *et al.* 2010).

A contrasting example is provided by diversity. It is a reliable, naturally occurring characteristic of almost every native ecosystem, not because of natural selection, but more because of limits on the ability of natural selection to produce organisms that perform optimally under all environmental conditions in time and space. A diverse native plant community necessarily includes diversity of root architectures, leaf tissue chemistries, and other features. And when functioning together, these diverse plant attributes help prevent nutrient loss, explosion of insect herbivore populations, invasion of noxious weeds, and other ecological outcomes highly beneficial to agriculture (Ratnadass *et al.* 2012, Vandermeer, 2012). If insects and weeds are not to be controlled with pesticides, and prevention of soil erosion is to be independent of herbicide use, and if nutrient losses are not made up by application of non-renewable fertilizers, the ecological derivatives of diversity become even more important.

Perennialism per se, as suggested above, does constitute a significant mimicry of nature, and likely will bring with it a range of beneficial ecosystem functions. But it is important that we do not settle for the degree of improved ecosystem function that would be conferred, for example, by single-species stands of grain-producing perennial grasses. There is a reason why such an ecosystem is never seen in nature: it is not sustainable over time. Therefore, two strains of perennial grain research—breeding and ecology—must be carried out jointly.

BREEDING PERENNIAL GRAIN SORGHUM

Researchers aiming to develop food-producing ecosystems based on perennial grain crops face a chicken-and-egg situation: the perennial crop breeder would like to know more about the system into which the new species will be incorporated, but to study alternative systems, the ecologist needs the new crop species that do not yet exist. Nevertheless, much can be learned from experimental systems that incorporate the intermediate products of perennial grain breeding. Perennial sorghum provides one of many examples.

Sorghum is a tropically adapted genus. To survive and produce grain for more than one season in a temperate climate, a sorghum plant must not only produce rhizomes; those rhizomes must also be cold-tolerant enough to survive through the winter at between 2 and 20 cm below the soil surface and produce ramets that emerge in the spring. The Land Institute launched its research on perennial sorghum in the early 1980s by making hybrids between induced tetraploids of *Sorghum bicolor* and various rhizomatous, winterhardy accessions of the tetraploid grass *S. halepense*. Populations derived from those crosses, as well as from backcrosses to the *S. bicolor* parent, were evaluated in the field in Kansas, and the results were published by Piper and Kulakow (1994). They concluded that breeding of a perennial grain sorghum was feasible but would require repeated cycles of selection for perenniality and backcrossing to improve yield and other traits. Meanwhile, using RFLP mapping, Paterson *et al.* (1995) showed that genomic regions associated with rhizomatousness and perenniality in a diploid population derived from a *S. bicolor* x *S. propinquum* cross, when evaluated in a south Texas field environment, were scattered across at least nine of sorghum's ten linkage groups.

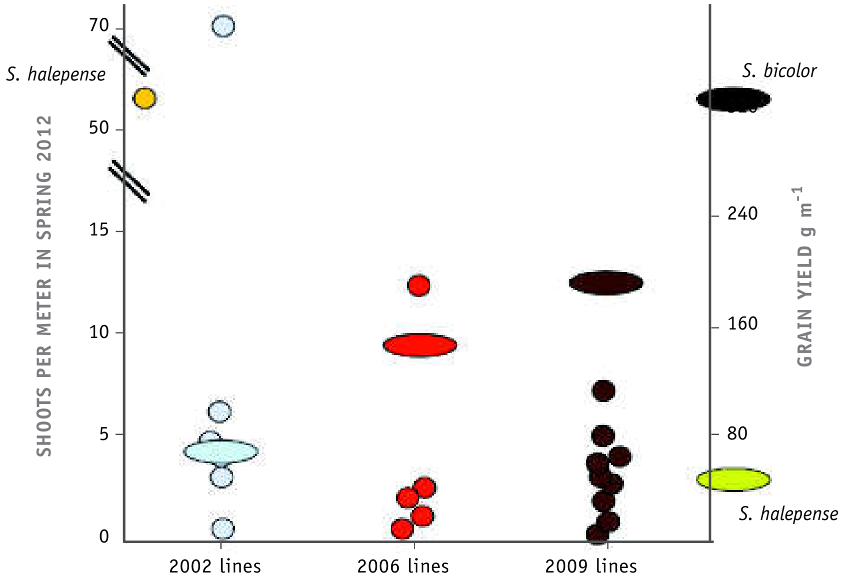
These basic studies were followed by the initiation, in 2001, of a perennial sorghum breeding programme at The Land Institute. The initial crosses were made between perennial selections from Land Institute populations and diploid grain sorghum inbred lines, to produce tetraploid segregating populations. Each year, we have selected perennial plants with improved cropping traits from annual x perennial or perennial x perennial populations and then backcrossed them to a range of annual lines, to capture more diversity from the *S. bicolor* gene pool. We have also introduced additional *S. halepense* accessions as parents.

