

PERSPECTIVE

Missing domesticated plant forms: can artificial selection fill the gap?

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Abstract

In the course of their evolution, the angiosperms have radiated into most known plant forms and life histories. Their adaptation to a recently created habitat, the crop field, produced a novel form: the plant that allocates an unprecedented 30–60% of its net productivity to sexual structures. Long-lived trees, shrubs and vines of this form evolved, as did annual herbs. Perennial herb forms with increased allocation to asexual reproduction evolved, but there are no examples of perennial herbs with high sexual effort. We suggest that sowing seed into annually tilled fields favored shorter-lived herbs because of trade-offs between first-year seed production and relative growth rate and/or persistence. By propagating cuttings, people quickly domesticated tuber crops and large woody plants. Perennial herbs were too small to be efficiently propagated by cuttings, and the association between longevity, allogamy and genetic load made rapid domestication by sexual cycles unlikely. Perennial grain crops do not exist because they could not have evolved under the original set of conditions; however, they can be deliberately developed today through artificial phenotypic and genotypic selection.

Introduction

If developed through breeding, perennial grain crops could reduce soil erosion while maintaining production of food staples (Glover and Reganold 2010). High yielding, large-diaspore perennial food crops, including oil palm, banana, coconut, and apple, already exist (see Table 1). However, it would be difficult to substitute those species for annual grain commodities, because they are much more difficult to harvest, transport, store and process mechanically. Herbaceous perennials could be harvested and handled as are existing domesticated grains. Among herbs, perennials generally have a lower annual sexual reproductive effort than annuals, but we and other authors have identified herbaceous perennials with high annual seed production and have argued that domesticating perennials should be possible (Wagoner 1990; DeHaan et al. 2005; Cox et al. 2006).

However, through 10 000 years of plant domestication, not one perennial species was domesticated for grain production. The prevalence of annuals among domesticated, grain-bearing species is often thought to warrant little discussion. For example, Blumler and Byrne (1991) wrote simply that perennial grains were not domesticated because they 'are less subject to selection pressures since

stands are not replaced each year. In addition, perennials usually outcross.' But a more detailed look at the differences in susceptibility to domestication of perennial and annual species 10 millennia ago can provide additional insights into that process while at the same time informing present-day attempts to domesticate perennial herbaceous species for grain production.

In the first two parts of this paper, we consider natural selection that occurred in early agricultural ecosystems. We treat historical plant domestication as a Darwinian process in which plants and humans coevolved (Rindos 1984). This coevolution involved initial unconscious selection for larger-seeded genotypes with reduced shattering and dormancy, augmented, subsequently, by conscious selection for other traits (reviewed by Cox 2009). Both unconscious and conscious selection are 'natural' in the sense that they immediately increased the individual fitness of the plants (and humans) in an agricultural environment. In the second part, we consider whether the prospects for perennial grains are different under artificial, scientifically informed selection, and what might motivate plant breeders to develop them. We consider scientific selection in the modern era to be artificial because it does not increase individual fitness but, rather, increases the productivity of the crop per unit area. This

Table 1. Dry matter yield of reproductive products and annual net reproductive effort in field trials of seven perennial species.

Crop	Product	Dry matter yield* (kg ha ⁻¹)	Annual net reproductive effort†	Basis of reproductive effort	Source and location
<i>Malus × domestica</i> (apple)	Fruit (diaspore)	13 000–17 000	0.65	Mass	Palmer (1988), New Zealand
<i>Elaeis guineensis</i> (oil palm)	Fruit plus seed	5000–9000	0.34	Mass	Corley (1983), Malaysia
			0.52	Energy	
<i>Cocos nucifera</i> (coconut palm)	Copra (seed endosperm)	3000–6000	0.20	Mass	Corley (1983), Malaysia
			0.31	Energy	
<i>Elaeis guineensis</i>	Oil (kernel & mesocarp)	6800	0.32	Energy	Wahid et al. (2004), Malaysia
	Bunches (fruit & peduncles)	16 800	0.55	Energy	
<i>Olea europaea</i> (olive)	Fruit (whole, with seed)	4600	0.54	Mass	Villalobos et al. (2006), Spain
<i>Musa</i> spp., genomes AAB (plantain)	Fruit (whole, seedless)	–	0.60	Mass	Baiyeri (2002), Nigeria
<i>Vaccinium corymbosum</i> (highbush blueberry)	Fruit (whole fruit & seed)	–	0.55	Mass	Pritts and Hancock (1985), USA

*Mean or range of means rounded to nearest 100 kg ha⁻¹.

†Proportion of total annual energy or mass accumulation allocated to the designated product.

often comes at the expense of individual fitness (Denison et al. 2003).

Morphospace as a metaphor

Plotting the existing combinations of reproductive effort against life-form creates a morphospace (McGhee 2001; Hall 2008) with a large empty region because there are no herbaceous perennials with very high reproductive effort (Fig. 1). This void stands out because there are longer- and shorter-lived life forms with much higher reproductive effort. There are several kinds of hypotheses to explain regions of unused morphospace. We will explore the morphospace metaphor first and later consider the evidence in the case of angiosperm domestication.

We have formulated five hypotheses that purport to explain the void in this morphospace. Under Hypothesis 1, perennial grains would be impossible on logical or thermodynamic grounds. In this case, the space that would be occupied by perennial grains is not unused morphospace; rather, the theoretical morphospace is simply not a rectangle. Under Hypotheses 2 through 5, there is a theoretical morphospace for perenniality combined with higher reproductive effort but it has never been stably occupied. According to Hypothesis 2, there has not been enough time for all logically possible trait combinations to have evolved. Incomplete sampling of morphospace alone could leave gaps in morphologies represented by fossil and extant species. Would perennial grains have been domesticated by unconscious selection—like the annual grains—given enough time or efficient sampling? Under Hypothesis 3 a morphospace can remain unoccupied because the organisms under consideration are

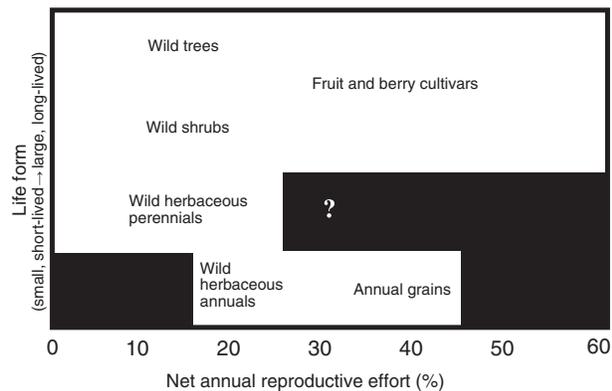


Figure 1 A morphospace is the ‘hypothetical universe of all conceivable phenotypes’ (Niklas 1997, 215). Here, a two-dimensional plane in angiosperm morphospace shows combinations of life form and reproductive effort (including asexual reproduction). Modified from Harper (1977) with the addition of values for woody crops from the sources listed in Table 1.

developmentally canalized to the extent that the combination of traits is impossible to achieve (McGhee 2001). The burden of proof will be heavy in the case of the angiosperms, given their proliferation into ‘...every known plant body-plan and growth form....and habitat across the face of the planet...’ (Crepet and Niklas 2009) Hypothesis 4 allows that the empty region of morphospace could have been briefly occupied repeatedly, but such morphologies experience a high extinction rate because of low fitness in any environment present during the time period under consideration. However, genotypes with low fitness value in one adaptive landscape could have high fitness value if the adaptive landscape changed. Could herbaceous perennial genotypes with high yield

potential have arisen from time to time only to be eliminated by natural selection in natural or early agricultural environments? Hypothesis 5 is a weaker version of Hypothesis 4: the empty morphospace could again have been transiently entered from time to time but never occupied because while the morphology was novel, the adaptive function was not (Wainwright 2007). Another lineage would already have been occupying the functional space, preempting the latecomer.

Annual grain morphospace

The domestication of cereals represents a recent and rapid colonization of morphospace in the reproductive-allocation dimension among graminoids. Though increased fecundity is a major component of fitness, and larger seeds almost always produce more vigorous, competitive seedlings (Leishman et al. 2000), trade-offs with other components of fitness may have prevented annual plants from colonizing this space prior to human involvement.

