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Perennial grain crops: A synthesis of ecology and plant breeding

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Abstract

Perennial grain crops would address many agricultural problems, including soil erosion, nutrient loss and pesticide contamination. Doubts about the possibility of perennial grain crops rest upon two assumptions: (1) that the relationship between yield and longevity is a fixed function that cannot be influenced by selection, mutation or environmental changes; and (2) that yield and longevity trade off in a bivariate manner to the exclusion of all other traits. These assumptions are consistent with the phenotypic trade-off model, but recent research suggests that a quantitative genetic model is a more appropriate approach to trade-offs. In the quantitative genetic model, environmental and genetic changes can result in increases in two traits simultaneously even when a trade-off, or negative correlation, exists between the two traits. Empirical evidence that the trade-off between perenniality and reproductive allocation is not fixed comes from wild, herbaceous perennials that can produce more than 2000 kg seed ha^{-1} in the temperate zone, and herbaceous perennial crops that produce on average 8900 kg fruit ha^{-1} in the tropics. Ecological literature suggests that most perennials produce small amounts of seed relative to their vegetative growth not as a physiological absolute, but rather as a result of natural selection in a stable, competitive environment favoring longevity. By selecting strongly for seed yield in a population of perennial plants, the plant breeder can likely achieve that which is rare in nature—a high seed-yielding perennial plant. The same general methodologies that have allowed annual grain breeders to increase grain yield and push many combinations of negatively correlated traits to levels of expression not seen in nature are available to the perennial grain breeder. Perennial grain breeders are integrating ecological principles and traditional plant breeding methods in their efforts to develop perennial grain wheat (*Triticum* spp.), sorghum (*Sorghum* spp.), sunflower (*Helianthus* spp.), Illinois bundleflower (*Desmanthus illinoensis*) and rice (*Oryza* spp.).

Key words: trade-off, carbon allocation, perenniality, life history, plant domestication

Introduction

Perennial grain crops would provide significant benefits to society and farmers[1]. New technologies and recent research make success more likely, but the task of breeding perennial grains remains formidable. Although strategies have been developed[2], plant breeders, working with other scientists, now need to establish and expand perennial grain breeding programs. The current structure of our public research institutions and a misunderstanding of the ecological and genetic principles that apply to perennial grain development impede that goal.

Specialization of scientific disciplines contributes to the problem. Ecologists and soil scientists have identified links between annual grain agriculture and environmental problems[3–7]. However, in formulating solutions involving plant breeding, they seldom look beyond a plant breeder's ability to increase the efficiency of existing systems[3]. Conversely, public plant breeders traditionally focus on the immediate needs of farmers, and allocate few resources to the longer-term project of breeding perennial grain crops. Privately funded or career-oriented plant geneticists are unlikely to invest in relatively long-term projects such as new crop development.

Attracting scientists to the field of perennial grain breeding requires articulation of the ecological and genetic principles central to the endeavor and securing funding sources sufficient to carry through the 25- to 50-year project required for developing a new crop. This paper provides a framework in which to consider these principles and describes their application in current efforts to breed several perennial grain crops.

Alternative Approaches to Trade-off Theory

Supported by observations that wild annuals generally have greater reproductive allocation than wild perennials[8], some researchers conclude that perennial grain crops will be less productive than annual grains because of their greater allocation of assimilated carbon to storage organs[9]. Although we are unaware of any research that would rule out development of perennial grains, it is appropriate that we provide a theoretical foundation for their feasibility as we launch new breeding programs.

Much of the misunderstanding about trade-off theory has its roots in the phenotypic trade-off model. However, the phenotypic model—the older of two fundamental approaches to trade-off—has been shown to be inadequate, if not misleading[10,11]. In this model, the relationship between two traits is defined as a fixed function. Selection moves the main trait value along a curve defined by the function, but the function itself never changes. Only if trade-offs are held to be static and bivariate can the phenotypic model be applied to perennial grain breeding.

The alternative approach is the quantitative genetic model, in which the trade-off is described by a bivariate normal distribution[10]. In this approach, selection, drift and mutation can produce changes in the slope and intercept of the trade-off function. In this model, as in practical plant breeding, trade-offs are dynamic rather than static relationships, and multi-factorial rather than simply bivariate[10].

Photosynthate Production and Allocation

According to the phenotypic trade-off model, the exclusive use of annuals as grain crops was inevitable. Even if discussion is restricted to the allocation of a given amount of carbon for either seed or perennating structures, a gram-for-gram trade-off should exist only in the first year. After perennial roots and crowns are built, they need not be fully reconstructed in subsequent seasons (although portions die, regrow and respire). New buds which develop each year require energy, but energy is also present in the seed of annual plants. Much of the carbon allocated to perennation is not spent, because it is remobilized in the following season.

Perennials, starting the growing season with an extensive living root system, have the potential for greater photosynthate production than annuals. Perennial root systems better use water and nutrients in a greater volume of soil than annual roots not yet fully developed or that have already senesced[7]. Perennial sorghum (*Sorghum* spp.) plants in our Kansas nurseries emerge from large, starchy and cold-tolerant rhizomes 4 weeks before annual sorghum plants display their first leaves. Cool-season perennial grasses, such as intermediate wheatgrass (*Thinopyrum intermedium*) and perennial wheat (*Triticum* spp.)[12], also lengthen the growing season by tillering and photosynthesizing after harvest, through late summer and fall.

Plants can pay the energetic cost of perennation by harvesting a much larger fraction of the seasonally available photosynthetic energy. Furthermore, in an agricultural setting, the risk of poor establishment—frequently an issue with annual crops—is avoided in the years when perennials are regrowing. Stand thinning, which makes resowing necessary in perennial forages like alfalfa (*Medicago sativa*), may also limit the longevity of perennial grain crops. However, rhizomatous perennial forages can be very long lived[13], indicating that rhizomatous perennial grains may be a reasonable solution to the problem of stand thinning.

