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A GRAIN AGRICULTURE FASHIONED IN NATURE'S IMAGE: THE WORK OF THE LAND INSTITUTE

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Abstract: *Modern industrialized agriculture is based on monocultures of annual crops requiring massive levels of biocide, fertilizer, and fossil fuel inputs. This form of agriculture has led to soil erosion and chemical contamination of soil and ground water. The Land Institute is studying a new model for grain agriculture, based on the prairie ecosystem, involving diversified plantings of perennial seed crops. Species we have studied include eastern gamagrass, wildrye, Illinois bundleflower, wild senna, Maximilian sunflower, hybrid perennial sorghum, and hybrid perennial rye. The Land Institute's research program develops perennial polycultures based on basic questions concerning high seed yield, overyielding, nitrogen supply by a legume component, and biological management of weeds, insect pests, and plant diseases. Results to support the model are presented.*

Environmental Problems of Industrial Agriculture

In terms of return on labor, North American style modern agriculture is a highly productive form of seed, fruit, and fiber production. Over the last few decades, however, it has taken increasingly more energy to produce a unit of grain with industrial farming methods, with a ratio of energy expended to food energy consumed in the U.S. of about 10 to 1 (Lovins et al. 1984). In addition to high fossil fuel energy requirements, this productivity has arisen largely through simplifying agroecosystems to feature monocultures and tailoring them to maximize a single component, yield, while ignoring or disrupting many of the links between organisms, the soil, and the physical environment that serve to regulate natural communities. The industrialization of agriculture has led to such profound problems as soil loss, depletion and contamination of water supplies, loss of genetic diversity in cultivars, fossil fuel dependency, pesticide poisoning of farm workers and non-target wild species, and development of pesticide resistance in pests.

A sustainable agriculture for the Great Plains, then, ought to address simultaneously several key problems of agriculture. The successful model should feature reduced or eliminated soil erosion, efficient use of land area and soil nutrients, improved water use efficiency, reduced reliance on synthetic nitrogen fertilizer, decreased risk of pest and disease epidemics, effective chemical-free weed management, reduced fossil energy requirements, and the opportunity for farmers to hedge their bets among several agricultural products.

Some important steps have been taken recently in the move toward a more sustainable agriculture. Such processes as conservation tillage, crop rotations, and integrated pest management incorporate several sustainable aspects of natural ecosystems. Ultimately, each is an inadequate solution to the problem of sustainability. Conservation tillage saves soil, but involves herbicide use and energy needed for mechanical cultivation. Although crop rotations help provide nitrogen (N) and reduce pest buildup in fields, such rotations fail to address the problems of monocultures in any given year. Finally, integrated pest management (IPM) incorporates important principles of predator-prey theory and understanding of vulnerable life cycle stages of target organisms, but as it is typically practiced integrated pest management is not yet completely free of pesticide use, but focuses instead on more effective application.

Nature as Measure for Sustainable Agriculture

To use Nature as a model or standard for sustainable agriculture requires first appreciating the features of natural ecosystems that promote sustainability or permanence. For example, how natural ecosystems regulate crucial nutrients so that inputs approximately equal outputs in a "steady state" is a primary concern in studies of natural ecosystems. A terrestrial ecosystem consists not only of plants and animals, and the fungi and microbes crucial for decomposing organic material and recycling nutrients, but also the parent material beneath the soil that provides minerals essential to the systems, water that enters as precipitation, and the solar energy captured through photosynthesis and transferred from organism to organism within the community. If agriculture is to remain productive without exhausting its resource base, there must be such a balance for agricultural ecosystems. Hence, natural ecosystems provide our best models for the structural patterns necessary to achieve the tight nutrient cycling, and solar driven energy flow, that will be crucial to agricultural sustainability.

TABLE 1

COMPARISON BETWEEN CONVENTIONAL, INDUSTRIAL AGRICULTURE AND THE NATIVE PRAIRIE ECOSYSTEM FOR SOME FACTORS THAT CONTRIBUTE TO SUSTAINABILITY

	Conventional agriculture	Native prairie
Fragility	high	low
Resilience	low	high
Species and genetic diversity	low	high
Rate of nutrient flux	high	low
Degree of biotic interdependence	low	high
Energy source	solar and fossil fuel	solar
Nutrients	from fertilizers	local, recycled

Source: Soule and Piper 1992.

Conventional agricultural ecosystems differ from natural ecosystems in several important ways (Table 1). The study of natural ecosystems has shown that, to a large extent, system resilience is enhanced by high species and genetic diversity, tight nutrient cycling, and interdependence of species whose niches complement one another in space and time.

Perennial Polyculture Modelled on the Prairie Ecosystem

Because of the various sustainable features of natural ecosystems, The Land Institute's research is attempting to develop an agricultural model that mimics the vegetation structure, and hence the functioning, of natural plant communities. Agroecosystems that are functional analogs of natural ecosystems should feature species adapted to local seasonal precipitation patterns, tight or closed nutrient cycles, compatibility in resource use among species, soil preservation, and biological methods of crop protection.