Human farmers, by providing a regular disturbance regime, dispersing seeds, and suppressing interplant competition created a novel environment: the agroecosystem. This new ecosystem presented a novel suite of trade-offs and opportunities; the adaptive landscape had changed, with an adaptive peak mapping to an unoccupied region of morphospace. Annuals from several families rapidly converged towards the new phenotype associated with the domestic grain. In recent decades breeding of annual crops has further increased their reproductive allocation by bringing previously unavailable genetic variation (e.g., for dwarfing in *Oryza* and *Triticum*) into elite populations and continuing artificial selection under conditions of improved fertility, weed and disease control (Evans and Fischer 1999).

Woody perennial morphospace

Although Harper (1977) suggested that trees might allocate up to 25% of their net annual assimilation to sexual reproduction, the literature indicates that values of 5% are more common for wild trees (Bazzaz et al. 2000). Therefore, wild trees and wild perennial herbs had similarly low reproductive allocation. That several domesticated trees and palms allocate more than 50% to reproduction—higher than maize, the most productive annual crop—illustrates the remarkable transformation in allocation possible through domestication (Table 1). The first woody domesticates were achieved in the Near East long after grain agriculture was well established (Zohary and Spiegel-Roy 1975). Because all of the woody domesticates are highly heterozygous, their early domestication

and subsequent spread depended completely on the ease with which the species could be vegetatively propagated. Zohary and Spiegel-Roy (1975) state that olives, grapes, figs, dates and pomegranates were essentially preadapted to domestication because of their ease of vegetative propagation, and that yield was increased through subsequent cloning of fortuitous hybrids between domestic clones and wild populations.

The perennial-grain void in morphospace

Hypothesis 1

We argued previously (DeHaan et al. 2005) that the issue of perennials' low reproductive effort is something of a distraction. Whereas plant ecologists focus on reproductive effort, agronomists focus on yield *per se*. In a classic study showing a negative correlation between longevity and reproductive effort among species, Primack (1979) stated, 'Perennial species of *Plantago* have larger average leaf areas than the annual species of *Plantago*. This larger vegetative size allows the perennial species to produce greater weights of seed per plant than the annual species, more than compensating for the lower reproductive effort of the perennial.' Simply by being more productive, perennial plants could conceivably put forth a rather modest reproductive effort and still yield as much seed per acre as a domesticated annual grain.

Why is it reasonable to expect that perennials might often be more productive than annuals in the same environment? Dohleman and Long (2009) compared the above-ground productivity of two grasses, *Z. mays* (annual) and *Miscanthus gigantea* (perennial). They concluded that the perennial intercepted more of the available light by establishing a full canopy more quickly in the spring and remaining photosynthetic later in the season. The perennial invested in rhizomes, lost some below-ground biomass via respiration during the Illinois winter, and still produced considerably more aboveground biomass than maize.

Nevertheless, the question of whether perennials could match domesticated annuals in reproductive effort is worth addressing because it may help answer the question of why perennial grain-producing species did not become domesticated. We consider possible thermodynamic problems with the concept of perennial grains below:

Hypothesis 1a

Survival is energetically very expensive, so 'perennial systems may be destined to lower yield...' (Ewel 1999).

Among wild species, lifespan has frequently been observed to be negatively correlated with reproductive effort (Harper 1977; Primack 1979; Hautekeete et al.

2001). Ecologists often assume 'a tradeoff between rejuvenation through seeds (reproduction) and investment in new vegetative tissues (survival)' (Van Dijk 2009) because 'carbon allocated to stature and perennial organs [is] unavailable for reproduction' (Ewel 1999). However this has been difficult to demonstrate (Hautekèete et al. 2002; Aragon et al. 2009). Even where blossom removal increased the survival rate of a short lived perennial, it did not affect reproductive effort (Aragon et al. 2009). Two closely related species of *Lesquerella*, one perennial and the other annual, were found to have indistinguishable allocation to seed (Ploschuk et al. 2005) and within perennial *Beta* species, lifespan and reproductive effort were unrelated (Hautekèete et al. 2001).

Deductions about tradeoffs in wild populations must be balanced against inductive observations: some plants that combine longevity and high reproductive effort. Table 1 includes several domesticated woody and herbaceous species capable of allocating more than 50% of their net annual assimilation to reproductive sinks. This is higher allocation to reproduction than is made by most annuals, yet these perennials must also expend resources to keep vegetative meristems alive year-round, a cost that annuals do not have. Does the annual habit incur other costs? Dohleman and Long (2009) suggested that plants with re-usable roots may have lower annual capital costs than do annual plants.

Hypothesis 1b

Some mature perennials may have high annual allocation to reproduction but only because of low reproductive effort during establishment years: lifetime reproductive effort is always lower for perennials than annuals.

Tree crops clearly have a low-yielding establishment phase. In blueberries and olives, 4 years were required to achieve maximal yield (Pritts and Hancock 1985; Villalobos et al. 2006), some commercial apple orchards begin to bear after 3 years (Glover et al. 2002). However, given fairly short establishment periods or many years between replanting of tree or shrub crops, average reproductive effort could approach or even exceed the average for annual crops. Assuming zero reproductive allocation for 3 years and 0.65 net reproductive effort thereafter, an apple orchard's lifetime average annual reproductive allocation will match that of maize (0.45, Tollenaar and Lee 2002) in 10 years. It is hard to know if this is relevant to understanding the conditions under which annual and woody crops became domesticated. In any case, even if true, this hypothesis cannot explain why woody crops were domesticated for harvest of reproductive structures but herbaceous perennials were not: herbaceous perennials reach peak production much more quickly than do woody ones.

Hypothesis 1c

The cost of multi-year survival is much higher for herbs than for woody plants.

This hypothesis would certainly explain the unoccupied morphospace, but we can deduce no mechanisms that would explain the necessity of wood. Induction suggests otherwise. Many perennial herbs allocate a high percentage of their net annual assimilate to 'disposable' structures used either for competition or asexual reproduction. The energy-rich reproductive herbaceous culms of *Miscanthus*, sugarcane and plantain can be harvested annually without sacrificing the ability of these plants to overwinter or regrow. Beal and Long (1997) reported 28 Mg ha⁻¹ annual dry matter productivity for *Miscanthus* in England. Rhizome mass declined to an annual minimum of 5 Mg ha⁻¹ in early summer, and in autumn achieved a maximum of about 10 Mg ha⁻¹ suggesting that 5 Mg ha⁻¹, or about 18% of annual productivity, supported winter rhizome survival, spring re-growth, and clonal expansion.

When the chief reproductive organ is an underground vegetative structure, crop plants often allocate to it far more carbohydrate than would be needed for reproduction in the wild. In an Idaho trial, two *Solanum tuberosum* (potato) cultivars fertilized at recommended rates allocated a mean of 80% of total plant dry weight to tubers, producing a mean 11.5 Mg ha⁻¹ of tuber dry weight. We estimate less than 0.2 Mg ha⁻¹ dry matter is required for potato to overwinter in California (as 'seed' tubers), using recommended planting rates (Bishop and Wright 1959) and assuming 80% moisture content. In Japan, two *Ipomoea batatas* (sweet potato) cultivars allocated a mean 81% of dry weight to harvestable roots, producing almost 13 Mg ha⁻¹ (Sulaiman and Sasaki 2001). In two studies that included a total of four *Manihot esculenta* (cassava) cultivars, a mean 56 percent of total dry weight was partitioned into harvestable roots (Veltkamp 1985; Sagrilo et al. 2008).

Hypothesis 1d

Net annual biomass partitioning to fruit (see 1a, above) or harvestable stems (see 1c, above) cannot be compared directly with partitioning to seeds, which are protein and oil-rich.

Different kinds of biomass have different construction and translocation costs depending on their composition (Penning de Vries et al. 1989). While some fruit dry matter may well be relatively low in protein and oil, the fruits of some of the woody plants in Table 1 are oil-rich. Villalobos et al. (1994) reported that olive (fruit oil) commonly yields 3 Mg ha⁻¹ of oil while sunflower (seed oil) yields 2.25 Mg ha⁻¹ in the same region of Spain.

If a perennial biomass crop like *Miscanthus* could be bred to produce maize-like grain, how much reallocation of existing production from stems to seeds might be necessary? Assuming the same leaf to stem ratio as seen in a previous study with similar biomass yield (Beale and Long 1997), in 2007, in Illinois *Miscanthus* produced about 24 Mg ha⁻¹ of stalks; maize produced 12 Mg ha⁻¹ of seeds (Dohleman and Long 2009). The listed 'glucose equivalent value' for stem biomass is slightly higher than the value for maize reproductive structures (Penning de Vries et al. 1989). Assuming that breeding changes only allocation of dry matter, from stem to ear, a hypothetical grain *Miscanthus* could produce as much seed as maize and still have the capacity to invest in 12 Mg ha⁻¹ of stalk. That should be more than enough stalk mass for plant support: maize stem and leaf material at the time of grain harvest amounted to about 7 Mg ha⁻¹ both years of the Dohleman and Long (2009) study.