Ecologically, the costs of being a perennial are offset by the advantages. Globally, natural systems, primarily dominated by perennials, had greater mean net primary productivity than the anthropogenic systems that replaced them[14]. Within the USA Corn Belt, comparing near-wild perennials such as switchgrass (*Panicum virgatum*) to elite maize (*Zea mays*) cultivars in a high-input system may lead to the erroneous conclusion that perennials have inherently lower yields than do annuals. Comparing the productivity of domesticated crops within a family is more appropriate. For example, across diverse environments in the USA, the perennial forage crop alfalfa consistently produces more biomass than the annual soybean (*Glycine max*) (Table 1). The comparison is appropriate because both species are nitrogen-fixing legumes and the biomass of both species contains approximately the same level of crude protein[15,16]. Although at a disadvantage during its establishment year, alfalfa produces greater biomass yield than soybean, even when yields are averaged over the entire four-year lifespan of the alfalfa stand (Table 1).

If perennials can fix an adequate amount of carbon to make them viable crops, the question becomes one of harvest index rather than trade-off. The abundant seed yield of some wild herbaceous perennials lends support to the feasibility of perennial grain breeding. The perennial legume Illinois bundleflower (*Desmanthus illinoensis*) has had seed yields up to 1700 kg ha^{-1} in Kansas[17] and 3000 kg ha^{-1} in Florida[18]. *Senna marilandica*, another perennial legume, has had seed yields exceeding 2000 kg ha^{-1}[19]. These plants have yet to be used as grains, due to shattering and the need for extensive utilization research, not because of a yield trade-off. Further evidence comes from domesticated herbaceous perennials such as bananas (*Musa* spp.) and strawberries (*Fragaria × ananassa*) that, in Central America, 1999–2003, had an average annual reproductive allocation of 8900 and 2400 kg ha^{-1}, respectively[20]. The annual grains, maize (*Zea mays*), sorghum (*Sorghum bicolor*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*), yielded an average of 2100, 2600, 3000 and 4200 kg ha^{-1}, respectively, in the same region and time period[20].

Table 1. Comparison of alfalfa and soybean biomass yields and standard deviations (SD) obtained in diverse environments.

Location	Alfalfa		Soybean[4]	
	Average	SD	Average	SD
	------------------------ kg ha^{-1} yr^{-1} ------------------------			
Urbana, Illinois, research station 2001–2003[1]	14,672		10,619	
Central Minnesota research station 2001–2003[2]	12,343		10,045	
Central Illinois on-farm production 1993–2003[3]	9,682	671	8,626	655
East-central Oklahoma on-farm production 1993–2003[3]	7,557	1,372	4,411	1,058
Northwest Minnesota on-farm production 1993–2003[3]	6,829	577	5,494	534
Average	10,216		7,839	

[1] Data from the University of Illinois Variety Testing Program, http://vt.cropsci.uiuc.edu/index.html. Alfalfa yields include an establishment year.

[2] Data from Minnesota Agricultural Experiment Station, http://www.maes.umn.edu/maespubs/vartrial/vt-cntnt.html. Alfalfa yields include an establishment year.

[3] Data from the United States Department of Agriculture National Agricultural Statistics Service, http://www.usda.gov/nass/

[4] Calculated based on a harvest index of 0.40.

Natural Versus Human-directed Selection

Most perennials produce small amounts of seed relative to their vegetative growth not because of inherent physiological constraints, but rather as a result of natural selection. The evolutionary concept that predicts higher average seed yield in annuals has been described as *r*-selection[21]. Wild annuals are typically found in less competitive (often disturbed), resource-rich, hazardous or changing environments. They typically evolve to use resources quickly and produce abundant seed that is widely dispersed and remains dormant until abundant resources are again available[22].

In a stable, undisturbed environment, competition results in resource limitation. Annuals are then mostly displaced by comparatively *K*-selected perennials, which have greater competitive ability and often dominate more resource-limited environments[21]. (To clarify, competition can result in resource limitation despite fertile soil and abundant rainfall.) To survive and reproduce in such a habitat, a perennial plant may develop a deep, spreading, long-lived root system. In order to shade its neighbors, a plant may grow tall and have horizontal leaves. Its leaves may contain more lignified tissues to increase leaf persistence[23]. In order to live in one place for many years, a plant must have robust mechanisms to fend off or tolerate herbivores and pathogens. Natural selection may have produced adaptations that allow the perennial plant to live through periods of extreme heat, drought or flooding.

Instead of producing seeds as its primary mode of dissemination, a perennial plant may instead invest in rhizomes that result in vegetative spread into favorable environments[24]. In response to stress, a perennial plant may shift allocation from seed production in a single season to rhizome production that increases the odds of survival[25]. Generally, low levels of dormancy in the seeds of perennials compared to annuals[26], combined with the scarcity of long-lived grass seeds found in seed banks[22], leads to the conclusion that seeds of perennials are used more for dispersal than for survival through time[27]. Seed production is only one of many traits important to the perennial plant's overall fitness under natural selection. If natural selection is not acting strongly for seed yield relative to the aggregate of many other traits in a perennial plant, low seed yield is expected. Indeed, there is evidence that fitness in perennial plants tends to depend more heavily upon survivorship than on fecundity[28].

Because *r*- and *K*-selection are comparative terms[21], their use in separating species into neat categories is a misapplication. Even wild plant species cannot be segregated in such a way, and with artificial selection in agricultural fields, a much wider range of trait combinations is possible. For example, annual types of wild rice (*Oryza* spp.) typically produce more seed than related perennial types, because of their long history of *r*-selection[29]. Annuals produce more seed in response to selection for a greater rate of population increase, while perennials 'show greater vegetative allocation which helps them maintain themselves in crowded habitats'[29]. Allocating a larger proportion of resources to seed and less to vegetation would be one avenue for obtaining a high-yielding perennial grain in an environment where less vegetative growth is needed.

Much of the yield gain in annual grains has come by reducing intra-specific competition, increasing tolerance to crowding stress, increasing responsiveness to high inputs, reducing height and/or increasing harvest index[30–32]. Modern grain plants have a narrow plant profile that reduces competitiveness, and they are often short, in order not to waste resources on vegetative biomass or lodge when nitrogen fertilizer is applied (Fig. 1). In contrast, most wild perennials are extremely competitive. Perennial grain plants should be selected to expend less energy on competition and more on seed production. The goal is a perennial grain crop with deep, durable roots with an above-ground structure that resembles that of annual grain crops more closely than it does that of wild prairie plants (Fig. 1).

