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OPINION & POLICY

# A Pipeline Strategy for Grain Crop Domestication

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## ABSTRACT

In the interest of diversifying the global food system, improving human nutrition, and making agriculture more sustainable, there have been many proposals to domesticate wild plants or complete the domestication of semidomesticated orphan crops. However, very few new crops have recently been fully domesticated. Many wild plants have traits limiting their production or consumption that could be costly and slow to change. Others may have fortuitous preadaptations that make them easier to develop or feasible as high-value, albeit low-yielding, crops. To increase success in contemporary domestication of new crops, we propose a pipeline approach, with attrition expected as species advance through the pipeline. We list criteria for ranking domestication candidates to help enrich the starting pool with more preadapted, promising species. We also discuss strategies for prioritizing initial research efforts once the candidates have been selected: developing higher value products and services from the crop, increasing yield potential, and focusing on overcoming undesirable traits. Finally, we present new-crop case studies that demonstrate that wild species' limitations and potential (in agronomic culture, shattering, seed size, harvest, cleaning, hybridization, etc.) are often only revealed during the early phases of domestication. When nearly insurmountable barriers were reached in some species, they have been (at least temporarily) eliminated from the pipeline. Conversely, a few species have moved quickly through the pipeline as hurdles, such as low seed weight or low seed number per head, were rapidly overcome, leading to increased confidence, farmer collaboration, and program expansion.

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New crops could provide a wide array of benefits to farmers, consumers, and the environment (Bates, 1985; Janick et al., 1996). New grains with novel life histories (perennial or winter annual) could have particularly high potential impact given the large economic and environmental footprint of current grain crops

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and the potential to remedy environmental challenges in agriculture with perennial crops (Brummer et al., 2011; Cox et al., 2006, 2010; Glover et al., 2010). New perennial crops for forage or biofuel could provide environmental benefits, but here we restrict our consideration to grain crops capable of providing food directly to humans.

Although much has been written about the need for new crops—and many new crops have been proposed—we are unaware of a comprehensive strategy for domesticating new crops published in the last 30 yr. Here, we will briefly review some of the older and most relevant literature. Jain (1983) laid out systematic approaches for domesticating and breeding new crops, and the article provides an excellent review of domestication work and thinking in the 1970s. More recent publications on new domestications have focused on tree crops or energy crops (e.g., Jaenicke et al., 1995; Leakey, 2007; Sang, 2011). New domestication has also been addressed in a theoretical context (Diamond, 2002). Strategy for new crop development has been approached from a policy perspective to obtain sustained support for the work (Jolliff, 1989; Knowles, 1960). Some practical efforts have sought to identify candidates for domestication by determining mean values of important traits from a large number of species (e.g., Earle and Jones, 1962; Wagoner, 1990). Others have reviewed ongoing work with a range of potential species (McKell, 1983). However, no effort has been made to develop a strategy based on experiences gained in the past decade of work on new grain crop domestication (e.g., Cox et al., 2006, 2010; Glover et al., 2010).

The reflective plant breeding paradigm (Runck et al., 2014) has been developed as a robust and potentially effective approach to developing new crops. This approach closely couples germplasm development with coordinated commercialization and involves interactions among scientists, government, farmers, and other stakeholders to consider not only the economic viability of a potential new crop but also its social and environmental impacts. This approach, developed in the context of an existing research and development program, only identifies a strategy to move a single crop from domestication through to commercialization. The paradigm does not provide specific criteria for evaluating potential species to domesticate outside of the stakeholder engagement process or existing breeding programs nor does it provide a strategy for prioritizing specific species in the context of limited budgets. Ultimately, the reflective plant breeding paradigm provides a useful idealized model but lacks the pragmatism required within a real breeding program where certain candidates for domestication will be abandoned as the research and development process progresses. Here, we explicitly define the stages and targets that domestication projects will need to go through to achieve successes.

In the past 30 yr, many species representing a wide array of plant growth forms and taxa have been described as candidates for domestication (Janick et al., 1996). Additionally, the list of domesticated crops has been revised to include many more species (Meyer et al., 2012; Fuller et al., 2010; Smith, 2006; Smith and Yarnell, 2009). Yet few species have become viable modern crops despite initial agronomic trials and germplasm evaluation and, often, no publication record exists to document the work that was done. Rather than viewing these efforts as failures, we suggest that they were inevitable because the domestication pipeline resembles the pharmaceutical one; the odds of any given candidate having all the qualities required for full commercialization are low. To obtain a single successful drug (or new crop), many candidates must be screened and rescreened, resulting in rejections at each stage of development (Payne et al., 2007). Knowing that there will be surprises and setbacks along the way, domesticators of new grain crops could increase their chance of success and the rate of new crop development by designing and following a logical set of evaluation and development steps as they begin and execute each domestication program. In retrospect, aspects of the domestication pipeline have been used in our domestication efforts over the past decade, but the model we are proposing here has yet to be fully implemented.