After 100 years of applying monoculture farming to the prairie soils of North America we have lost 50% of our topsoil's latent productivity. In contrast, the native prairie built and maintained soil and supported large herds of grazers. Perhaps before we use up the remaining 50% of our topsoil, we should consider a model for the future for our "breadbasket" that mitigates soil erosion while providing edible seeds.

The Prairie Archetype

In various parts of the world, successful agricultural mimics of natural ecosystems have been designed or established to produce vegetables, fruits, nuts, and grains (Soule and Piper 1992). Since people are primarily grass and, secondarily, legume seed eaters, however, we should look to an ecosystem that features grasses as the dominant type of plant for our best example. On the Great Plains of North America, we look to the prairie as the most appropriate natural model for seed agriculture.

The North American prairie is characterized by wide open landscapes of primarily herbaceous vegetation. As farmers replaced arrays of native grasses and forbs with such annual species as wheat, sorghum, and soybeans, North American landscapes were modified to accommodate the biological requirements of these crops. Yet the few remnants of intact prairie serve as prime examples of inherently sustainable biotic communities in which complex webs of interdependent plants, animals, and microbes garner, retain, and efficiently recycle critical nutrients.

Prairie soils are among the richest soils in the world. Seasonal drought cycles, involving warm moist springs and summers favorable to luxuriant grass growth followed by dry summers and autumns, have led over the millennia to an accumulation of soil organic matter via root turnover. As much as 60 to 75% of the prairie's total plant biomass occurs underground as roots, rhizomes, and crowns. In some prairies, 30 to 60% of root biomass may turn over each summer, leaving a rich store of deep, dark organic matter that has made the highly productive U.S. grain belt possible. In depleting the soil's natural fertility, our productive agriculture has essentially been mining over decades the fertility built up by the prairie ecosystem.

Prairie vegetation is a grass-dominated mixture consisting primarily of perennial cool-season (C_3) and warm-season (C_4) grasses, legumes, and composites growing oftentimes side by side. On a broad geographic scale, the ratios of different types of plants vary over the Plains in response to climatic patterns, with cool-season grasses increasing in importance with latitude and drought-tolerant shortgrasses increasing westward toward the Rocky Mountains.

Differences in plant architecture, type of resource use, and seasonality allow species coexistence. Under the ground, one plant may produce a deep taproot, whereas its neighbor produces shallow, fine roots. Some species, legumes primarily, fix atmospheric nitrogen in addition to taking up available nitrogen in the soil. Timing of resource use differs among species across the entire growing season, thereby reducing competition for soil water and nutrients. Grasses with C_4 photosynthesis and drought-hardy forbs are able to withstand the hot, dry conditions of summer. Others, cool-season grasses and forbs, persist by growing in the spring and setting seed before the onset of summer drought. The diversity of plant species with complementary niches contributes in large part the resilience of prairies in the face of climatic extremes.

The particular assemblage of plants forming prairie communities varies across soil types. For example, four prairie sites studied during seven years at The Land Institute represent a productivity gradient determined by soil characteristics. Since the categories C_4 grasses, C_3 grasses, legumes, and composites represent most of the prairie's plant species as well as four important functional groups, it may be important to examine how relative proportions of these groups change across a range of soil types. The vegetation of the two most productive sites, 1 and 2, is composed of nearly 90% grasses, primarily C_4, although C_3 grasses and sedges can represent as much as 20% of the aboveground biomass in some cases (Table 2). In contrast, Site 3, a low-nitrogen soil, supports 60% grasses, almost exclusively C_4, and composites average 7% of the biomass, but the legume component may be as high as 26% in some years. The relative amount of legume biomass may represent the benchmark percentage needed to support perennial grass/legume mixtures. Site 4, where growth is limited by dryness rather than by low nitrogen, averages almost 80% grasses, but with 19% composites and few legumes (Table 2). Hence, C_3 and C_4 grasses dominate deep, fertile soils whereas a dry, infertile site exhibits a high proportion of legumes but virtually no C_3 grasses. A fertile, but dry site features few legumes and C_3 grasses, but many composites.

A related question concerns how diverse prairie communities are, and how diversity patterns differ on different soil types. In general species diversity is higher on sites of lower soil quality (Table 2). This indicates that poor soils somehow allow, maintain, or even promote greater species diversity than more favorable soils. It is interesting that Site 1 displays a species diversity equivalent to that of a three species mixture with each species equally represented. The diversity of Site 4 would be achieved with a mixture of five equally abundant species.

Moreover, prairie communities are dynamic in time, with relative importance of species changing in response to year-to-year as well as long-term

TABLE 2

COMMUNITY ATTRIBUTES OF FOUR PRAIRIE RESEARCH SITES, 1986-1992

Site	All grasses (%)	C_3 graminoids[1] (%)	Legumes (%)	Composites (%)	Peak biomass (g m^{-2})	Diversity[2]
1	86.9	18.5	0.2	4.8	574	3.15
2	87.2	10.9	0.0	8.0	418	3.70
3	58.9	0.0	16.0	7.2	276	4.12
4	75.9	2.9	1.0	18.7	279	4.97

[1] Graminoids = grasses and sedges

[2] The exponential of the Shannon Index (H'), which factors in species richness and evenness. This value represents the number of equally common species required to produce the value of H' given by the sample. For a monoculture, exp(H')=1.0. for a biculture, with two species of equal biomass, exp(H')=2, and so on.

climatic cycles. During the past seven years, peak aboveground biomass has at some sites varied four-fold depending on annual precipitation, with shifting relative dominance of such species as big bluestem, little bluestem, and sideoats grama. During the drought of the 1930s, western wheatgrass supplanted tallgrasses on much of the eastern Kansas prairie while many shortgrasses moved eastward. When normal precipitation resumed in the 1940s, the prairies reverted to their pre-drought species compositions (Weaver 1954). Long-term studies of this sort have documented the prairie's great resilience to changes in weather.