Hypothesis 1e

Even if the carbon costs of overwintering are small (1c, above) seeds are nitrogen-rich, and nitrogen molecules cannot be two places at the same time.

At first glance, this line of logic would seem also to preclude the domestication of annual grains, however, it is combined with the observation that annual plants undergo programmed senescence of nitrogen-rich leaves, translocating most of the nitrogen to the developing seeds (Denison 2009). Perennials usually stay green after seed fill and could not, under this hypothesis, deposit as much protein in the grain. But at second glance, this appears to be merely a delay in timing rather than a completely different nitrogen-use strategy. The leaves of perennial herbs do senesce, and translocatable nutrients are salvaged from them just as with annuals (Munné-Bosch 2008). Some nitrogen is stored in perennating organs instead of being translocated directly to seeds, but it could end up in seeds the next year. Beale and Long (1997) observed that the apparent 'inverse relationship between above-ground and below-ground nutrient contents suggests translocation between the rhizome and canopy, and vice versa.'

Hypothesis 2

Most evidence favors rejection of the first group of hypotheses; therefore, the morphospace for herbaceous perennial grains exists, but it remains unoccupied. The second category of hypotheses has to do with time and chance: High yielding perennial herbs are possible, perhaps even inevitable, but their ancestors were somehow missed by those who carried out the first agricultural revolution.

Hypothesis 2a

Perennials were not domesticated because people did not harvest their seeds.

Many plant species were cultivated extensively in many parts of the globe without ever becoming domesticated (Weiss et al. 2006); then, as some species did achieve domestic status, the nondomesticated cultigens were gradually dropped from the human food inventory. Over the past 20 centuries, hunter-gatherer societies have consistently collected and eaten the seed of many herbaceous perennial plant species. At least 38 perennial grass species have been so utilized (Table 2). Yet *Bromus mango* and *Coix lachryma* were the only perennial grasses that were even partially domesticated by early cultivators; neither became a major crop, and *Coix* was probably treated mostly as an annual. *Oryzopsis hymenoides* has been commercially grown in Montana in recent years, following the discovery of a nonshattering accession (Jones and Nielson 1992; Cox et al. 2002).

Savard et al. (2006) found that just prior to the wave of crop domestication in the northern Fertile Crescent, small-seeded grasses, including perennial species, were an important component of the diet of sedentary hunter-gatherers. Indeed, people were consuming seeds from annual and perennial plants of more than 20 different genera, encompassing not only small- and large-seeded grasses but also legumes, sedges, composites, other forbs, and nut trees.

Humans gathered and ate seeds from both annual and perennial herbs, domesticating only the former. However, had they not experienced an episode of extreme climate change, humans might not have come into the kind of prolonged, intimate contact with annual, grain-bearing herbs that led to the domestication of cereals. Through the history of modern humans, until the warming of the Earth's climate that occurred 11 000 years ago following the last Ice Age, the regions that were to be the sites of crop domestication were covered primarily in perennial vegetation. Whyte (1977) proposed that 'annual species/ecotypes/genotypes which could be regarded as prototypes of the cultivated cereals and grain legumes were absent or insignificant in the vegetation of specific parts of Asia before the end of the Pleistocene.' But that changed when, after the retreat of the ice sheets, summers on the fringes of Asia's 'arid cores' became both very hot and very dry, increasing the fitness of species that propagate primarily through seed. In west and southwest Asia, hunter-gatherers 'began to note the new resource in the form of large-grained annuals.' Species of *Hordeum* and *Triticum* 'would have become established on the bare ground between the perennial species of a climax grassland that had become impoverished by desiccation and overgrazing.' Without this climate-induced change in species

Table 2. Thirty-eight perennial grass species from which seed has been harvested by humans as a source of food, with the geographical region in which they were harvested.

Reference	Region (present-day)	Species
Bohrer (1972)	Poland	<i>Glyceria fluitans</i>
	Mongolia	<i>Elymus giganteus</i> <i>Arundo villosa</i>
Bye (1985)	Southwestern N. America	<i>Festuca octoflora</i> <i>Distichlis palmeri</i>
	Southwestern N. America	<i>Oryzopsis hymenoides</i> † <i>O. miliacea</i> <i>Sporobolus</i> spp. <i>Eragrostis oxylepis</i> <i>Glyceria</i> spp. <i>Poa</i> spp. <i>Elymus canadensis</i> <i>Melica imperfecta</i> <i>Stipa speciosa</i> <i>Muhlenbergia asperifolia</i>
Powers (1875)	California	<i>Bromus carinatus</i>
Chamberlin (1911)	California	<i>B. marginatus</i>
De Wet (1992)	Chile	<i>B. mango</i> ‡
Vaughan et al. (2008)	China	<i>Oryza rufipogon</i> §
Guo et al. (2007)	China	<i>Zizania latifolia</i>
Griffin and Rowlett (1981)	Scandinavia	<i>Leymus arenarius</i>
Weiss et al. (2004)	Israel	<i>Puccinellia distans</i> <i>Alopecurus arundinaceus</i>
		<i>Elymus panormitanus</i> <i>Secale montanum</i>
Bar-Yosef and Kislev (1989)	Israel	<i>Piptatherum holciforme</i> <i>Puccinellia gigantea</i> <i>Hordeum bulbosum</i>
Willcox et al. (2007)	Syria	<i>H. bulbosum</i>
Hillman et al. (2001)	Syria	<i>Stipa</i> spp.
Harlan (1989)	North Africa	<i>Aristida pungens</i> <i>Panicum turgidum</i>
	West Africa	<i>Latipes senegalensis</i> <i>Oryza longistaminata</i> <i>Paspalum scrobiculatum</i>
	India	<i>P. scrobiculatum</i> <i>Coix lachryma</i> ¶
Hillman et al. (1989)	Southwest Asia	<i>S. montanum</i> **
O'Connell et al. (1983)	Australia	<i>Eragrostis eriopoda</i> <i>Panicum decompositum</i>

*Doebley (1984) listed 20 additional perennial grass species that were used as food sources. Only those he classified as 'important' are listed here.

†Has undergone domestication and commercial production in modern times following the discovery of a nonshattering accession (Jones and Nielson 1992).

‡Has undergone domestication.

§Underwent domestication, resulting in cultivated rice, *O. sativa*. Rice's direct ancestor may have been an annual form of *O. rufipogon*.

¶Has undergone domestication.

**Contributed to domestication of rye (*S. cereale*). Rye's direct ancestor may have been an annual form of *S. montanum*.

composition, Whyte asserted, 'people would have had to continue to devote their time to the laborious collection of enough seeds from perennial plants to feed themselves.'

In 13 000-year-old charred remains at the Abu Hureyra archaeological site in present-day Syria, Hillman et al. (1989) consistently found seeds of *S. cereale*'s perennial relative *S. montanum* in mixtures with seeds of wild annual rye (*S. cereale* ssp. *vavilovii*) and *Triticum boeoticum* (wild einkorn). Based on data collected at the site, they concluded that 'all three cereals were harvested from the same wild stands.' Three to four centuries after its establishment, Abu Hureyra, like much of southwest Asia, was suddenly hit with a prolonged cool, dry period coinciding with the Younger Dryas climatic episode. Among charred remains, Hillman et al. (2001) found a rapid decline in formerly abundant wild grass seeds coinciding with the drought. But seeds of wild annual grasses persisted among food remains long after they were no longer able to survive in the wild in the vicinity of Abu Hureyra and after the remaining wild stands had retreated far to the north ahead of the expanding zone of aridity. Furthermore, much larger rye seeds appeared prominently in the remains. Hillman et al. (2001) concluded that with virtually all of their annual and perennial food crops dying out around them, residents had begun cultivating wild annual cereals. Although they were likely to have collected seeds of both annual and perennial wild rye, the annual species would have had a great advantage in the new cultivated environment.

Hypothesis 2b

Perennial seeds were harvested but never planted.