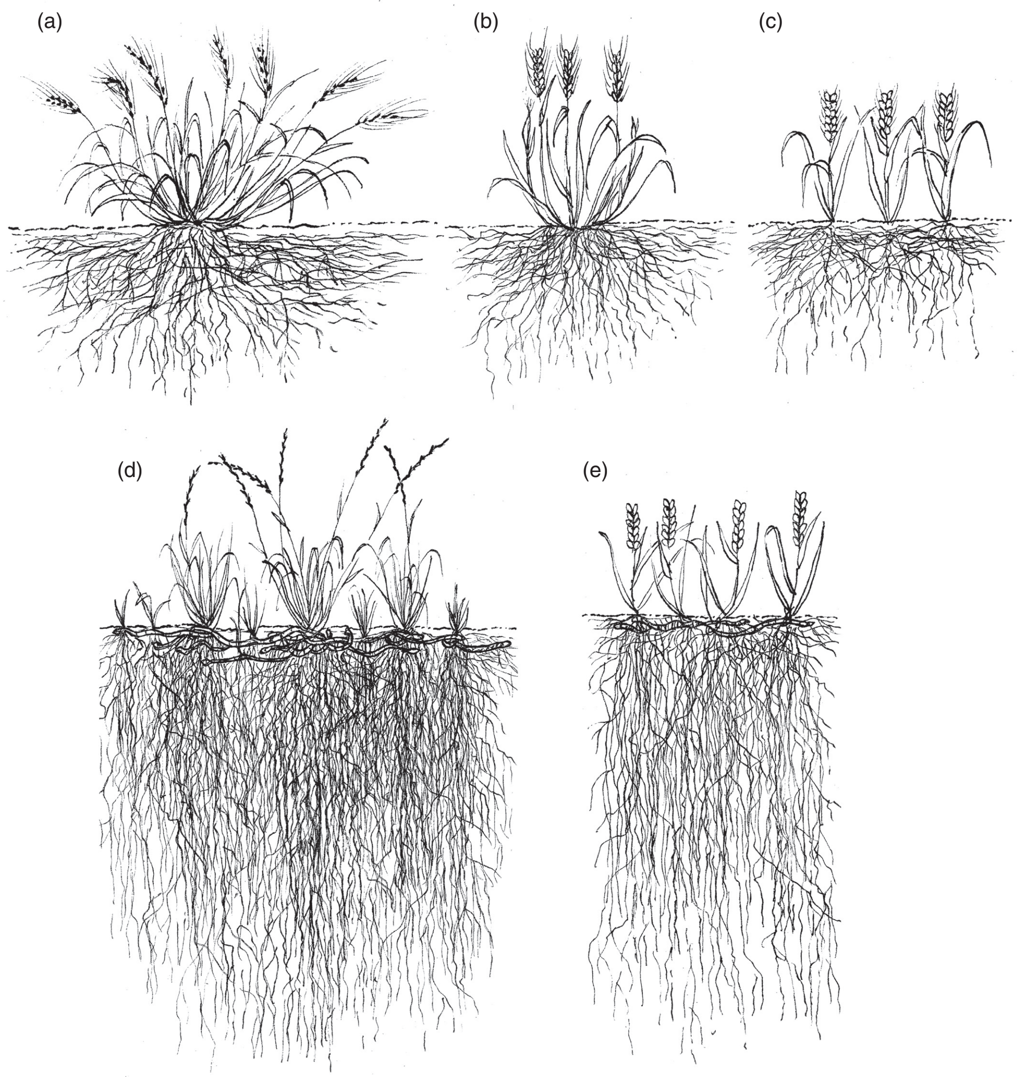

Figure 1. Archetypal morphology of (a) wild annuals; (b) early annual grain crops; (c) modern annual grain crops; (d) wild perennials; and (e) future perennial grain crops.

Anticipated Difficulties

Because perenniality[33] and yield are both polygenic traits, we do not expect that a 'yield gene' can be inserted into a wild perennial, or a 'perenniality gene' into an annual crop plant. Rather, perennial grain breeders are pursuing two parallel strategies: domesticating promising wild perennials and hybridizing annual crops with perennial relatives. In either case, one of the major obstacles we face is the anticipated negative correlation (or trade-off, properly understood) between yield and longevity.

In most cases, multiple traits associated with fitness are expected to be negatively correlated. This is because alleles conferring a positive effect on multiple fitness traits have been largely fixed within a population, leaving those responsible for negative correlations at more intermediate frequencies[34]. Therefore, we fully expect seed yield and longevity to be negatively correlated in perennial grain populations. Selecting to increase seed yield and longevity simultaneously will be slower than selection for either yield or longevity alone. Plant breeders are familiar with the challenge of selecting against negative correlations, as when they attempt to improve concentrations of oil or protein in the seed[35,36] without reducing grain yield. Despite negative correlations, breeding has increased seed yield in perennial forage species[37], while simultaneously increasing forage yield[38]. (The typically small increases in forage and seed yield observed in perennial forages are due to unique challenges in the forage industry[39] that should not be generalized to the breeding of perennial grains.)

Hybridization between annual crops and wild perennials, with the goal of perennial grain development, is made more difficult by genetic and cytological divergence of the parents. Wide hybridization often produces highly sterile progeny. Restoring fertility can be a lengthy process, or even end in failure. Whether or not fertility is restored by chromosomes doubling, lack of pairing between chromosomes derived from different parents can mean that linkages between genes conferring perenniality and genes that limit yield are difficult or impossible to break.

An Integrated Conceptual Framework

Even as we make the case that breeding perennial grain crops is a realistic objective, the relationship between perennial grain development and ecological trade-off theory remains unsettled. Plant breeding literature generally assumes a human-modified environment and artificial selection. Ecological literature has often focused on a single natural ecosystem, seldom considering the role of artificial selection. In an effort to explain perennial grain breeding in a manner that is equally satisfying to ecologists and plant breeders, we have developed a framework that integrates plant breeding and ecology through the quantitative genetic approach to trade-off theory.