Tight nutrient cycling is another sustainable feature that arises largely from the prairie vegetation's perennial nature. Because most nutrients are tied up in living biomass and soil organic matter year round, they are not vulnerable to leaching or erosion loss. Nutrients are cycled seasonally within plants, stored in organic matter, and quickly taken up once mineralized by decomposers.

Description of Perennial Polyculture

An agroecosystem modelled on the prairie would comprise mixtures of perennial grasses, legumes, and composites as seed crops, whose species composition should vary across soil type and climate. Polycultures of herbaceous perennial seed crops would be composed of plants that differ in seasonal nutrient use and would thereby play complementary and facilitating roles in the field. A polyculture might emphasize warm-season grasses, legumes, or cool-season grasses depending on climate and soil conditions.

Research on a prairie analog for agriculture is more complex than conventional studies of crop mixtures because it goes beyond simple two- or three-component systems and uses perennials instead of annuals. Very little ecological or genetic information on crop varieties appropriate for polyculture designs has been gathered, and plant breeders are only beginning to approach the problem of how to apply such knowledge to designing viable intercropping systems. Different crops would flourish in different years. Because perennial crops will be required to maintain themselves in the field for a period of years instead of months as with annual crops, it is necessary to incorporate multiple year demographic patterns of growth and seed yield into crop development research. Unlike the grower of annual crops, who has some flexibility in changing crops or modifying field conditions after each growing season, farmers establishing perennial polycultures will have to forecast over several possibly very different growing seasons.

Research Questions

Ongoing Land Institute research encompasses four primary questions critical to the development of viable perennial polycultures (Jackson 1985).

Question 1: Can a herbaceous perennial seed crop yield as well as an annual crop?

Presumably, annual species were domesticated originally because they possessed certain characteristics that made their seed inviting as food. As early agriculturalists purposefully sowed and harvested these plants they consciously or unconsciously selected for favorable characteristics. On the other hand, many perennial plants, though producing very nutritious seeds, lack the other characteristics that would lend them to immediate usefulness as crops. Despite this drawback, however, many wild perennial grasses have provided food for hunter-gatherer societies in the past (Bohrer 1975; Doebley 1984; Kindscher 1987; Harlan 1989).

Two general approaches are possible in the modern development of perennial grains. The first approach involves the conversion of a wild perennial into a seed crop by selecting for such agronomic characteristics as high seed production, reduced seed shattering, uniform time of maturity, ease of threshing, and large seed size. In this case, the potential crop already has the desired perennial habit, but lacks most of the characteristics that would make it a good grain crop. The difficulty facing the plant breeder is to overcome undesirable traits of the plant while maintaining the perennial habit and good nutritional qualities of seed.

The second approach starts with annual grain crops and attempts to turn them into perennials via wide hybridization with perennial relatives. The rationale for this approach is that annual crops have already undergone domestication over the last several thousand years. Hence, they already show such agronomically favorable characteristics as edibility, high yield, large seed size, ease of threshing, synchronous maturity, and resistance to shattering and lodging.

With either approach, obtaining high seed yield from perennials is more complex than it is with annuals. Not only must the yield be high in one year, but yield must be maintained at sufficiently high levels for several years after the crop is established.

Seed yields of perennial crops need to be at some acceptable level to make the perennial polyculture model compelling. For comparison, the bench-mark yield for Kansas wheat is about 1800 lb/acre, or about 2000 kg/ha. It is promising that several trees (Smith 1953), shrubs (Pasternak et al. 1986), and herbaceous perennial grasses and legumes (Brown 1943; Ahring 1964; Thornberg 1971) approach or exceed this bench-mark yield.

Does the fact that a species is perennial per se set a limit on its seed yield? While it is true that a perennial must devote some resources to constructing and maintaining its permanent organs, an expense an annual does not bear, it is not clear that high seed production and the perennial habit are in any kind of strict trade-off relationship within a plant. Increasing seed production is probably more complex than merely shifting allocation of resources and energy from roots and stems to reproductive structures, as there is evidence that reproductive structures themselves can stimulate growth and photosynthesis. Several studies have indicated little or no vegetative "cost" to future reproduction or differences in survival as a result of increased sexual reproduction in the present (Bazzaz and Ackerly 1992). These are promising results for the effort to breed for higher seed yield without losing a plant's perennial nature.

Question 2: Can a perennial polyculture display overyielding?