The pipeline model of domestication that we propose begins by defining an agricultural target to be met with a type of crop that does not yet exist. In the same way, drug development begins by defining a particular pathogen, symptom, or disease for which current treatments are inadequate. A research pipeline for delivering at least one crop that addresses the target is then conceptualized, and finally, large numbers of wild plant species are screened and several candidates are fed into the pipeline with the expectation that not all will pass through to become successful crops. Agricultural targets could include seasons where soil is left fallow in standard crop rotations (see the pennycress case study, below), food with enhanced nutrition, food security in drought-prone environments, N fixation in difficult soils and climates (see the lupin case study, below), and soil conservation and restoration (see the perennial grain examples, below). Additional considerations, including production scale (e.g., subsistence vs. commodity), technology (e.g., mechanization, irrigation, genetic engineering), end use (e.g., cereal, oil, animal feed or forage), and broad soil or climatic targets, will further narrow the breeding requirements thereby increasing the rate of progress through the pipeline. Once domesticated, a crop can then be bred for adaptation to different environments.

In contrast to the pipeline model, a species-centric approach attempts to find a purpose for a preidentified, promising, favorite, or popular plant instead of finding a plant to meet a predefined purpose. One danger with this method is that the best niche for a particular wild or semidomesticated plant may be already saturated. New crops (new in the sense that farmers in a region do not

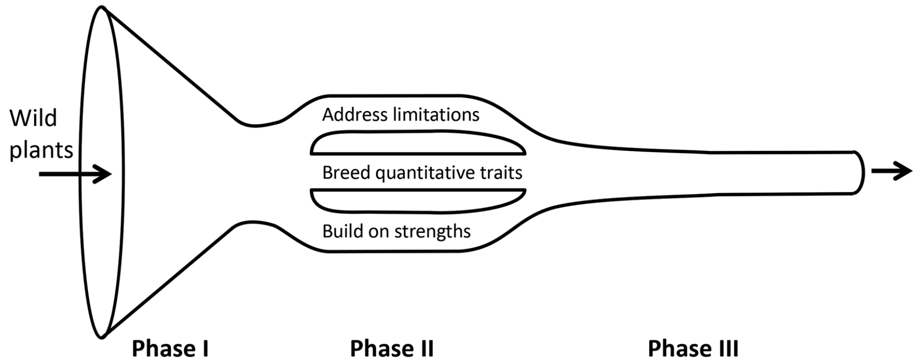


Fig. 1. Domestication pipeline. Vertical width of the narrowing pipeline depicts the relative number of species contained within. Phase I: Screening of many plant species to discover candidates. Screening may require several cycles of selection to evaluate evolvability and domestication potential. Phase II: Each candidate is developed according to one of three general development strategies designed to produce a partially domesticated species usable as a new crop. Phase III: Domestication proceeds through integration of strategies to develop a commodity crop.

currently grow them), such as buckwheat (*Fagopyrum esculentum* Moench), amaranth (*Amaranthus*, spp.), and spelt [*Triticum aestivum* L. subsp. *spelta* (L.) Thell.], are annual plants very similar in an agroecological sense to existing, fully domesticated and high-yielding cereals. We predict that they will struggle to attract sufficient investment to attain substantial acreage planted if a novel growth habit (e.g., perennial or winter annual) or unique quality, such as flavor or nutrition, is not identified.

The pipeline approach differs substantially from past screening efforts where properties of numerous species were compared to identify the most promising candidates (e.g., Bell et al., 2011). While these checklist approaches are a necessary first step, they may not be adequate to select the species most amenable to domestication. Instead of a one-time evaluation, we propose initiating domestication of many species and performing ongoing evaluation. Each particular strength and weakness of a species is less critical than whether an overall domestication strategy can be developed given the strengths and weaknesses of a species. The economic and political realities surrounding a domestication effort are just as important to consider as are mean values for a few key traits.

Our proposed pipeline approach proceeds in three phases (see Fig. 1). First, a high-throughput screening process identifies promising candidates for domestication. Second, one develops and executes a strategy to prioritize the research and development activities necessary to understand, breed, and market the species. Third, the Phase II strategies are integrated to facilitate continued optimization. Although we briefly describe this third stage, crop improvement to optimize traits after initial domestication (transformation from wild plant to useful crop) is beyond the scope of this paper.