The context of a stable environment, in which natural selection acts in a constant way, provides a useful starting point for discussion. Assuming no mutations, selection will eventually exhaust additive genetic variance for fitness, and fitness will no longer increase. At that point, the population is said to be at equilibrium. Falconer and Mackay state that:

> Since the array of gene frequencies in an equilibrium population is the best, in the circumstances, for maximizing fitness, it follows that if selection is applied to any metric character that is not fitness itself, the gene frequencies at loci affecting the character must change if there is a response. Fitness must therefore be reduced as a correlated response, unless the character selected is controlled entirely by genes with no effect on fitness.[34]

In other words, natural selection will, in a stable environment, result in the optimal allocation of resources. By definition, the highest value of any character that is not fitness itself will not result in the highest fitness.[34]

A brief note on the terms ‘fitness’ and ‘stability’ is appropriate at this point. In natural systems, fitness integrates virtually all plant traits. On an agricultural research station, the plant breeder selects certain individuals or families based on any character or combination of characters, thereby defining fitness. And, of course, no environment is truly stable. The adaptive landscape model of selection deals with this fact[40]. However, making the assumption of a stable environment allows easy conceptual consideration of the quantitative genetic principles involved in trade-off theory.

As Lack[41], the father of trade-off theory, was careful to state, a trade-off must hold only in a specific environment[41,42], and Falconer and Mackay[34] further stipulate that the concept of an equilibrium population includes the assumption that mutation does not occur. But environments fluctuate and mutations do occur, so trade-offs are never absolute.

The conceptual model depends upon an understanding of annuality and perenniality as quantitative traits that respond to selection in the same manner as more commonly considered quantitative traits, such as seed yield or seed protein content. Thomas et al.[43] have made a strong argument that although perennials and annuals may appear to be dramatically different, vastly different life histories can occur as the result of minor quantitative changes. They conclude that ‘annuality and perenniality are traits that recur time and again across the taxonomic range and that, with the right selection pressure, the propensity to generate either form of phenotype can be realized without the need for large-scale genetic innovation’[43].

Domestication and the Breeding of Annual Grains

For greater clarification of a topic that spans several disciplines, our conceptual model can be used to examine how trade-off theory applies to wild and domestic forms of annual and perennial plants (Fig. 2). The model is not quantitative, and the steps in the model are not inevitabilities. Rather, the model is intended to provide a framework in which to consider what is possible and, perhaps, likely due to natural and artificial selection.

The model assumes that carbon allocation is completely partitioned among five types of organs and functions: (1) seeds, (2) storage organs, (3) defense structures and compounds, (4) leaves and stems, and (5) roots. The metric used is the average annual carbon irreversibly allocated for each function, averaged over the life of the plant. This allocation includes the carbon used for respiration in that organ or function, averaged over the life of the plant, but not carbon that is remobilized for a different function. Carbon allocation is assumed to represent allocation trade-offs accurately. Where equilibrium populations are considered, we also assume that environments are completely stable and that there is no mutation.

The starting population (Fig. 2a) is one of short-lived perennial plants (with ‘short-lived’ defined relative to other populations in the model) in an environment with moderate disturbance and resource availability. Through natural selection the population has achieved maximum fitness within the constraints of its genetic variation by allocating nearly equal amounts of carbon to roots, leaves and stems, defense and storage, and a small amount to seed. Therefore, it is considered to be in equilibrium.

Water, light and nutrients are more abundant in an agricultural field than in the starting environment (Fig. 2b), due to regular disturbance and a variety of inputs. If a short-lived perennial population invades the field and is able to avoid cultivation during the growing season, the greater resource availability will cause an increase in growth in all structures except roots, which typically do not grow as large relative to above-ground biomass in nutrient-rich environments[44,45]. Because natural selection has not yet