The second basic question is whether a polyculture of perennial seed crops can overyield the same crops grown in monoculture. Overyielding is the phenomenon in which crop mixtures yield more per unit area than their components yield in monoculture. This can occur, for example, when interspecific competition in a plant community is less intense than intraspecific competition, or where one species enhances the growth of another. Where crop varieties have been grown together for centuries, as in the maize-bean-squash polycultures of traditional Mexican agrarian cultures, crop compatibility has increased through coevolution.

Conceivably, many factors can lead to overyielding. For instance, canopies of component crops might occupy different vertical layers, with tall crops tolerant of strong light and shorter crops requiring shade and/or relatively high humidity. Or roots of different species may explore different soil layers. Additionally, crop species may have complementary nutrient requirements. For example, mixtures of legumes with nonlegumes typically overyield, especially in soils where the nitrogen supply is limited. Finally, differences in the length of the growing period or in the seasonal periods of nutrient uptake among crops can promote overyielding.

The Land Equivalent Ratio (LER) is a way of expressing the yield advantage of intercropping over monoculture. The LER, the sum of the fractions of the various intercrops relative to their yields in monoculture, represents the land area required to obtain from monocultures the yield obtained in polyculture. If LER is greater than 1, then there is overyielding. An LER of 1.2, for example, indicates that a farmer would have to plant 20% more land area to achieve in monoculture the yields obtained in polyculture.

Some interactions between plants are competitive, that is one species hinders the performance of its neighbor such that overall growth in the field is lowered. Other interactions, such as nitrogen sharing between legumes and grasses can be positive, leading to improved performance in fields. A wise polyculture farmer could design planting arrangements to maximize the frequency of beneficial contacts and minimize the frequency of suppressive contacts between components in intercropped fields.

Question 3: Can a perennial polyculture provide much of its own nitrogen fertility?

Specifically, to what extent can nitrogen-fixation by legumes compensate for nutrients removed in harvested seed? To answer this requires careful documentation of nutrient pools in the soil, rates of uptake by plants, nutrient content of harvested seed, and the capacity of crop plants and associated symbionts to enrich the soil over time.

The correct mix of species in polyculture can maintain soil fertility by tapping not only the benefits of non-overlapping resource use, but also the ways species in mixtures benefit one another directly. In particular, legumes can benefit other species in mixtures through their special ability to fix atmospheric nitrogen. The nitrogen fixed by their symbiotic bacteria becomes available to other species in the mixture when the legumes' roots decay or via direct mycorrhizal transfer (Mallarino et al. 1990; Fujita et al. 1992).

Despite sometimes lower yields than are obtained with synthetic nitrogen, legume nitrogen can prove both energy efficient and cost effective. Studies have consistently shown higher dry matter yields in grass/legume mixtures than in grass monocultures (Barnett and Posler 1983; Brophy et al. 1987). A survey by Thomas (1992) suggested a need for 20 to 50% of herbage dry matter in legumes for tropical and temperate pastures, depending on desired level of animal production, dry matter production, or forage protein yield.

Question 4: Can a perennial mixture successfully manage weeds, insect pests, and plant pathogens?

Perennial polycultures can take advantage of crops' overlapping growth periods to block light or usurp soil nutrients before weeds can take hold. Another biological mechanism of weed control available with perennial mixtures is "allelopathy." This term refers to any direct or indirect harmful effect that one plant has on another through the production of chemical compounds that escape into the environment. Allelopathy would be especially valuable during the vulnerable establishment phase until the perennial canopy became established.

Research on the effects of diverse cropping systems on insect pest control confirms that polycultures tend to reduce densities of insect pests relative to monocultures (Risch et al. 1983). Crop diversity can provide physical barriers and masking odors that can interfere with colonization, movement, feeding efficiency, and reproduction of phytophagous insects (Tahvanainen and Root 1972; Tukahirwa and Coaker 1982). In addition, a polyculture environment often attracts greater than expected numbers of beneficial predators and parasitoids. Lastly, a polyculture can include a trap crop, which attracts pests away from other, more important crops.

It is well established that disease problems in agriculture often result from extreme genetic uniformity of crops (Adams et al. 1971; Horsfall et al. 1972; Barrett 1981). Thus, an increase in genetic diversity created by planting mixtures of species, and mixtures of genotypes within species, can reduce the spread of some plant diseases. Altieri and Liebman (1986) and Thurston (1992) have reviewed the literature showing reduced disease levels in intercrops. Likely mechanisms include physical barriers to aerial dissemination, reduced amount of tissue vulnerable to infection and thus amount of inoculum available for subsequent dispersal, altered microclimate, induced resistance of host, and increased spacing between susceptible plants.

The Species

Development of new perennial seed crops is necessarily a long-term process. Work at The Land Institute to domesticate perennial seed crops began in 1978 with an inventory of nearly 300 herbaceous perennial species for their suitability to the environment of central Kansas and promise of high seed yield. A second inventory studied the agronomic potential in 4300 collections (accessions) of perennial grass species within six cool-season genera. From these inventories, a handful of perennial species was chosen for potential crop development (Jackson 1990). The following list of crop candidates includes five species of wild perennials and two wide hybrids.