In these populations, degree of perenniality is not associated with grain yield but is negatively correlated with kernel weight. Furthermore, most perennial selections tend to have traits that are generally undesirable in a crop plant: often excessive tillering and branching, non-synchronous flowering and maturity, excessive plant height, and small, hulled, brown kernels. Some of these associations, such as between rhizomatousness and aboveground tillering, may result from pleiotropy. Others, such as between winterhardiness and low kernel weight, may result from a low frequency of recombination between chromosomes of the two species in regions surrounding the genes required for perenniality. With Andrew Paterson at the University of Georgia, we have studies underway to elucidate more fully the basis for these negative associations (Paterson, this volume).

Despite the negative trait associations, selection and backcrossing have succeeded in increasing productivity while maintaining perenniality. In 2011-13, we ran a field trial comparing perennial families selected at three stages of The Land Institute's breeding program: 2002 (the original perennial parents), 2006, and 2009. Grain yield and kernel weight have increased with backcrossing and selection, but have not attained the levels of commercial grain sorghum (Figure 1). Perenniality is not as strong as that of *S. halepense*, but here, moderation is desirable; for a crop plant, the aggressive rhizome development displayed by the weedy parent would be an unnecessary and unproductive waste of resources. Among these selected lines, there was no correlation between degree of perenniality and grain yield; however, perenniality was associated with low weight of individual kernels (r=-0.46**).

FIGURE 1. NUMBER OF SHOOTS EMERGING IN SPRING PER METRE OF ROW IN SPRING, 2012, FOR 'GYPSUM 9' (*SORGHUM HALEPENSE*) AND 27 PERENNIAL SORGHUM FAMILIES SELECTED FROM THREE STAGES (2002, 2006, AND 2009) OF THE LAND INSTITUTE'S BREEDING PROGRAMME (CIRCLES AND LEFT Y-AXIS), TOGETHER WITH MEAN GRAIN YIELDS OF THE THREE GROUPS OF SELECTIONS (OVALS AND RIGHT Y-AXIS, WITH YIELDS OF GYPSUM 9 AND A COMMERCIAL GRAIN SORGHUM HYBRID, PHILLIPS 664, INDICATED ON THE AXIS.)

Yields are from first-year harvests of Salina, Kansas, retrospective trials in 2011 and 2012, with each year's trial in a randomized complete block design with four replicates. The experimental unit was a 3 m row.



Recently, we have selected lines potentially superior to those that were evaluated in the retrospective trial. These have come from crossing the *S. bicolor* inbred line BTx623 with plants from 'Gypsum 9', a *S. halepense* population collected near the town of Gypsum, Kansas in 2009. This cross was initiated to create populations for mapping loci associated with perenniality and other traits and monitoring recombination frequencies in interspecific hybrids of tetraploid sorghum (Paterson, this volume). But these populations have also become a valuable source of perennial breeding parents that have a more domesticated plant type and higher grain production. In these populations, associations between perenniality and deleterious wild traits appear to be weaker. Forty-nine partially winterhardy F_2-derived F_3 families derived from a BTx623 × 'Gypsum 9' cross and evaluated in 2011-2012 did not differ in mean height, flowering date, grain yield, and threshability from their winter-tender siblings (Table 1). However, strength of perenniality, expressed as the proportion of plants in a family that re-emerged in spring, had loose negative correlations with grain yield per plant and threshability.