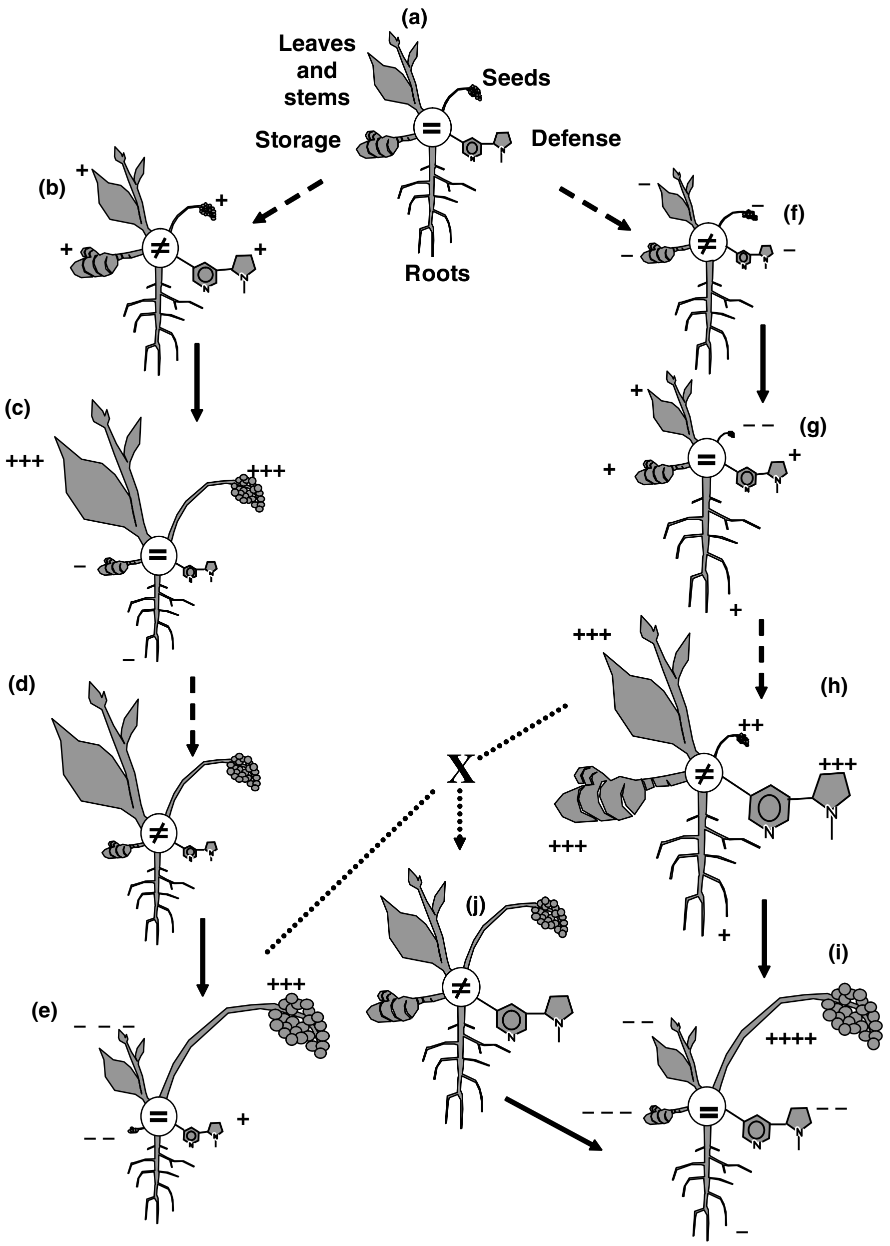

Figure 2. Relative increases (+) and decreases (–) in carbon allocation among seeds, storage, defense structures and compounds (Defense), leaves and stems, and roots due to environmental changes (solid arrows), selection (dashed arrows) and hybridization (dotted arrows) in the hypothetical domestication of annuals and perennials. Populations are in equilibrium (=) or disequilibrium (≠). The populations presented are: (a) a short-lived perennial in an environment with moderate resource availability and competition; (b) a weak perennial in an agricultural field; (c) an annual weed in an agricultural field; (d) a wild annual placed in a plant breeding nursery; (e) a domestic annual grain crop; (f) a weak perennial in a competitive environment; (g) a strong perennial in a competitive environment: (h) a wild perennial placed in a plant breeding nursery; (i) a domestic perennial grain crop; and (j) a hybrid between a wild perennial and a domestic annual, placed in a plant breeding nursery.

acted to maximize fitness, the population is now in disequilibrium.

Given time and natural selection pressure, the population may reach a new equilibrium, becoming an annual weed (Fig. 2c). Plants in disturbed habitats typically allocate reduced amounts of carbon to roots, storage organs and defense, because these are generally less important to a fast-growing annual plant experiencing low competition[22,46,47]. Carbon allocation to stems and leaves increases under selection pressure, to take advantage of the available resources[47], and finally, allocation to seeds typically increases because of the critical importance of seed to fitness in an annual plant[22] in a frequently disturbed (i.e., hazardous) environment.

Next, consider an annual weed that is to be domesticated as a new grain crop. Its morphology is initially unchanged, because environmental conditions are similar. But it is no longer an equilibrium population (Fig. 2d), because fitness

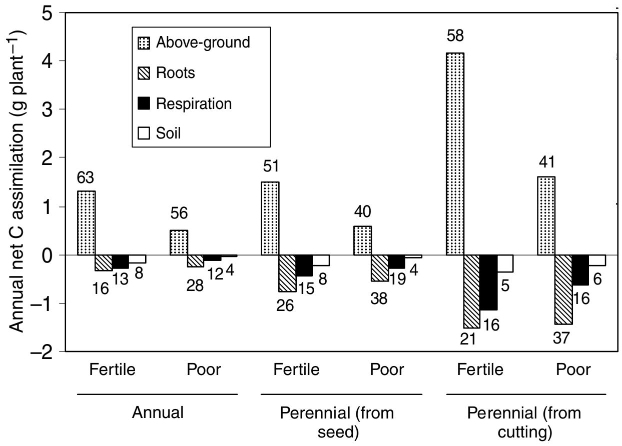

Figure 3. The relationship between nutrient availability and the partitioning of carbon assimilates in annual and perennial grain plants (data from Warembourg and Estelrich[45]).

is now defined by the plant breeder, who favors plants or families that produce maximum seed yields under high density.

The plant breeder's definition of fitness results in selection that produces an equilibrium population with high seed yield, adequate defense allocation and reduced allocation to stems and leaves (Fig. 2e). This population will avoid intense intraspecific competition[48], enabling it to be grown at a high density, as most modern annual crops are grown (Fig. 1c). Some allocation to vegetative storage is likely to remain as a means to tolerate stress[31].

Because modern varieties can have higher yields than landraces, even in low-fertility environments[49], plant breeders may be tempted to conclude that the trade-off concept does not apply to artificial selection. Modern wheat varieties seem to be a case in point, but they have the benefit of newly introduced yield, dwarfing and disease resistance genes that were not present in the original landrace equilibrium population. The expansion of available genetic diversity has allowed plant breeders to increase yield without producing readily identifiable trade-offs.

Even though the high-yielding crop in this model is an equilibrium population, future yield increases are not precluded. If the environment is changed via improved management, selection can once again be used to increase seed yield. Furthermore, additional genetic variation can arise from mutation or hybridization with other high-yielding varieties, landraces or related species.

Domestication and Breeding of Perennial Grains

There are two possible scenarios for the development of a perennial grain crop. First, we consider the evolution of a long-lived perennial. If the short-lived perennial starting population (Fig. 2a) is subjected to reduced resource availability due to increasing competition (Fig. 2f), its total growth is likely to be reduced. When nutrient availability is low (perhaps due to root competition), total carbon fixation is often reduced, and roots now require a greater proportion of available carbohydrate (Fig. 3) to obtain the limiting nutrients[44,45,50]. In this instance, resource scarcity refers to available rather than total resources. For example, soils can have high organic nitrogen content but little nitrogen available for plant growth.