Eastern gamagrass (*Tripsacum dactyloides* (L.) L.) is a warm-season grass native to the region stretching from the southeastern United States and Great Plains to southern Nebraska southward to Bolivia and Paraguay. Although eastern gamagrass is acclaimed as a select forage, it shows much promise also as a human grain crop. Gamagrass grain is both tasty and nutritious, being about 27 to 30% protein and 7% fat (Bates et al. 1981, Bargman et al. 1989). It can be ground and used like corn meal. It begins flowering in central Kansas in late May and seed harvest begins in July. The major limitations of eastern gamagrass as a grain crop are low seed yield and enclosure of the grain in a hard fruit case. The Land Institute has explored in enclosure of the grain in a hard fruit case. The Land Institute has explored in its breeding program a gynomonoecious or "pistillate" variant, forma *prolificum*, which produces exclusively female flowers and thus has the potential to increase seed yield considerably (Dewald et al. 1987).

Wildrye [*Leymus racemosus* (Lam.) Tsveler, Gramineae], is a member of the tribe Triticeae which also contains wheat, rye, and barley. It is a rhizomatous, cool-season grass native to Bulgaria, Romania, Turkey, and parts of the former Soviet Union, that has been planted in the western U.S. to stabilize sandy soils. Grain of this species was eaten by Asian and European people historically, especially in drought years when annual grain crops faltered. Flour of wildrye seed could be used as a substitute for wheat or rye flour. As is typical of cool-season plants, it displays most of its growth in late autumn and early spring. Flowering in plots at The Land Institute takes place in May and seeds mature by late June.

Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM., Leguminosae] is a nitrogen-fixing plant that forms a deep taproot in its first year. It is native to the Great Plains and its range extends northward into Minnesota, east into Florida, and as far west as New Mexico. It grows best during warm weather, flowering from late June onward; the small seeds are borne within clusters of brown legumes beginning in late July. The nutritional quality of the seeds [38% protein, 34% carbohydrate (Piper et al. 1988)] suggests great potential as a seed crop for human or livestock consumption. It could be used much like soybeans. This species appears capable of fixing appreciable amounts of atmospheric nitrogen (Kulakow et al. 1990). As with other wild legumes, the pods open (dehisce) and disperse their seeds upon maturity. A non-shattering type identified by Peter Kulakow, The Land Institute's plant breeder, in 1988 has been crossed with accessions displaying consistent high seed yield, and these crosses have been planted for further evaluation.

Wild or Maryland senna (*Cassia marilandica* L., Leguminosae) is a legume native to the southeastern region of the Great Plains. Flowering in Kansas takes place from late August to early September, producing racemes of insect-pollinated yellow flowers that become brown-black legumes later in the fall. Plants may grow up to 2 meters tall. *Cassia marilandica* produces thick, deep roots, but does not appear to form symbioses with nitrogen-fixing *Rhizobium* bacteria. Although The Land Institute is not working to develop this species as a crop, because the seed appears to have low value as food, much information on its long- term patterns of seed yield has been gathered to address the biological question of whether a herbaceous perennial could produce sustained, high seed yield. It provides a good model for studying the population dynamics of a high seed-yielding perennial.

Maximilian sunflower (*Helianthus maximilianii* Schrad., Compositae) is native throughout the Great Plains. Its range extends eastward to Maine and North Carolina, and westward to Texas and the Rocky Mountains. Flowering begins in late August and September; achenes begin to ripen in October. In addition to its potential value for direct consumption as a seed or oil crop (seed is 21% oil) (Thompson et al. 1981), Maximilian sunflower appears to inhibit weed growth allelopathically, and may therefore be especially important during the establishment phase of a perennial polyculture.

Grain sorghum [*Sorghum bicolor* (L.) Moench, Gramineae], a native of the African continent, is a successful seed crop for animal feed in the southern Great Plains. It is weakly perennial in tropical regions, but is killed by frost at higher latitudes. Johnsongrass [*Sorghum halepense* (L.) Pers.], a weedy relative of cultivated sorghum, is a troublesome weed in the U. S. that overwinters by production of rhizomes, fleshy underground stems capable of winter survival. Peter Kulakow is exploring the feasibility of converting a tetraploid variety of grain sorghum from an annual to a perennial growth habit by combining in hybrids good grain quality with the ability to produce winter-hardy rhizomes. The ease of making this transfer will depend on the number of genes controlling the production of rhizomes and whether overwintering ability is genetically associated with poor agronomic characteristics.

Hybrid perennial rye, "Permontra," is a hybrid between common rye (*Secale cereale* L.) and perennial *S. montanum* Guss., a native to the steppe regions of southwest Asia. This hybrid variety was developed in Germany for use as cereal crop for human consumption or as a perennial forage or hay crop. It was first planted at The Land Institute in 1990, with the first harvest in 1991. We will need to evaluate whether it can both overwinter and survive the hot summer in central Kansas.

Research Results

Question 1: Seed Yields of Perennials

Selection and domestication of plants for use in polyculture is more complex than selection of varieties for monocultures. Initially, scientific plant domestication involves collection and evaluation of wild germ plasm, then selection for stable high seed yield, harvestability, adaptation to mixed species plots, and suitability for use as a human or livestock food. Moreover, these characteristics need to be evaluated for several years in the life span of a perennial species.