De Wet and Harlan (1975) noted, 'The knowledge of plant propagation and cultivation as a means of increasing population size and yield probably was widely known among hunter-gatherers long before plant domestication.' As people moved from simple gathering to more intensive cultivation, perennial plants re-growing from vegetative structures would have been much more vigorous than seedlings, whether volunteering or intentionally sown; therefore, if there was any cultivation of perennials, it might have entailed weeding, watering, or control of grazing, but probably not re-seeding.

Vegetative propagation of perennials, even if practiced intentionally, would only have maintained fully wild populations unless fortuitous mutants were noticed and consciously propagated. We suggest several reasons this was more unlikely with herbs than with woody plants (or large, tree-like herbs): first, seed traits are more difficult to see in the field with the naked eye than fruit traits; second, the rhizomes of herbs in a field intermingle making it difficult to distinguish between genets and ramets,

whereas tree cuttings or suckers more obviously come from a particular genotype. Finally, a mutant genotype would have to be cloned repeatedly and transplanted in large numbers to have any use as a grain. Return of grain on investment of labor and time would have been low using vegetative propagation of small herbs. In contrast, a large tree bearing large, high-value fruit can regenerate from a single transplanted clone.

Hypothesis 2c

Even if planted, perennial seedlings would not have been noticed.

If there ever were attempts to grow perennial species through yearly sowing, the slow-to-establish, often relatively unproductive first-year perennial plants would not have been at all attractive.

Most of the staple crops were domesticated in biomes with very well-defined seasons differing markedly in rainfall and humidity (Whyte 1977; Gepts 2004). In such regions, the optimum times for initiation of growth and harvest of food plants would have been obvious to human gatherers. For those who eventually decided to sow a portion of their harvested seed, the motive may have been to increase plant density and thereby improve harvested yields (Gepts 2004). Furthermore, intentionally sown crops 'did provide a buffer against environmental uncertainties' (Zeder et al. 2006). Tillage and sowing provided people much more influence over the timing of crop growth and harvest. Sowing annual species in an environment similar to that to which they were adapted provided humans a high degree of control over plant growth even before domestication of the plants could occur. On the other hand, any perennial plants growing wild in the vicinity would not constitute an easily regulated buffer crop. The perennials' growth and development would depend upon immediate environmental conditions and their history of natural selection, not upon a human desire to produce more seed in that year. Seed dormancy and slow seedling growth would have compounded this effect, making it difficult to detect—let alone depend upon—this new growth during a given year.

Hypothesis 3

It is easy to see how perennials could have been harvested for food but simply never replanted, and therefore were never domesticated by natural selection during the first phase of the agricultural revolution. A second opportunity for domestication may have occurred as people in fully agricultural communities experimented with new fruit, forage and fiber crops. Perennials like alfalfa have been deliberately harvested and sowed for several thousand

years. Why did seed size not increase? Genetic exchange with longer-lived wild relatives should have provided an opportunity for altering the life-history of domesticated grains. Were the particular domesticates subjected to selection pressures for increased lifespan or allocation to seed yield simply unable to respond?

Hypothesis 3a

Perennials are predominantly allogamous. Sexual reproduction in out-crossing species can involve conflict between the maternal, paternal and filial genomes. Relatively inflexible developmental pathways in reproductive structures evolved to minimize this conflict.

Reason and experimental evidence supports the idea that self-fertilization avoids conflict among mother plant, pollen parent and offspring (Shaanker et al. 1988), whereas cross-fertilization can precipitate conflicts that ultimately limit seed and fruit set. Although it may be in the best interest of the mother to maximize seed set, offspring of diverse phenotypes can engage in fratricide to improve their own dispersal or increase seed size (Shaanker et al. 1988), often at cost to maternal fitness. Maternal plants may place upper limits on seed size in an effort to suppress genomic conflict, and such limits may ultimately restrict reproductive allocation (Sadras and Denison 2009). Although genomic conflicts may limit reproductive allocation in allogamous plants, evolutionary solutions that allow consistent production of abundant seeds have been observed: many angiosperms have uniovulated ovaries that limit contact between siblings, seed coats of maternal tissue can restrict seed size, and triploid endosperm is genomically biased toward the maternal parent (Shaanker et al. 1988). The existence of allogamous annual crops with high reproductive effort, such as maize and rye, is evidence that outcrossing is not a strict barrier to use as a grain crop.

Hypothesis 3b

The herbs people had begun domesticating had no genetic variation for longevity within their gene-pool making increased longevity impossible even if it had been desirable.

Ancestors of some grain crops harbored genetic variation for life history. *O. rufipogon* (wild rice) is a species with many ecotypes, ranging from ones that propagate almost entirely vegetatively to ones that produce large quantities of seed (Morishima et al. 1984). *O. rufipogon* grew in abundance after the end of the Pleistocene in what is now east-central China and was gathered as a grain source (Fuller 2007; Vaughan et al. 2008). There, as in southwest Asia, rapid climate change favored domestication of more annual forms. The cooling of east Asia's climate that began approximately 8000 years ago greatly reduced populations of *O. rufipogon* in north and

central China. That probably provided people an incentive to practice more intense cultivation, and to save and sow seed in order to maintain stands of what had become an important food staple (Fuller 2007). In doing so, the early farmers most likely would have focused their attention on the more prolific seed-producing plants lying toward the annual end of the species' 'perennial-annual continuum' (Morishima et al. 1984).

Domesticated *Sorghum bicolor* is slightly perennial—like rice, it can be ratooned—but is probably much shorter lived than its wild ancestors. A number of crops are perennials but are almost always grown as annuals (Table 3). The list includes plants grown for grain and other purposes. For annuals descended from perennials or perennials treated as annuals, genetic variation for longevity was present but not utilized so we infer that the annual lifespan was more attractive to farmers.

Hypothesis 3c

Herbaceous perennial cultigens had no genetic variation for increased yield and were unable to respond to the new set of selection pressures associated with the agroecosystem.

This hypothesis lacks empirical support. Most perennial grasses and legumes that have been selected by humans for seed production have responded dramatically. Indeed, the heritability estimates for seed yield are often over 50% (reviewed by Falcinelli 1999). A single cycle of selection for seed yield in perennial grasses has increased yield by 20–47% (Bean 1972), vastly exceeding the rate of progress in annual grain breeding programs. However, perennial forage breeding programs typically place little emphasis on seed yield—modern cultivars often have lower seed yield than older forms (Falcinelli 1999). This

explains the continued low seed yield of perennial forage species.

Hypothesis 4

The fourth group of hypotheses assumes that perennial herbs probably have 'experimented' with increased allocation to sexual reproduction or that short-lived perennials and annuals with gene-flow from perennial relatives have 'experimented' with increased lifespan, but that the forms with intermediate lifespan and reproductive effort never had increased fitness because of tradeoffs. There is a large body of literature on these tradeoffs in natural ecosystems (e.g., Bazzaz et al. 1987). We do not attempt to review this literature because here we are more interested in the tradeoffs that would have been manifested in the early agricultural setting than in a potentially completely different set of tradeoffs associated with herbaceous perennials in genetic equilibrium in natural grasslands and forests. We accept that increased reproductive allocation entails tradeoffs in competitive ability or defense for both annuals and perennials in nonagricultural environments and that these tradeoffs were more severe for perennials. We must still explain why the new agricultural environment eliminated these tradeoffs for many annuals used as grain crops but not for similarly exploited perennials.

Hypothesis 4a

Tradeoff between asexual and sexual reproduction is difficult to eliminate.

Even if frequency of alleles favoring increased reproductive allocation had begun to increase in a perennial grain, ramets bearing somatic mutations that reversed this effect

Table 3. Domesticated perennial species* grown as annual field crops.

Reference	Common names	Part harvested	Species
Bailey†	Beet	Root	<i>Beta vulgaris</i>
	Pigeon pea, red gram	Seed	<i>Cajanus cajan</i>
	Hyacinth bean, lablab	Seed	<i>Dolichos lablab</i>
	Sweet potato	Tuberous roots	<i>Ipomoea Batatas</i>
	Tomato	Fruit	<i>Lycopersicon lycopersicum</i>
	Cassava, manioc, tapioca, yucca	Tuberous root	<i>Manihot esculenta</i>
	Runner bean	Seed	<i>Phaseolus coccineus</i>
	Lima bean	Seed	<i>Phaseolus lunatus</i>
	Castor-bean	Seed	<i>Ricinus communis</i>
	Potato	Tuber	<i>Solanum tuberosum</i>
Ploschuk et al. 2005	Bladderpod	Seed	<i>Lesquerella fendleri</i>
Smartt 1990	Chickling pea, khesari dhal	Seed	<i>Lathyrus sativus</i>
	Goa bean	Seed, roots, fruit	<i>Psophocarpus tetragonolobus</i>

*Includes species with annual or short-lived perennial populations and freezing intolerant perennials.