TABLE 1. MEANS OF SIX TRAITS FOR GROUPS OF SORGHUM FAMILIES

49 families that had a percentage of spring emergence greater than zero, and 122 families with zero emergence, in a 2012-2013 field trial in Salina, Kansas. The families were F_3 progenies of 171 F_2 plants from a BTx623 (*Sorghum bicolor*) × Gypsum 9 (*S. halepense*) hybrid. They, together with parents, were evaluated in randomized, nonreplicated three metre rows with 1 metre between rows. Standard errors of means were based on variances of families within groups. Free-threshing index was the ratio of the weight of an approximately 5 g dehulled grain sample to the weight of the sample before dehulling; therefore, it has a possible range of 0 to 1. Correlations are rank correlations over 50 data pairs: 49 pairs of means of the families containing surviving plants, plus a single pair of means computed over all families that had zero survival.

		MEAN					
GROUP, BY SPRING EMERGENCE	No. OF FAMILIES IN GROUP	PROPORTION OF PLANTS EMERGED, SPRING	No. RAMETS, AUTUMN	PLANT HEIGHT	FLOWERING, DAYS AFTER 30 JULY	GRAIN YIELD PER PLANT, DEHULLED	FREE-THRESHING INDEX
No plants emerged	122	0	0.75	236	25.9	42	0.71
Some plants emerged	49	0.28	1.38 a	247	24.4	45	0.68
Correlation versus proportion of plants emerged			0.25	0.10	0.10	-0.34*	-0.31*

a Significantly different from the mean of the “no plants emerged” group (P<0.05)

* Significantly different from zero (P<0.05)

We still struggle to select for perenniality independently of other wild traits; however, among perennial BTx623 × ‘Gypsum 9’ selections, and among rhizomatous but cold-sensitive selections from other crosses, it has been possible to identify much more croplike lines that prove winterhardy in the warmer southeastern United States. These selections presumably would be perennial in the tropics as well. Therefore, we have been generating a second gene pool as a base population for breeding perennial sorghum for the tropics and semitropics. Breeding for tropical adaptation, which would start with crosses between temperately adapted perennial lines and tropically adapted annual lines, has not yet started. When it does, a medium-term outcome along the way to developing a rhizomatous perennial sorghum could be an improved rattooning sorghum that grows more vigorously and produces higher yields in the second (and possibly subsequent) season than do current annual cultivars (Paterson, this volume).

The current perennial sorghum gene pool bears only a loose resemblance to the annual grain crop. Dwarf plants are rare, and tillering is excessive. Ramet emergence, tillering, flowering, and maturity all are highly asynchronous, tending to extend over periods of weeks. Until these characteristics are adjusted through breeding, perennial sorghum in temperate regions will remain unsuitable for mechanized cultivation and harvest, whatever the degree of improvement in grain yield. However, in regions where hand harvesting and crop polycultures are the norm and where tall stover is harvested for fodder or other uses, tall plants and asynchronous maturity would not necessarily be obstacles to adoption. And perennial cultivars could have advantages beyond erosion prevention. In many parts of the tropics, one of the most dire problems facing sorghum farmers is poor stand establishment, thanks to adverse soil and moisture conditions. With perennial sorghum, there would be no need to achieve a good seedbed and precise seed placement under adverse conditions; furthermore, the shoots and roots of ramets emerging from deep rhizomes would be much more robust than those of seedlings.

But while presenting opportunities for adoption of perennial sorghum, tropical regions raise new challenges as well. Tropical environments are very diverse, and with seasonal variation in temperature and rainfall, most are not friendly to sorghum cultivation year-round. Research is needed to determine which environmental signals will be required to keep perennial sorghum plants alive but not actively growing during the off-season. In temperate zones, the onset of cold weather enforces several months of dormancy, after which new perennial plants emerge much earlier in the spring and grow more rapidly than do annual plants. But in the semiarid tropics, for example, would a perennial sorghum plant's rhizomes be able to survive deep in the soil through a long dry season and emerge with the return of rains? Answers to these and other questions have not yet been sought.