Over 16 accessions of wildrye and its relatives, over 250 accessions of eastern gamagrass, and about 150 accessions of Illinois bundleflower have been collected, documented, and/or evaluated in the ground at The Land Institute. The next step, describing the available variation in plant growth and agronomic performance within each species, is also underway for these three species. Favorable genotypes are then tested in a set of cropping systems that includes monocultures and polycultures.

Some of the highest yields for perennials at The Land Institute have been for Illinois bundleflower and wild senna in which plots produced high yields around 200 g/m^2 (2000 kg/ha) (Table 3). Peak yields of wildrye, eastern gamagrass, and Maximilian sunflower have been somewhat lower. Moreover, in contrast to an expected general yield decline in subsequent years from an initial peak, yields have improved in some stands of eastern gamagrass, Illinois bundleflower (Fig. 1), and wild senna (Piper and Towne 1988; Piper 1992).

The best example of our perennial hybrid approach is the perennial sorghum work, directed by Peter Kulakow, in which interspecific hybrids have been developed using tetraploid lines of grain sorghum and collections of Johnsongrass from Kansas and California. The work thus far has demonstrated that it is possible to retain rhizome production in BC_0 (50% grain sorghum genes), and BC_1 (75% grain sorghum genes) and BC_2 (87.5% grain sorghum genes) backcross generations. Although rhizome production tends to decrease with each backcross, 88% of BC_1 and 57% of BC_2 plants produced rhizomes in 1990. Seed yields of both backcrosses were over 150 g m^{-2}, compared to 179 g m^{-2} in the grain sorghum. In another planting, in 1992, mean yields were even higher: 171.9 for BC_0, 471.6 for BC_1, and 396.7 g m^{-2} for BC_2 rows. Interestingly, there was a positive correlation between seed yield and rhizome mass in BC_1 plants in 1990, indicating that particularly vigorous plants had both high seed yield and rhizome production (Jones 1991). Overwintering has not yet been observed in these backcross lines. As this work proceeds, it will be important to determine whether there is a necessary loss of rhizome production as good agronomic qualities are selected for, or whether these two sets of traits can be combined.

The other hybrid observed at The Land Institute is permontra rye, which yielded 195.4 g m^{-2} in its first year (Wittig 1991). Here, the limitation to this crop is heat and drought-intolerance after seed production. In 1991, only 15 to

TABLE 3

HIGHEST SEED YIELDS IN SELECTED EXPERIMENTS INVOLVING PERENNIAL SEED CROP CANDIDATES AT THE LAND INSTITUTE YIELDS ARE EXPRESSED AS G M^{-2}

Species	Type of experiment	Duration (years)	Highest yield	Year of highest yield[1]
Illinois bundleflower	Density	5	197	1st
Eastern gamagrass	Germplasm	3	24	3rd
	Effects on soil	2	25	2nd
Wild senna	Density	5	209	2nd
Wildrye	Germplasm	2	83	2nd
Maximilian sunflower	Comparison with annual	2	77	1st

[1] Wildrye and gamagrass are vegetative in the first year if established from seed.

[2] Estimate based on seed yield as 27% of uncleaned fruitcase yield (Piper and Towne 1988).

20% of the stand regrew after harvest. Future breeding work with this hybrid needs to identify drought-tolerant material suited to the Kansas climate.

Plant breeding for polyculture must consider that some lines behave differently when grown in different planting arrangements or with different species for neighbors. When there is an accession by cropping system interaction, the best performing accessions may differ among cropping systems, and selections should therefore be made within the intended cropping system. These sorts of interactions need to be evaluated as a breeding program for polycultures progresses.