Through natural selection, the population becomes adapted to its stable, highly competitive environment and is able to increase total carbon fixation relative to its unadapted condition (Fig. 2g). Under low resource availability, selection is expected to reduce allocation to seeds and increase allocation to structures that will increase competitive ability[21], such as roots, stems, defense and storage. A resource allocation strategy that improves the plant's survivorship will be likely to maximize its fitness in a competitive resource-scarce environment[28]. Although allocation to seed is reduced, this does not mean that seeds are of little value to the perennial. Rather, fitness is maximized by sustained production of smaller numbers of seeds per year.

A long-lived prairie plant placed in a plant breeding nursery would be likely to greatly increase growth and allocation to storage, defense, leaves and stems (Fig. 2h). Allocation to seed may increase only slightly, because the plant is genetically programmed for longevity rather than seed production in a single year. This pattern of greatly increased growth and above-ground allocation was observed when the perennial *Bromus madritensis* was grown on fertile compared to poor soil (Fig. 3).

Under the new environmental conditions of the breeding nursery, the population is now in disequilibrium and being selected for increased seed yield and longevity. After many selection cycles, the population attains equilibrium, with an average seed yield approaching that of annual crops (compare Fig. 2e and i). Compared with annual crops, however, there will be greater allocation to defense structures and compounds, because a long-lived perennial plant must be able to tolerate environmental extremes and defend itself against herbivores and pathogens, populations of which can build up over time. Although we expect the perennial grain to have a much larger root system than the annual grain (Fig. 1), proportional allocation to roots may not need to be much larger after the first year. For this to be true, annual respiration and root turnover in the perennial root system must not exceed the cost of building a complete root system in an annual. According to Weaver, root turnover in prairies is about 40% annually[51] and respiration can easily equal 50% of root mass annually (Fig. 3). Therefore, allocation below ground level will exceed that of annual crops unless the root systems of perennial grain crops are somewhat smaller (Fig. 1) or more efficient than in wild perennials. Net allocation to storage is modest because much of the stored photosynthate and nutrients can be remobilized in the following year. The resources stored by perennials can enable them to sustain seed production even in stressful conditions[52].

If a wild perennial has low seed yield, the time required for domestication will likely be long. If the species can be hybridized with a related domestic annual, interspecific crossing may speed perennial grain development. The hybrid is expected to have a resource allocation pattern that is intermediate to the two parents (Fig. 2j) because hybrids are generally intermediate in longevity, seed yield and allocation patterns[12,53]. Furthermore, the genetic variance for traits affecting both seed yield and longevity will increase over either parent, allowing more rapid progress in selection for yield and longevity simultaneously. The large genetic variance is beneficial because it is due to the presence of useful 'domestication alleles' from the crop and 'perenniality alleles' from the wild plant.

The development of a perennial grain crop should not be viewed as simple modification of an annual grain crop (Fig. 1c). The latter is fixing as much carbon as possible during its short lifespan and allocating as much of that carbon as possible to harvestable seed. Therefore, it cannot be expected to maintain the level of durable defense against pathogens and pests that is common in perennials, let alone store enough carbon to regrow in the following season. The high-yielding annual grain crop is an equilibrium population resulting from selection for seed yield. Because negative correlations between fitness components are the rule in equilibrium populations, selection for any other trait, including those that could increase longevity, must necessarily come at the cost of reduced seed yield.

Crossing the annual crop with a perennial species changes the genetic constitution, so that the progeny comprise a disequilibrium population, in which trade-offs are not necessarily fixed. A hybrid between the perennial and the annual crop may be able to acquire water and nutrients from greater depth throughout the year, and harvest light energy earlier in the spring and later in the fall. As a result, the perennial plant is able to fix more total carbon (Table 1, Fig. 3), which can be allocated to storage, below-ground allocation and defense. The trade-off of carbon among various functions is avoided if the total pool is increased in the more efficient perennial plant.

The framework also explains how high-seed-yielding herbaceous perennials could be developed through selection, despite their rarity in natural ecosystems. In their native, resource-scarce environments, where perennials have a competitive advantage over annuals, plants maximize fitness via allocation to roots, storage, leaves, stems and defense/tolerance. This allocation pattern increases competitive ability and longevity to maximize fitness. In contrast, a plant breeder can develop a perennial plant with reduced competitive ability by selecting for shorter stature, a less spreading root system, reduced tillering and more erect leaves.

It is important to remember that the allocation patterns arrived at in equilibrium populations (Fig. 2) are not necessarily the optimal allocation imaginable, but rather the optimal allocation possible for the population under consideration. If additive genetic variance for a trait, such as seed yield, is low, other traits that increase breeder-defined fitness may show a greater response to selection. Furthermore, strong negative correlations between traits can limit the ability of selection to increase fitness components simultaneously.

Promising Perennial Grain Programs

At the Land Institute, four perennial taxa are being domesticated and selected for grain production: intermediate wheatgrass, Illinois bundleflower, Maximilian sunflower (*Helianthus maximiliani*) and *Silphium* spp.[2,54]. A recurrent selection program to improve kernel size, yield per unit area and threshability of intermediate wheatgrass is under way. Hybridization methods for Illinois bundleflower, a species with no human-directed breeding history, are being developed in order to begin recurrent and pedigree selection. The sunflower and *Silphium* programs are at the initial germplasm evaluation stage.

With some of these and other species, there is an opportunity to combine grain production with perenniality through interspecific and intergeneric hybridization[2,54]. Work with amphiploids and backcrosses derived from crossing wheat (*Triticum aestivum* and *T. turgidum*) and triticale (× *triticosecale*) with three wheatgrass species (*Thinopyrum elongatum, Th. intermedium* and *Th. ponticum*) is under way, and initial crosses with members of the genera *Elymus, Leymus* and *Agropyron* are being made. By 2002, 1500 intergeneric hybrids between annual small grains and wild perennial relatives had been made, and by 2003 more than 600 progeny had been obtained by backcrossing or chromosome doubling to restore fertility. The wheat breeding program at Washington State University is evaluating more advanced perennial wheat germplasm[12].