PROSPECTS FOR ECOLOGICALLY SOUND PRODUCTION

In trying to visualize agricultural ecosystems that include perennial sorghum and other perennial grains, the chicken-and-egg problem remains. How do we design ecologically sound production systems for new crops as long as the best of their germplasm is still half-wild? Will data gleaned from experiments using proto-perennial grains be applicable to cropping systems for fully domesticated cultivars once they are developed? We cannot know the answers to those questions in advance, but some insights could come from forging ahead with field research that employs today's crops-in-the-making.

Throughout tropical and semitropical regions, supplying grain crops with biologically fixed nitrogen, together with other nutrients, is an urgent need. If, as a first step toward a full-blown food-producing ecosystem, perennial sorghum is to be incorporated into a biculture, the obvious choice of partner species would be legumes—preferably perennial. The sorghum plant would derive the greatest fertility benefits from a non-grain legume that is included solely in a nitrogen-fixing role. But where increased food production per hectare and diet diversification are top priorities, an cereal-plus-grain legume intercrop is more appropriate. In Malawi, for example, Snapp *et al.* (2010 and this volume) have been investigating systems for growing pigeon pea (*Cajanus cajan*) as a perennial grain legume intercropped with annual maize (*Zea mays*). They have shown that "Semiperennial rotations provided twofold superior returns, whereas diversification of maize with annual legumes provided more modest returns" as compared with maize monocrops. These and other results provide an incentive, once perennial sorghum germplasm has been screened for adaptation to local conditions in areas where pigeon pea is well-adapted, to run small-scale pigeon pea intercrop experiments that include preliminary breeding lines of perennial or enhanced-rattooning grain sorghum. Such studies could proceed across a range of environments, in parallel with continuing breeding efforts until acceptable perennial sorghum cultivars are developed.

We are also investigating whether in this or other systems, perennial sorghum might supplement its nutrition through endophytic nitrogen fixation. It has been found, for example, that *S. halepense* harbours in its rhizomes nitrogen-fixing endophytic bacteria that also can make phosphorus more available and chelate iron (Weiman, 2012). As a genus, *Sorghum* also has a strong tendency to form associations with arbuscular mycorrhizal fungi and thereby increase its phosphorus uptake under certain conditions (Neumann and Eckhard, 2004); perennial sorghums for low-input systems should be evaluated for their ability to gain access to phosphorus and other nutrients through mycorrhizal associations.

With perennial sorghum, the development not only of farm-ready cultivars but also of ecologically-based cropping systems will probably be achieved first in the tropics. In many regions of Africa, Asia, or Latin America, a biculture of a perennial or rattooning cereal like sorghum with a perennial pulse could be a highly effective system for providing staple foods while reducing soil degradation, during the transition to more ecologically durable systems. Meanwhile, both resistance breeding and ecological research will be needed to address yield losses to pathogens, pests, and weeds, especially parasitic weeds like striga in the case of sorghum. More complex perennial polycultures involving a range of plant families will need to be evaluated, not only for productivity but for ecological functioning as well. For example, soil water and nutrient uptake efficiencies can be increased in polycropping arrangements where soil resources are partitioned in time or space.

Where agro-forestry is already being employed, integration with herbaceous perennial grain crops should be explored. Trees can improve crop microclimate conditions and provide nutrient inputs through biological N fixation and in some cases by bringing phosphorus and other rock-derived nutrients to the surface via roots from deep in the soil profile (Buresh, 1995). This could be particularly important in tropical regions with highly weathered, nutrient depleted topsoils. Some of this work can inform the eventual development of new cropping systems in the temperate zones, but much location-specific work will be required there as well.

The details will differ for other perennial crops, for other combinations of crops, and for every environment. But the ultimate goal remains constant: by adding perennial grain crops to the agricultural inventory, we can finally create opportunities for a deep synthesis of agriculture and ecology.

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