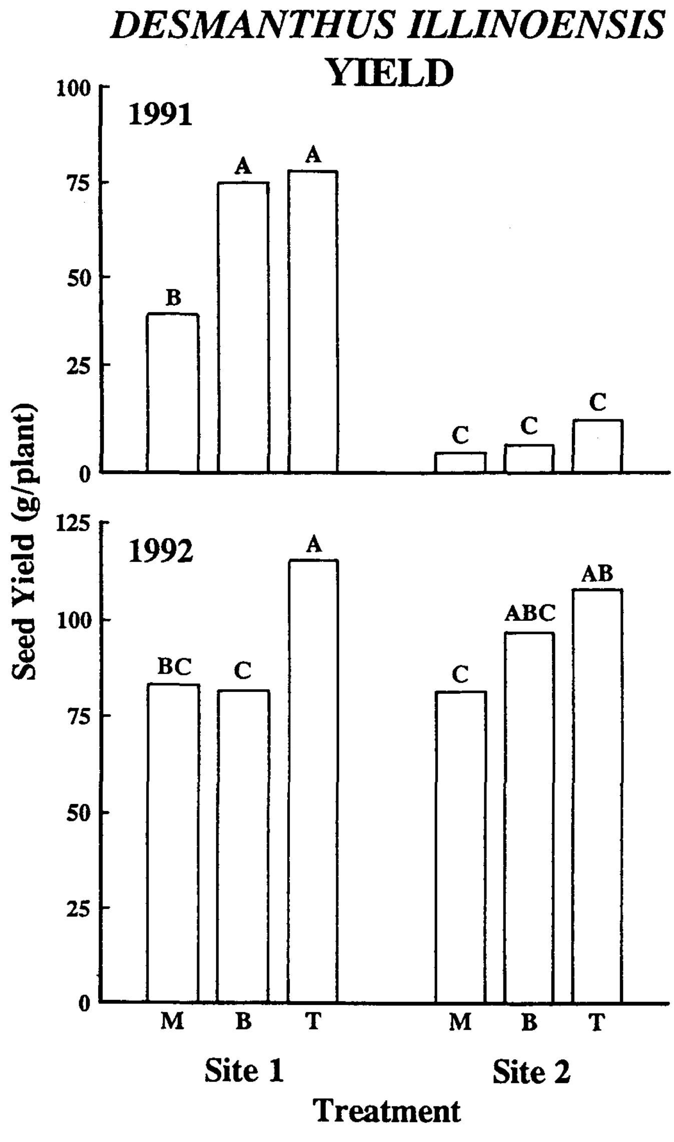

Figure 1. Mean seed yield for Illinois bundleflower in three cropping system treatments in two environments over two years. Initially, soil of Site 1 was higher in available and total nitrogren than Site 2. Previous 12-month precipitation was 56.7 cm in 1991 and 93.7 cm in 1992. For each year, bars subtended by the same letter do not differ at $p<0.05$ (ANOVA, Duncan's multiple ranges test).
Key: M = monoculture, B = biculture with eastern gamagrass, T = triculture.

Several polyculture studies at The Land Institute (Muto 1990; Piper et al. 1991; Schuur and Haigh 1992; Piper 1993b) have revealed striking context-specific yield and growth patterns of species, positive and negative associations between species, and change in the direction (positive or negative) of interactions in different years. Successful mixtures of perennial crops will have to accentuate net positive while minimizing any net negative associations between species.

Question 2: Overyielding in Perennial Polyculture

Three studies at The Land Institute have examined the question of overyielding with perennials. The first study comprised a series of mono- and bicultures of wild senna, which does not fix nitrogen, and Illinois bundleflower, a legume that potentially fixes appreciable amounts of nitrogen. Significant overyielding occurred in this experiment by the second year, and appeared to increase with time. The increase was most dramatic in an alternate plant biculture (i.e. plant species mixed within each row) in which overyielding averaged 161% by the third year. Essentially, absolute yields declined in monocultures whereas yields in bicultures remained fairly constant or declined more slowly over time (Braun 1985). This study indicated the benefit to a perennial of association with a nitrogen-fixing species. It also showed that polycultures can counteract the trend, observed in some perennials, toward decreasing yields in subsequent years.

In another study, summarized by Muto (1990), 28 different accessions each of Illinois bundleflower and eastern gamagrass were grown in a series of monocultures and bicultures to estimate overyielding. In the first year in which gamagrass produced seed, LER based on the average yields across genotypes in monoculture and biculture was 1.25, or a 25% yield advantage in biculture. The LER based on the best yields in monoculture and biculture was 1.19, a value similar to that derived from the average yields. In the next year, overyielding based on best yields was 1.08. These favorable results demonstrate that overyielding, typical in many polycultures of annual crops, can also occur in perennial polycultures and can occur in more than one year.

Mixtures of wildrye, eastern gamagrass, and Illinois bundleflower should overyield because of the species' distinct spatial and seasonal differences in pattern of soil water and nutrient use (Piper 1993a). A third, ongoing, study is examining overyielding in bicultures and tricultures of the three species. Moreover, the study is replicated on a favorable and unfavorable site. In 1992, the first year in which all three species flowered, 5 to 6% overyielding occurred in both bicultures at both sites (Schuur and Haigh 1992). Surprisingly, however, overyielding was not seen in either triculture treatment, a consequence perhaps of wildrye's slow rate of establishment, vulnerability to early shading by the taller gamagrass and bundleflower neighbors, or both.

Question 3: Internal Supply of Fertility

A mechanism that can contribute to overyielding is the ability of a nitrogen-fixing legume to provide much of its own nitrogen requirements via symbiosis with nodulating bacteria. The mean acetylene reduction rate, an estimate of nitrogen fixation under laboratory conditions, measured in 70-day old Illinois bundleflower plants was 141 nmoles min^{-1} (Kulakow et al. 1990). This value is similar to or somewhat higher than values reported elsewhere for this species and also for 68-day old soybeans (Lofton 1976; Lindemann et al. 1982). Ideally in an intercrop, the period of maximum nitrogen mineralization in soil would overlap or coincide with the period of maximum uptake in a companion crop. The benefit from a nitrogen-fixing companion crop should be greater on poor soil than on a more fertile soil. Yields of Illinois bundleflower reveal that differences in plant performance on fertile versus less fertile soils can disappear when precipitation is adequate (Fig. 1).

Question 4: Management of Weeds, Insect Pests, and Plant Diseases

Effective weed control has occurred in two separate experiments at The Land Institute. In one study, a plot containing rows planted with five densities of Maximilian sunflower and a control (no sunflowers), weed biomass was significantly reduced in the sunflower plots relative to the control (Gernes 1986). By the second year, a sunflower density of 3.6 plants m^{-2} reduced weed biomass between rows to levels only 25 to 50% of the control. In the third year, weed biomass in sunflower rows was 44% of weed biomass in the control during May. Here, effective weed control was maintained across years despite changes in the weed community from predominantly annuals in the first year to perennials by the third year.