†Staff of the L.H. Bailey Hortorium, Cornell University, 1976.

by increasing allocation to rhizome growth or plant height could have outcompeted other ramets. Similar competition led to excessively tall cultivars in many annual crops (Donald and Hamblin 1983), but tall annual genotypes still experience selection for seed production, while mutant rhizomes could invade fields despite (or because) of much reduced seed production. Farmers do not allow large perennials grown for their tubers (e.g., potato) or propagated by cutting (e.g., cassava) to self-propagate vegetatively. Tree crops domesticated by the cloning of fortuitous genotypes are susceptible to invasion by shoots from undomesticated rootstocks, but these can be readily pruned.

Hypothesis 4b

Tradeoff between below-ground competition and reproduction.

For the hypothetical Neolithic perennial grain crop, unconscious selection of high-yielding individuals several years after establishment could have increased competition for below-ground resources, indirectly selecting for greater allocation to roots. This would have counteracted selection pressure for increased reproductive effort in the same way that intraspecific competition for height prevented further increases in harvest index of annual crops. In addition, early seedling investment in roots reduces specific leaf area, thereby reducing seedling growth rate (Poorter and Remkes 1990). Reduced seedling growth rate may be only a first-year trade-off, but it would make establishment in weedy conditions more difficult.

Hypothesis 4c

Shifting cultivation exaggerates first-year yield tradeoff.

Frequent habitat disturbance favors sexual over asexual recruitment among wild plants (Silvertown 2008). Likewise, more sexual (annual) grain species or genotypes may have experienced stronger selection for domestication when people began tilling new land year after year to sow harvested seed, perhaps as a part of shifting cultivation to avoid buildup of weeds (Hillman and Davies 1968). Longer-lived (less sexual) plants that may have produced valuable harvests as semi-permanent plantations would have been much more poorly adapted to shifting cultivation because there is often a tradeoff between investment in rhizomes and seeds in the first year. Any move toward full-field tillage and sowing would have made easily established annuals much more attractive. Selection for seed production might often have happened in the first season even when the crop was capable of regrowing in subsequent years. Even if persistence in subsequent years carried no penalty in the first year, the ability to perennate might erode through genetic drift. On the other hand, if first year yield and lifespan are negatively correlated, genetically, selection for yield would rapidly lead toward the annual habit.

Hypothesis 4d

Tradeoff between plasticity and harvestability.

Another key trait of domestication was determinacy of growth and the ‘compaction of seeds in highly visible terminal stalk-branch ‘packages’’ (Zeder et al. 2006). Wild plants often produce smaller and more numerous inflorescences than do crop plants, and both fertilization and seed maturation occur over longer time periods (Harlan et al. 1973). Among wild annuals in southwest Asia, *Avena sativa* (oat) provides lower seed yields because even within a panicle, seeds can differ greatly in degree of maturation (Ladizinsky 1995). During the domestication of wild *Triticum* and *Hordeum*, species in which maturation is compressed into a shorter timespan, oat was left behind. Fuller (2007) shows how, in harvesting nondomesticated plants, people needed to harvest early enough to catch most of the grains before they shattered but late enough that they did not take too many unripe grains. If human societies developed regular harvesting and sowing routines that were consistent year to year, selection for greater synchrony of maturation would result (Fuller 2007). When humans became dispersal agents for the plants they cultivated, the resulting selection pressure in those plant populations came to favor traits that increased a plant’s ability to disperse seed. According to Rindos (1984), ‘Many domesticated plants, notably the grain crops, have used aggregation of propagules into larger units as their prime means of ensuring quality dispersals... they have sacrificed the greater part of the propagule population for attraction and rely only on a small portion of the crop for reproduction.’ So even unconscious selection tended to reduce the numbers and increase the size of inflorescences, a development that would have been compatible with narrowing the maturation window.

As with other traits, selection for inflorescence size and synchrony of maturation proceeded more quickly in annuals than it would have in perennials. The rate of selection for harvestability in perennials would have been retarded by a negative correlation between degree of perenniality and synchrony of maturation that is expected because strongly perennial herbs have a long growing season and large energy reserves enabling many to flower early in the season and continue until killed by frost or drought. Furthermore, winter survival may be related to general stem indeterminacy: the odds of at least one meristem surviving increase with greater rhizome number and depth in soil (related to rhizome length). In The Land Institute’s current breeding programs to develop perennial sunflower and sorghum from annual \times perennial crosses, perennial progenies tend to have a more indeterminate growth pattern; when some inflorescences on a plant have reached harvest maturity, others may just be undergoing anthesis.

Hypothesis 4e

Tradeoff between maintenance of sexual reproduction and vegetative vigor.

Is it coincidental that many of the most productive cultigens, e.g., *Miscanthus*, *Musa*, *Saccharum*, are polyploids with reduced sexual fertility? Cultigens like apple with high reproductive allocation have been propagated asexually since early in the domestication process. Though sexually fertile, selection has altered maternal tissues (fruit) rather than seeds. Is there a cost to sexuality beyond reproductive allocation? Silvertown (2008) noted, 'Sexual reproduction can take place only in circumstances where vegetative growth is possible. However this dependence is not symmetrical.' Thus, domestication for sexual seed production requires simultaneous selection on many more traits than selection for vegetative traits alone. Quantitative genetics (see Falconer and Mackay 1996) predicts that adding a trait to a selection index reduces the selection intensity on each trait (unless the new trait has a genetic correlation of 1 with an existing trait in the index). We suggest that this partitioning of selection intensity is a kind of trade-off with consequences for the rate of domestication.

Diplontic selection, in which cell lineages with greater vigor outcompete slower growing lineages within or between meristems on the same plant (Klekowski 2003), provides a mechanism for the elimination of dominant, deleterious somatic mutations and the fixation of novel beneficial mutations in clonally propagated cultigens (McKey et al. 2010). Diplontic selection may rapidly and efficiently improve the yield and even productivity of clonal cultigens, but the gains are reversed by episodes of sexual reproduction, which break up favorable genetic associations. However, without some sexual cycles, there is no opportunity for selection that improves seed production; therefore, mutations deleterious only for sex are predicted to accumulate (Klekowski 2003). The evolution of perennial grains would have required simultaneous selection for both vegetative and sexual vigor and deliberate selection during alternating cycles of asexual and sexual reproduction to prevent invasion of the population by higher-yielding sexual annuals or asexual perennials.

Hypothesis 5

Finally, even if perennial herbs had not experienced more tradeoffs than annuals in early agroenvironments, could annuals and clonally propagated trees have simply adapted to the novel environment faster than perennials, thereby pre-empting them? Similarly, domesticates from the primary centers of domestication preempted the domestication of new annual crops in neighboring

regions, as hunters and gatherers switched directly to agriculture using the imported crops or were overrun by farmer immigrants bringing their native crops with them (Diamond 2002). Secondary domesticates, which became crops after agricultural systems based on the primary domesticates were already widespread, also were annuals or trees, not only for the same reasons that primary domesticates were annual but also because people had by that time come to associate grain with annual plants and fruit with trees or woody shrubs. Why would perennials herbs have evolved more slowly?

Hypothesis 5a

There are more annual species and they evolve faster in the wild.

Crepet and Niklas (2009) state that many of the species-rich plant families are dominated by annual species and suggest that annuals evolve faster because of their lower generation time and their smaller, more isolated populations. Molecular evolution rates were higher in annual than in perennial mallow species (Andreasen and Baldwin 2001).

Hypothesis 5b

Perennials do not need to go through a sexual generation each year.

Many perennial herbs do produce seed the first year, but if stands can be harvested for several years before replanting, the rate of evolution would certainly be slower than for annuals, which must be grown from seed every season. As De Wet and Harlan (1975) and many others have emphasized, only one type of propagation—sowing of harvested seed—could lead to domestication of grains. Sowing increased the frequencies of alleles conferring seed retention and reduced dormancy.

Hypothesis 5c

Annual tillage increases the rate of domestication.

Tillage, presumably practiced to clear wild vegetation and prepare a seedbed, also increased nitrogen mineralization. Seed production in wild perennials and annuals is often limited by nitrogen availability. Annual tillage decreases the environmental variation between plants by providing more uniform fertility. Phenotypic variation for seed production is increased because of higher fertility. Response to selection is expected to be greater under conditions of reduced environmental and increased phenotypic variance (Falconer and Mackay 1996).