The Land Institute's first hybridization project was to develop perennial sorghum from crosses between grain sorghum (*Sorghum bicolor*) and johnsongrass (*S. halepense*). Since 2001, we have been broadening the base of that perennial gene pool by crossing with newly released grain sorghum germplasm having superior grain quality. Crosses are also being made between annual, cultivated sunflower (*H. annuus*) and Maximilian sunflower (*H. maximiliani*), Jerusalem artichoke (*H. tuberosus*) and other perennial sunflower species with the intent to produce a perennial grain sunflower.

Development of perennial grains from the species and hybrids listed above will take several decades. A promising, shorter-term prospect for tropical regions may have been the International Rice Research Institute's (IRRI) perennial rice breeding program, which ran from 1995 to 2001. Yields of many of the hybrids were large, indicating good potential for perennial rice to exceed yields of 1000–2000 kg ha^{-1} in South-East Asian upland conditions[55]. Some of the most strongly perennial families had the highest grain yields, and there was not a negative correlation (trade-off) between yield and survival. Particularly promising was the ability of the perennial hybrids to produce a dry-season crop, which could be extremely important to the welfare of farmers in South-East Asia. Researchers concluded that 'Breeding perennial cultivated rice should be feasible but it will likely take five to ten more years'[55]. Despite excellent prospects, the program was discontinued, primarily due to priorities within IRRI and lack of funds (Erik Sacks, personal communication, 2004).

Conclusions

The primary issue addressed in this paper is whether there exists solid evidence or theory demonstrating that an inevitable trade-off between perenniality and seed production precludes the breeding of perennial grain crops. The answer to this question is clear. Trade-off theory, when approached from a quantitative genetic perspective, does not rule out perennial grains.

Because perennial plants can be inherently more efficient and productive than annuals, resources may well be available for both grain production and perennation. The larger question of whether specific perennial grains such as sorghum, sunflower or wheat can be developed remains unanswered. This question depends upon a host of genetic factors and can be answered only by attempting to breed these perennial crops.

The potential benefits of perennial grains, in terms of soil conservation, reduced agricultural inputs and improved wildlife habitat are great, while the risks are comparatively modest. For example, breeding programs in numerous perennial grain species could be conducted using only a small fraction of the United States Department of Agriculture's annual budget. Indeed, several perennial grain breeding programs have been initiated and are progressing well. If progress is sustained and funding expanded, perennial grains could be widely available within decades.

For maximum benefit, perennial grain programs must be expanded and initiated in the immediate future. The process of breeding perennial grains will itself generate data crucial to the debate about a trade-off between yield and the perennial habit. A call for further theoretical discussion is therefore an argument for accelerating rather than postponing serious breeding efforts.

References

1 Glover, J.D. 2005. The necessity and possibility of perennial grain crops. Renewable Agriculture and Food Systems 20: 1–4.

2 Cox, T.S., Bender, M.H., Picone, C., Van Tassel, D.L., Holland, J.H., Brummer, E.C., Zoeller, B.E., Paterson, A.H., and Jackson, W. 2002. Breeding perennial grain crops. Critical Reviews in Plant Science 21:59–91.

3 Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.

4 Gantzer, C.J., Anderson, S.H., Thompson, A.L., and Brown, J.R. 1990. Estimating soil erosion after 100 years of cropping on Sanborn Field. Journal of Soil and Water Conservation 45:641–644.

5 Dinnes, D.L., Karlen, D.L., Jaynes, D.B., Kaspar, T.C., Hatfield, J.L., Colvin, T.S., and Cambaradella, C.A. 2002. Nitrogen management strategies to reduce nitrate leaching in tile-drained Midwestern soils. Agronomy Journal 94:153–171.

6 Randall, G.W., Huggins, D.R., Russelle, M.P., Fuchs, D.J., Nelson, W.W., and Anderson, J.L. 1997. Nitrate losses through subsurface tile drainage in conservation reserve program, alfalfa, and row crop systems. Journal of Environmental Quality 26:1240–1247.

7 Huggins, D.R., Randall, G.W., and Russelle, M.P. 2001. Subsurface drain losses of water and nitrate following conversion of perennials to row crops. Agronomy Journal 93:477–486.

8 Silvertown, J. and Dodd, M. 1996. Comparing plants and connecting traits. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 351:1233–1239.

9 Wagoner, P. 1990. Perennial grain development: Past efforts and potential for the future. Critical Reviews in Plant Science 9:381–408.

10 Roff, D.A., Mostowy, S., and Fairbairn, D.J. 2002. The evolution of trade-offs: Testing predictions on response to selection and environmental variation. Evolution 56:84–95.

11 Roff, D.A. and Gelinas, M.B. 2003. Phenotypic plasticity and the evolution of trade-offs: the quantitative genetics of resource allocation in the wing dimorphic cricket, *Gryllus firmus*. Journal of Evolutionary Biology 16:55–63.

12 Scheinost, P., Lammer, D., Cai, X., Murray, T.D., and Jones, S.S. 2001. Perennial wheat: a sustainable cropping system for the Pacific Northwest. American Journal of Alternative Agriculture 16:147–151.

13 Sheaffer, C.C. and Marten, G.C. 1991. Kura clover forage yield, forage quality, and stand dynamics. Canadian Journal of Plant Science 71:1169–1172.

14 Field, C.B. 2001. Sharing the garden. Science 294:2490–2491.

15 Sheaffer, C.C., Cash, D., Ehlke, N.J., Henning, J.C., Jewett, J.G., Johnson, K.D., Peterson, M.A., Smith, M., Hansen, J.L., and Viands, D.R. 1998. Entry × environment interactions for alfalfa forage quality. Agronomy Journal 90:774–780.

16 Sheaffer, C.C., Orf, J.H., Devine, T.E., and Jewett, J.G. 2001. Yield and quality of forage soybean. Agronomy Journal 93:99–106.

17 Kulakow, P.A., Benson, L.L., and Vail, J.G. 1990. Prospects for domesticating Illinois bundleflower. In J. Janick and J.E. Simon (eds). Advances in New Crops. Timber Press, Portland. p. 168–171.

18 Adjei, M.B. and Pitman, W.D. 1993. Response of *Desmanthus* to clipping on a phosphatic clay mine-spoil. Tropical Grasslands 27:94–99.