In the second experiment that examined weed growth, a triculture comprising wildrye, eastern gamagrass, and Illinois bundleflower at equal densities, species combinations differed in their ability to control weeds (Piper 1993b). Weed biomass was consistently lowest in rows with eastern gamagrass as a component, despite seasonal and yearly changes in species composition of the weed community. These results point to eastern gamagrass as the primary weed controller among the three species, probably via shading, although unmeasured underground interactions were also likely important throughout the three-year study.

Each of the perennial crop candidates harbors one or more obvious insect or fungal pests, whose effects on growth and yield can be substantial. For example, Illinois bundleflower flowers and leaves are eaten by a chrysomelid beetle, *Anomoea flavokansiensis,* which can reduce seed production dramatically in some years. Censuses of beetle density for the first two years on Illinois bundleflower in polyculture and monoculture plantings have not yet shown cropping system effects, although there is an indication that monocultures are colonized earlier and insect populations are more variable in polycultures. Since these years represent effectively the colonization phase for the insect, there is a need to monitor the plots for several years.

Eastern gamagrass, in particular, is subject to several pathogens, including maize dwarf mosaic virus (MDMV) (Seifers et al. 1993), which can reduce seed yield dramatically (Davis 1991). Studies over two years have shown that MDMV incidence is reduced in plots where bundleflower is present relative to gamagrass monocultures and bicultures with wildrye (Piper et al. 1991; Haigh and Schuur 1992). Hence, spread of the virus, by aphids, appears influenced by cropping system, a favorable result for the potential to manage plant disease levels within perennial polycultures.

Conclusions

In developing perennial grain polycultures, Land Institute researchers typically think in the 50- to 100-year time-frame. It is hoped that there will be successful varieties to release sooner, whereas much challenging work will continue beyond the next century.

Sustainable agriculture research will have to reach beyond the traditional plant sciences. Unfortunately, the largest knowledge gap by far is what happens below ground. Soil scientists will therefore need to understand the factors involved in maintaining soil fertility within perennial systems and to elucidate better the interactions among climate, vegetation, and soil organisms that affect decomposition, mineralization, uptake, and nutrient transfer between species. Other issues to explore include how to measure soil "health," how to develop management programs and cropping patterns appropriate for particular soils, understanding the relevant ecological functions of different groups of soil organisms, how to vary management practices to enhance beneficial soil organisms, and how climate and cropping practices affect soil processes. The large, remaining question concerns the extent to which soil of a perennial polyculture can behave like soil of native prairie.

Insect ecologists can contribute an understanding of the basic biology of problem species and how cropping design affects herbivore population density, levels of predators and parasitoids, and the dynamics of insect-plant and insect-insect interactions.

Farmers and agronomists will deal with the most practical aspects of perennial polyculture. How will such polycultures actually be implemented on existing farms? How will they be planted and harvested? How will they be used and managed? As we consider the whole farm we will need to examine the potential roles of livestock in the fertility and management of perennial plots. Thus, animal scientists will study the feasibility of incorporating large livestock, bison perhaps, into perennial polyculture, an appropriate goal since large grazers were an historical part of the original prairie ecosystem.

Beyond the need for purely scientific research, the development of sustainable agriculture requires that biologists, social scientists, farmers, historians, and many others work together to answer some crucial questions. What are the root causes of a problem? What are the short- and long-term costs and benefits of the proposed solutions? What will be the time and resources required to effect the proposed solutions? How will the recommended innovations be adopted by farmers? What are the risks associated with their adoption? What are the local and regional impacts of adoption? What is the role of the market? What forms will human communities take in a sustainable agriculture? What is the role of government policy?

The ultimate value of the research at The Land Institute is in its move toward an agriculture based on sunlight, with closed nutrient loops, that uses nature as its model. A diverse and stable agriculture based on mixtures of perennial seed crops would provide numerous environmental and social benefits. In addition to the savings in cost and soil, the practice and philosophy of science would benefit as ecologists merge their expertise with that of agronomists to develop new insights for ways of looking at nature and analyzing the complexity inherent in diverse biological systems. As we approach the issue of sustainability, it is important to keep in mind Wendell Berry's (1987) three questions to be asked concerning human economy in any given place: What is (was) here? What will nature permit us to do here? What will nature help us to do here?

Clearly, the long-term sustainability of agriculture, in the face of dwindling resources and environmental damage, will depend upon innovative, creative, and complex approaches that combine ecological theories with practical agricultural research to reduce fossil fuel dependency and pollution while maintaining adequate levels of production and enhancing soil fertility. The blend of ecology and agriculture broadens the justification for preserving pristine ecosystems, as these are the ecological standards for agricultural sustainability. The time is ripe for a humble search into natural ecosystems for the patterns and properties transferable to sustainable forms of agriculture. Thus, to create a domesticated prairie much new research ground remains to be broken, but hopefully, in the process, the broken ground of the prairie will be healed.

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