Hypothesis 5d

Whereas the density of meristems of annuals can be managed by seed placement and light hand tillage and of tree

crops by pruning, the below-ground meristems of herbaceous perennials would have been almost impossible to manage with stone-age technology.

Beyond an optimal plant density, seed yield per unit area declines in older cultivars of maize, and yield and seed size decline in the domestic sunflower. Reproduction is affected similarly in the rhizomatous perennial *Tussilago farfara* (reviewed by Harper 1977). If asexually spreading perennials were allowed to persist for more than 5 years, it seems likely that crowding would have reduced many yield components below their genetic potential. Self-thinning and size hierarchies develop with time (de Kroon and Hara 1992) causing genotypes to experience different levels of competition from neighbors. Automatic selection for increased yield would have been very inefficient under these conditions. As stands aged, stone-age tools—adequate for slash-and-burn agriculture—would not have been able to rejuvenate sod-forming perennial crops through plowing and replanting.

Hypothesis 5e

Genetic load and self-incompatibility in perennials makes improved, true-breeding cultivars almost impossible to obtain.

The seed production potential of plants has often been studied in relation to three connected characteristics: life-span, self-incompatibility, and genetic load (the presence of deleterious recessive alleles in a population). These three characteristics of plant populations are likely to be inextricably linked in complex ways. But for our consideration here, the causative relationship between these three characteristics and a fourth—ability to set abundant seed—is of primary importance. We consider this in greater depth below.

Hypothesis 5f

Wild annuals had a head-start, having larger seeds and higher yields than did wild perennials.

The array of annual herbaceous species that came to be domesticated was not determined solely on the basis of traits like seed size and yield that today's plant breeders evaluate in practicing selection. An annual growth habit does not guarantee that a plant will have large, attractive, easily accessible seed. Larger, longer-lived plants have larger seeds, on average (Baker 1972), and growth form explains more of the variation for seed mass than dispersal syndrome (Moles et al. 2005). However, dramatically large-seeded outlier species with relatively high grain yields per unit area were prominent among the annual grasses that were domesticated (Blumler 1998). Perennial species did not offer the efficient harvests of large, easily threshed seeds provided by stands of wild annual *Triticum* and *Hordeum* species. But neither did wild annual *Sorghum*,

Pennisetum, or *Helianthus*, which had small seeds and low yields yet gave rise to domesticates (Cox et al. 2006).

Hypothesis 5g

The head-start given to these outlier annuals with large seeds began even before cycles of planting and harvesting.

Once people discovered the positive impact of tillage on productivity, annual species' exclusive place in agriculture was ensured. The sorting among species that occurred with cultivation overlapped with and was followed by the intraspecific selection that led to domestication, and such selection within species reinforced the results of the sorting. It is possible that even spontaneously self-seeding populations under cultivation experienced some gene-frequency shifts at loci other than those controlling shattering (Fuller 2007; Brown et al. 2009). Purugganan and Fuller (2009) argue that in some, but not all, cereals under cultivation, selection for larger seed preceded selection for seed retention. With or without sowing by humans, seed size of wild annual species increased through generations of cultivation, they wrote, because 'larger seeds are... likely to be selected in open environments, where bigger seedlings are advantageous given the deeper burial in soils disturbed by human tillage.'

Hypothesis 5h

The reproductive systems of selfing annual and vegetatively propagated cultigens preserved rare selected gene combinations.

Self-fertilization and clonal propagation are both reproductive systems that have been characterized as evolutionary dead ends because of the potential for genetic degradation through accumulation of deleterious mutations and the loss of adaptive potential through reduced genetic variation (Klekowski 2003; Takebayashi and Morrell 2003). However, in the short-term, these forms of reproduction allow rapid response to directional selection because of their ability to preserve genetic associations that have been generated by recent selection (Haag and Roze 2007). As noted above, most perennials are allogamous and when they are propagated by seed, as would be essential for establishing grain fields, segregation and/or recombination load would reduce the average fitness of progeny of individuals selected during domestication.

The rapid domestication of the three cross-pollinated grains, rye, maize and pearl-millet, appears to contradict this hypothesis. However, whereas many perennial herbs are strongly self-incompatible, these annuals are really mixed-mating populations. Mixed-mating, the annual life-form, and small geographic distributions (characteristic of annuals populations, see 5a, above) are predictors

of high rates of population differentiation and low intra-population genetic diversity. In contrast, populations with greater longevity, wider geographic distribution and outcrossing are expected to have greater genetic diversity but less population differentiation (Hamrick and Godt 1997).

A synthesis

We suggest that the simplest explanation for the absence of perennial herbs with high reproductive effort is that, while biophysically possible, this lifeform could not have evolved by natural selection. We summarize this position below and go on to suggest the reasons that perennial grains could be developed using artificial selection in the next section.

Evidence does not support the proposition (our Hypothesis 1) that the combination of herbaceous growth, multi-year lifespan, and high seed yield in one plant species is impossible or that increased plant allocation to one function (e.g., longevity) will necessarily require a reduction in another (e.g., seeds). Sadras and Denison (2009) argue that the metaphor of conflict between plant parts (cells, vegetative versus reproductive organs, modules, ramets) is an 'incomplete argument' because it neglects the increased fitness that can be gained when intra-plant competition is restricted. They write, 'Competition by the definition above may occur, in the sense that a given carbon or nitrogen atom cannot be in the stem and reproductive structures at once. But this is managed competition whose outcome is shaped by developmental processes that enhance overall plant fitness.' (Sadras and Denison 2009).

We found many reasons why overall individual plant fitness would be reduced by increased expression of perennial tendencies (our Hypothesis 4) under Neolithic field-crop conditions. These conditions include propagation by seed, frequent replanting of grain fields (shifting agriculture or migration) and tillage as the primary method for managing weed and nitrogen fertility. The weakly perennial nature of several relatively productive seed or fruit crops (Table 3) suggests that selection against longevity has been weak. The fact that these species are almost always grown as annuals reflects the utility of annual cultivation and replanting in traditional cropping systems and supports our fifth group of hypotheses: that domestication of annuals (or plants treated as annuals) under natural selection would have been faster than—and probably pre-empted—the domestication of perennials. The domestication of perennial plants now grown as annuals shows that—at least in these cases, and probably more generally—perennial species have enough genetic and developmental plasticity for domestication and large shifts in net allocation to harvestable structures.

Perennials still grown as perennials also responded to natural selection for domestication and dramatically increased reproductive allocation (Table 1). However, none of these plants is propagated from seed. The perennial herbs sugarcane and banana are highly domesticated and highly productive, but also very large plants that can be efficiently propagated asexually. It appears that life-form *per se* was not the barrier to the evolution of perennial grains. Rather, it is the specific combination of method of propagation and lifespan.

The population ecology of many wild perennials reduces their ability to respond quickly to directional selection, a process that requires a population to quickly shed genetic diversity. Wild perennials excel at generating genetic diversity: somatic mutation generates heterozygosity in long-lived individuals (Morgan 2001) and allogamic recombination 'destroys the associations built by, and favored by, selection' (Agrawal 2006) yet inefficiently purges deleterious recessive alleles (Morgan 2001). Moreover, wild perennials are often ecologically dominant and therefore seldom found in small, isolated populations like annuals (Crepet and Niklas 2009). This is relevant because almost all contemporary examples of rapid evolution have involved colonization events: the occupation of new environment by a small, at least partially reproductively isolated population, followed by rapid population growth through sexual reproduction (Reznick and Ghalambor 2001).

As humans created new agricultural environments, perennial plants would have been slower to colonize than annuals, would have remained reproductively connected with the surrounding wild populations, and could have increased in population size by asexual reproduction. In this scenario, and perhaps in general, perennial plants are poor candidates for rapid natural selection except through clonal propagation.

Long-lived plants with high fertility are extremely rare and must be propagated clonally

Plant breeders working with perennial forage grasses face the challenge of increasing seed yield so that seed can be produced at reasonable cost. These breeders have long recognized improved seed-set as the single most important factor for increasing seed yield. In *Lolium perenne* (perennial ryegrass), for instance, only 10–65% of florets set seed, with production fields tending toward the lower end of the range (Hebblethwaite and Ivins 1977). If full seed set could be obtained and harvested, the yields of perennial forage grasses could potentially exceed those of annual small grains (Falcinelli 1999). If genetic load (perhaps in association with outcrossing) is at the heart of the low-seed-set problem in perennial crops, there is hope

for a mechanism to vastly increase seed yield: purging of the genetic load. We will now explore several lines of evidence that point to genetic load and self-incompatibility as being at the heart of low seed set in perennials herbs.