19 Jackson, W. and Jackson, L.L. 1999. Developing high seed yielding perennial polycultures as a mimic of mid-grass prairie. In E.C. Lefroy, R.J. Hobbs, M.H. O'Connor, and J.S. Pate (eds). Agriculture as a Mimic of Natural Systems. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 1–37.

20 FAOSTAT data. 2004. Food and Agriculture Organization of the United Nations http://apps.fao.org/faostat/collections?version=ext &hasbulk=0&subset=agriculture (verified 24 January 2005).

21 Gadgil, M. and Solbrig, O.T. 1972. The concept of *r*- and *K*-selection: Evidence from wild flowers and some theoretical considerations. The American Naturalist 106:14–31.

22 Harper, J.L. 1977. Population Biology of Plants. Academic Press, London, UK.

23 Garnier, E. and Laurent, G. 1994. Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. New Phytologist 128:725–736.

24 Abrahamson, W.G., Anderson, S.S., and McCrea, K.D. 1991. Clonal integration: Nutrient sharing between sister ramets of *Solidago altissima* (Compositae). American Journal of Botany 78:1508–1514.

25 Meyer, G.A. 1993. Effects of herbivorous insects and soil fertility on reproduction of goldenrod. Ecology 74:1117–1128.

26 Young, T.P. and Augspurger, C.K. 1991. Ecology and evolution of long-lived semelparous plants. Trends in Ecology and Evolution 6:285–289.

27 Wilson, M.F. 1983. Plant Reproductive Ecology. John Wiley and Sons, New York.

28 Crone, E.E. 2001. Is survivorship a better fitness surrogate than fecundity? Evolution 55:2611–2614.

29 Sano, Y. and Morishima, H. 1982. Variation in resource allocation and adaptive strategy of a wild rice, *Oryza perennis* Moench. Botanical Gazette 143:518–523.

30 Brancourt-Hulmel, M., Doussinault, G., Lecomte, C., Berard, P., Buanec, B.L., and Trottet, M. 2003. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. Crop Science 43:37–45.

31 Reynolds, M.P., Rajaram, S., and Sayre, K.D. 1999. Physiological and genetic changes of irrigated wheat in the post-Green Revolution period and approaches for meeting projected global demand. Crop Science 39:1611–1621.

32 Tollenaar, M. and Wu, J. 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Science 39:1597–1604.

33 Paterson, A.H., Schertz, K.F., Lin, Y.R., Liu, S.C., and Chang, Y.L. 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 of the United States of America 92:6127–6131.

34 Falconer, D.S. and Mackay, T.F.C. 1996. Introduction to Quantitative Genetics. Prentice Hall, Harlow, UK.

35 Loffler, C.M., Busch, R.H., and Wiersma, J.V. 1983. Recurrent selection for grain protein percentage in hard red spring wheat. Crop Science 23:1097–1101.

36 Burton, J.W. and Brim, C.A. 1981. Recurrent selection in soybeans. III. Selection for increased percent oil in seeds. Crop Science 21:31–34.

37 Knowles, R.P., Cooke, D.A., and Buglass, E. 1970. Breeding for seed yield and seed quality in smooth bromegrass, *Bromus inermis* Leyss. Crop Science 10:539–542.

38 Casler, M.D., Berg, C.C., Carlson, I.T., and Sleper, D.A. 1997. Convergent–divergent selection for seed production and forage traits in orchardgrass: III. Correlated responses for forage traits. Crop Science 37:1059–1065.

39 Wilkins, P.W. and Humphreys, M.O. 2003. Progress in breeding perennial forage grasses for temperate agriculture. Journal of Agricultural Science 140:129–150.

40 Wright, S. 1988. Surfaces of selective value revisited. American Naturalist 131:115–123.

41 Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford, UK.

42 Czesak, M.E. and Fox, C.W. 2003. Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. Evolution 57:1121–1132.

43 Thomas, H., Thomas, H.M., and Ougham, H. 2000. Annuality, perenniality and cell death. Journal of Experimental Botany 51:1781–1788.

44 Cheplick, G.P. 1995. Life history trade-offs in *Amphibromus scabrivalvis* (Poaceae): Allocation to clonal growth, storage, and cleistogamous reproduction. American Journal of Botany 83:621–629.

45 Warembourg, F.R. and Estelrich, H.D. 2001. Plant phenology and soil fertility effects on below-ground carbon allocation for an annual (*Bromus madritensis*) and a perennial (*Bromus erectus*) grass species. Soil Biology and Biochemistry 33:1291–1303.

46 Coley, P.D., Bryant, J.P., and Chapin, F.S. 1985. Resource availability and plant herbivore defense. Science 230: 895–899.

47 Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, New Jersey.

48 Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385–403.

49 Shroyer, J.P. and Cox, T.S. 1993. Productivity and adaptive capacity of winter wheat landraces and modern cultivars under low-fertility conditions. Euphytica 70:27–33.

50 Tilman, D. 1990. Constraints and trade-offs: toward a predictive theory of competition and succession. Oikos 58:3–15.

51 Weaver, J.E. 1968. Prairie Plants and their Environment. University of Nebraska Press, Lincoln.

52 Marshall, D.L., Levin, D.A., and Fowler, N.L. 1985. Plasticity in yield components in response to fruit predation and date of fruit initiation in three species of *Sesbania* (Leguminosae). Journal of Ecology 73:71–81.

53 Piper, J.K. and Kulakow, P.A. 1994. Seed yield and biomass allocation in *Sorghum bicolor* and F_1 and backcross generations of *S. bicolo*r × *S. halepense* hybrids. Canadian Journal of Botany 72:468–474.

54 Cox, T.S., Picone, C., and Jackson, W. 2004. Research priorities in natural systems agriculture. Journal of Crop Production 12:511–531.

55 Sacks, E.J., Roxas, J.P., and Sta. Cruz, M.T. 2003. Developing perennial upland rice I: Field performance of *Oryza sativa*/*O. rufipogon* F_1, F_4 and BC_1F_4 progeny. Crop Science 43:120–128.