Genetic load can be purged

Past success in purging genetic load through inbreeding has helped to demonstrate the role that genetic load can play in limiting fitness and sexual reproduction. In a review of purging, Crnokrak and Barrett (2002) demonstrated that inbred populations can show substantial levels of purging. Evidence of purging is also strong in domestic species such as maize, in which inbreeding with selection has produced inbred lines with greater seed production than was obtained by open-pollinated landraces (Crow 1998).

Highly heterozygous perennials can have high reproductive allocation

Trees typically have about 5% reproductive allocation (Bazzaz et al. 2000). However, early domesticators of woody plants quickly learned how to preserve maximum heterozygosity through cloning, which ‘covers’ the negative effects of recessive genetic load. Indeed, the sexually-derived offspring of clonally propagated crops are generally worthless for food production because of exposed genetic load (Zohary and Spiegel-Roy 1975).

Heterosis is high in outcrossing annual grains

Because of the genetic load that builds up in cross-pollinated species, heterosis is much larger in outcrossing than in selfing crops (more than 200% in maize, compared to about 10% in wheat) (Gallais 1988).

Polyploidy only reduces genetic load temporarily

Polyploidy has been suggested as a means for species to fix heterozygosity and reduce the effects of load. However, Otto (2007) has demonstrated that by having a larger numbers of copies of each gene, the mutational rate will increase and at equilibrium polyploids will suffer greater harm from recurrent deleterious mutations than will diploids. Therefore, many perennials may have experienced a reduction in genetic load immediately after polyploid formation, but subsequently suffered from increased genetic load.

Large perennial species have higher inbreeding depression

Scofield and Schultz (2006) found that large plants have a higher inbreeding depression than smaller plants, which is probably explained by a higher mutation rate per generation. Klekowski (1988b) states that genetic load is because of mutations accumulating in the apical initials during growth, and ‘is a function of the postzygotic accumula-

tion of mutations as well as mutations inherited from previous generations.’

Clonal spread is associated with self-incompatibility

The relationship between genetic load and plant size has been most easily studied in relation to height, but rhizome spread would also allow for the accumulation of mutations in apical initials during clonal spread. If deleterious mutations are accumulating during rhizome spread, we would expect greater self-incompatibility in rhizomatous species as a means to maximize heterozygosity. Indeed, numerous authors have reported a strong association between clonal spread and self-incompatibility (Stebbins 1957; Jonsson et al. 1996; Clements et al. 2004).

Older plants have less sexual fitness than young plants

If genetic load increases because of mutations during mitotic cell divisions, very old plants should have accumulated more recessive alleles that will be lethal to young developing embryos. Sexual fitness was observed to decline with increasing clone age of *Populus tremuloides* (Ally, 2008). Although the lifespan of a clonal plant is unlimited, its ability to reproduce sexually is not (Klekowski 1997).

Low seed set in long-lived plants has a genetic cause

Longer-lived, primarily outcrossing species have been observed to have lower seed/ovule ratios, which is most often and most easily explained by genetic load (Lamont and Wiens 2003; Meney et al. 1997; Wiens et al. 1987; Wiens, 1984; Marshall and Ludlam 1989). Other reasons such as pollen limitation, resource limitation, or maternal sanctioning exist, but none approaches the overriding influence of genetic load.

Genetic load in out-crossers impacts seed set more than it does other traits

Klekowski (1988a) states that mutational load in long-lived plants is expected to result in ‘reproductive cycles that enhance the loss of defective gametophytes, gametes and offspring’ because purging of load will be most efficient if it occurs via elimination of zygotes and young seeds. Furthermore, the ‘selective sieve’ (Morgan 2001) that is present during mitotic cell divisions will preferentially allow recessive alleles with large effect on zygotes or seeds to pass on while eliminating deleterious dominant mutations with effect on mature cell lines. Experimental support for these ideas has been found in evidence that a species with greater asexual reproduction had more genetic load with embryonic effects (Klekowski 1988a) and in the observation of more early-acting inbreeding depression in outcrossing than in selfing species (Husband and Schemske 1996).

Recessive mutations that severely limit seed yield are present in perennials

If outcrossing perennials suffer from low seed set because of recessive alleles, genetic studies should be able to identify the presence of these alleles. Infertility in *Decodon verticillatus* has been linked to a single mutation of strong effect (Eckert et al. 1999). In *Lolium perenne*, molecular markers have been used to identify two genomic regions with major influence on seed set, and one was identified as a recessive mutation that causes nearly complete sterility (Armstead et al. 2008).

Some plant populations may go extinct because of load

Plants that have completely lost the ability to reproduce sexually have been identified within a population of *Vaccinium corymbosum* with low mean sexual fertility (Krebs and Hancock 1991). Another shrub has a seed set of only 2.5%, despite high levels of heterozygosity (Wiens et al. 1989). These populations lack a means of asexual reproduction, and may go extinct because of sterility-inducing mutations.

Expression of genetic load is influenced by environment

Seed set in perennial grasses can be strongly impacted by environment (Falcinelli 1999). If seed abortion because of genetic load is only caused by genotype alone, then a strong environmental influence on abortion would rule out genetic load as an explanation for seed abortion. Helgenurm and Schaal (1996) found that in one species *Lupinus texensis* genetic load appeared to be due in part to deleterious genes that become lethal only in stressful environments. If this phenomenon is widespread, then genetic load may be at the root of the seed abortion that often occurs in stressful environments.

Reducing genetic load should increase seed set without sacrificing vegetative growth

If genetic load reduces over-all vigor along with seed set, its elimination represents an opportunity to increase seed production without sacrificing vegetative growth. Supporting this prediction, seed set of forage species has often been increased through selection with no reduction in forage yield (Falcinelli 1999).

Prospects for filling the gap in morphospace using artificial selection

We proposed (section III, above) that herbaceous perennial grains could not have evolved by natural selection under the agricultural conditions of early and traditional agriculture. Increased lifespan would not have increased fitness under these conditions, but we argue below that contemporary agriculture is a fundamentally different

environment. Even in the new agroenvironment, a domestic perennial grain would not be evolutionarily stable. We suggest that on-going, artificial selection lowering individual fitness through several tradeoffs is required to achieve and maintain an agriculturally useful combination of traits. We also suggest ways that artificial selection can overcome the problem of genetic load that we have argued is more serious for perennials than for annuals. Finally, we mention lineages that may have the genetic potential to fill this morphospace given the appropriate artificial selection.

The modern agroenvironment

Land tenure

Farmers practicing shifting cultivation and frequent migration, which may have been very common when human population density was low, would have had little interest in permanent crops. Today, continuous cropping is more common and farmers are quite familiar with establishing perennial crops for hay and, increasingly, for fuel.

Nitrogen fertility

Tillage was probably the easiest and most reliable way to make nitrogen available through increased nitrogen mineralization. Today, fertilizers can be applied to the soil or to the foliage in the absence of tillage. Annual grains are increasingly produced each year without tillage.

Traction

Plowing perennial sod requires great force and would have been avoided by early farmers, especially prior to the domestication of draft animals. Mechanical tractors and steel implements now make it relatively easy to break sod, an activity that would be required for replanting perennial grain crops. Heavy equipment and steel implements also make it possible to trim roots, thereby stimulating root turnover; to slice through rhizomes and crowns, releasing apical dominance in underground stems; and to cultivate the surface in strips as a means of controlling shoot density.

Weed control

The slow first-year growth that may be an inevitable tradeoff for some perennials makes them very susceptible to weed competition in the first year. In Neolithic fields, it would have been very difficult to find and pull weeds from among tiny seedlings following broadcast-sowing. Today, herbicides combined with no-till seed drilling equipment are widely used for prairie restoration and establishing perennial forage crops. It is not difficult, in our experience, to establish perennial grasses and forbs from seed without herbicides by planting the seed in precisely spaced rows and cultivating between the rows with

equipment designed for that row spacing. Mechanical mowers can be adjusted to remove weed material just above the height of the young crop seedlings with minimal damage to the seedlings.

Tradeoffs as opportunities

Many of the yield gains made by plant breeding have been traded for by sacrificing adaptation to irrelevant environments (Denison 2009). Our domesticated crops can no longer compete with wild plants in natural ecosystems. We reduce competition among individuals within the stand, thereby favoring genotypes that contribute to increased collective yield. In addition to obvious trades that are made by seed-propagated domesticates (reduced seed dispersal, reduced seed dormancy) and the well-known reductions in individual competitive ability made in recent times (reduced stem height, reduced phenotypic plasticity, increased determinacy) (Donald and Hamblin 1983), perennial grain candidates may have other traits that can be modified to increase yield.

Root mass

Although the massive root systems of perennial grasses may provide valuable ecosystem services (Glover et al. 2010), they are probably the result of a below-ground arms-race (Gersani et al. 2001; Craine 2006). Some reductions in allocation to root production may be acceptable without undermining soil-holding potential. This remains to be determined empirically.

Asexual reproduction

Many herbaceous perennials invest heavily in asexual reproduction in the form of spreading rhizomes, tubers or stolons. Other perennials increase in bunch size and stalk density each year. Neither strategy is helpful for an agricultural situation where constant plant density is desirable. Dramatic reduction in allocation to this kind of asexual spreading is both acceptable and desirable.

Extreme longevity

Some wild perennial plants are capable of surviving extreme droughts and living for hundreds, perhaps thousands of years. If this longevity requires large energy reserves, as seems likely, breeders will tend to select for increased allocation to seed production even if it results in reducing lifespan to the range of decades rather than centuries (see DeHaan et al. 2005).

Modern plant breeding strategies for purging load

Genetic load appears to severely limit seed yield potential of perennial outcrossing species. Recognition of this

factor points to several strategies for developing perennial grain crops. The first and most obvious approach is to domesticate those perennial species that are already self-pollinating. Although perennial species tend to be self-incompatible, selfing perennials do exist, and they should be considered as primary candidates for domestication.

If a promising selfing species is not available for domestication as a perennial grain crop, the next choice would be a species that has low genetic load even though it primarily outcrosses. Low genetic load may exist in some outcrossing species if they have recently passed through narrow genetic bottlenecks that have purged the most deleterious recessive alleles. This is presumed to be the cause of low genetic load in the domestic species of *Cucurbita* (Rick 1988).

Most modern crop plants are capable of self-pollination, even though they are generally believed to have had self-incompatible ancestors (Rick 1988). New selfing crops could possibly be developed from wild outcrossing species, but we expect that the process of inbreeding and purging genetic load would be lengthy.

A more rapid method of purging genetic load would be to develop numerous inbred lines by selfing with selection. Then the purged lines could be recombined in order to restore the benefits of heterozygosity. This approach has been used effectively in *Medicago sativa* to increase forage yield potential (Kimbeng and Bingham 1999). One concern is that the self incompatibility system not be degraded during the generations of selfing, or it will be difficult to obtain a final heterozygous population through outcrossing, because of the loss of self-incompatibility.

An extreme approach to dealing with genetic load through maximum heterozygosity is to develop F₁ hybrid varieties. This strategy will face numerous technical difficulties, but it has been achieved in several self-incompatible species, including *S. cereale* (Geiger and Miedaner 2009) and *M. sativa* (Robins et al. 2007).

In many self-incompatible species, inbreeding may prove to be impossible. For these cases, schemes have been devised that will allow breeders to capture the benefit of heterosis by producing semihybrids between diverse populations (Brummer 1999). Molecular markers could be of particular use in determining populations to combine for maximum heterotic effect.

Another approach would be to repeatedly select strictly for high seed/ovule ratios for many generations. If genetic load has accumulated because of few sexual cycles relative to mitotic divisions and if load is particularly detrimental at the stage of seed production in perennials (as was mentioned earlier), then strong selection for seed set could purge deleterious recessive alleles. Indeed, selection

for seed fertility has been shown to increase seed yield dramatically in perennial crops, sometimes producing a beneficial correlated response in other traits (Bean 1972; Knowles 1977; Wu et al. 2006).

Somatic embryos from tissue culture could perhaps be used to produce artificial seeds of cross-pollinated crops (McKersie and Brown 2008). If this technology becomes viable for use on a commercial scale, artificial seeds could be used to propagate genetically uniform plants in seed production fields and obtain varieties with reduced inbreeding depression.

A new generation of high-throughput molecular marker technologies may open opportunities to make rapid gains in purging deleterious alleles from populations of self-incompatible plants. Using traditional breeding approaches, determining which plants carry deleterious recessives in the heterozygous state can require many years, particularly in perennial plants. However, an effective high-throughput marker system could potentially allow the screening of thousands of seedlings so that many deleterious recessive alleles could be rapidly purged from a population.

Perennial grain candidates

Many annual grains have perennial species within their secondary or tertiary gene pools. Wide hybridization can bring together genes for domestication traits and the perennial life history. Initial interspecific populations have been made for rice, wheat, rye, sorghum and sunflowers (reviewed by Cox et al. 2002, 2006). The prospects for developing perennial rice appear particularly good. A perennial form of rice could mitigate pressing soil loss problems in uplands where rice is grown without terracing (Sacks et al., 2003). This work was begun at the International Rice Research Institute and is being continued at the Yunnan Academy of Agricultural Sciences (Fengyi Hu, personal communication). Wild perennial herbs that are being domesticated using genetic variation already existing in their primary gene pools include *Desmanthus illinoensis* (Michaux) MacMillan (Graham and Vance 2003) and *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey (Wagoner and Schauer 1990). Germplasm collections of grains grown as annuals but botanically (or originally) perennials (Table 3) could be screened for accessions that maintain high yields when allowed to regrow from crowns or rhizomes. Interestingly, perennial varieties of pigeonpea (*Cajanus cajan* (L.) Millspaugh), are being used for erosion control and reclamation of degraded cropland in southern China but it is not clear if this grain legume, which is an important food crop in India, is being used for food in China (Saxena 2008).

Conclusions

We have identified many possible reasons that natural selection of perennial herbs with high reproductive effort did not occur in the early agro-environment. The least likely of these reasons is that this combination of life-form and reproductive effort is not possible in any environment or evolutionary trajectory. The existence and productivity of life-forms larger, slower-growing and longer-lived than perennial herbs suggests otherwise. Some of these tree-like plants have attained the highest reproductive allocations ever reported (Table 1). The explanation we consider most likely is that long lifespan is associated with reduced seed fertility. Longevity is adaptive in competitive environments (*sensu* Grime 1977) but lethal recessive mutations accrue in perennial lineages because in the plant life-cycle, a large number of mitotic cell divisions occur between meiotic ones, and mutations accumulate from cycle to cycle. We believe that it is not coincidental that among domesticated perennial herbs that have extremely high productivity and allocate a high proportion of their net assimilation to nutritious storage compounds often associated with reproduction, e.g. *Saccharum*, *Musa*, and *Solanum*, none are grown for seed harvest. The few perennial species grown for their seeds (Table 3) are treated as annuals and may be in the process of becoming annual.

Fruiting trees and palms, often with good seed fertility, were domesticated by natural selection because they are propagated by clones rather than by seeds. Rare genotypes with exceptional fertility and fruit traits could be perpetuated in this way. Because they are highly heterozygous out-crossers, the domestic phenotype would be immediately lost if they were being propagated from seed. However, artificial selection, which allows selection of genotypes with reduced individual fitness, could be used to domesticate perennial seed crops. Tolerating reduced individual fitness allows two kinds of gains not available through natural selection: 1. purging of genetic load through inbreeding, which temporarily reduces plant vigor; 2. reducing inter-plant competition, which can increase crop yield per unit area.

In a paper on the productivity of plant communities, Westlake (1963) wrote: 'Agriculture based on plants grown from seed to harvest in 1 year is less productive than agriculture using perennial plants, even though the growing season productivity of the annual plants may be considerably higher.... Adaptation of agricultural techniques to increase the proportion of the year with the ground completely covered by leaves is probably the most rewarding change that could be made to increase the world's food supplies' Adding herbaceous grain type

crops to the inventory of existing, mostly tree-like, perennial food crops would give farmers additional options for balancing humanity's demand for both nutritional and ecological services. We predict that artificial selection will open previously inaccessible regions of plant morphospace to agriculture and will reveal that some promising taxa were under-sampled. The grass family, for example, has given us our most valuable grain crops, but 70% of the 8000 grass species are rhizomatous perennials (Crepet and Niklas 2009) and were almost certainly overlooked in the early rounds of domestication which relied on natural selection.

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