## RESEARCH PHASE I: EVALUATING CANDIDATE SPECIES

Below, we suggest criteria that can be used to evaluate species under consideration for domestication as a grain crop (defined as an herbaceous plant producing seeds used for food). Evaluating species according to this list is valuable in two ways. First, relative ranking of various species will be helpful in selecting species for additional investment. No unimproved wild candidate will meet all of these criteria, but the best candidates will have some fortuitous preadaptations or biological considerations that reduce the number of traits requiring major modification. Second, the relative strengths and weaknesses of a species in relation to these criteria will inform the strategy for domesticating that species (Phase II). We see this as a combination of the ideas of the domestication syndrome (Hammer, 1984) and ideotype breeding (Donald, 1968). In addition, we see this as an opportunity to expand on these ideas to bring new plant forms into use that were previously missed during domestication, leveraging what has been learned about the genetic architecture of these characteristic phenotypes (Doebley and Stec, 1991; Gepts, 2004; Li et al., 2006a,b; reviewed in Morrell et al., 2012).

Here we will consider a number of useful criteria for evaluating possible plants to domesticate and to use in continuous evaluation of species in the domestication pipeline. No candidate is expected to have all, or even many, of these traits. Indeed, in a candidate, we are not looking for traits at the fully domesticated level, but rather we are looking for species with traits that will make the process of domestication rapid and less difficult. The relative value of each characteristic that follows would be difficult to determine apart from evaluation of a particular candidate species. The important consideration here is that each of these points should be thoroughly explored and balanced against others to determine feasibility of the effort and to set goals before initiating a domestication program.

1. **Domestic Morphology and Phenology**. A promising candidate will germinate rapidly when sown, have rapid early growth to compete with weeds, and will be harvestable at the proper time in the target agroecosystem. Strong candidates will also have uniform ripening and shatter resistance, which is conducive to mechanical harvesting at a single time point. Moderate stature on robust stalks is useful to prevent lodging. As an integrative measure, a plant will be most easily used if it can be grown and managed using equipment currently employed in grain agriculture (e.g., have large, regularly shaped seed with low or readily breakable dormancy for ease of modern mechanical planting and harvesting).

2. **Ease of Breeding and Genetics.** The reproductive biology of each species is unique, resulting in a wide range of breeding techniques required for different crops. When considering a wild species, a primary requirement is for knowledge of reproduction. For instance, a species where outcrossing percentage, longevity of pollen survival, and key flowering cues are known would be preferred over a species where these basics are unknown. If the species is self-pollinated, easy emasculation is preferred. For making pollinations, species with adequate pollen production and accessible, long-lived stigmas are preferred. Ease of culture in the greenhouse or amenability to counter-season nurseries can be useful in a breeding program to allow for multiple generations of selection, selfing, or crossing per year. Perennial grain crops can provide the benefit to breeding of being able to save and propagate parental genotypes through clonal reproduction. But perennials can be more difficult to work with if they require a long establishment period or several years for trait evaluation. Obtaining DNA sequence information on candidate species has become affordable; however, the actual cost and difficulty of sequencing a new species is proportional to the size and complexity of the genome. An ideal case would be a candidate species with a small, diploid genome, in which case the development of genomic resources for breeding is less expensive and more tractable. As many candidate species possess large (up to 25 Gb) tetraploid or hexaploid genomes as a result of polyploidy or evolutionary duplication, this should be taken into consideration as a downstream limitation for molecular breeding. Although genomic information is not essential to domestication, it may be helpful in reducing the time required for domestication from centuries to decades through implementation of genomics assisted breeding (Runck et al., 2014).

3. **Easily Harvestable.** Ease of harvest is facilitated by seed that is large, smooth, dense, shatter resistant, easily threshed, and winnowed without difficulty. Harvest in many systems is facilitated when the grain is held near the end of rigid stalks that dry down completely before harvest. For mechanized production, the optimal plant will enable rapid harvest by conventional equipment and with minimal loss as a result of lodging, pod and seed shatter, or animal predators such as birds. In subsistence production, hand harvesting will be facilitated by seed borne in large clusters that can be easily gathered.

4. **High Yield.** Yield per area is driven by two primary factors: total biomass and harvest index. Harvest index is the proportion of total biomass that is allocated to the grain, and its increase has been critical to the yield of modern cultivars (Donmez et al., 2001; Singh and Stoskopf, 1971). Biomass accumulation is also of critical importance when evaluating a new species. Some candidates for domestication are so small that obtaining substantial grain yield will only be possible if total biomass production is increased. Increasing total dry matter yield has been a more important avenue to grain yield than raising harvest index in some crops (Tollenaar, 1989). In stressful environments, biomass accumulation may be necessarily limited to conserve resources and reduce premature mortality as a result of episodic stresses found in the target environment (e.g., frost, drought, wind).

5. **Grain Similar to that of Current Crops.** A new crop will be most easily integrated into existing commodity markets if the properties of the new grain are similar to a currently used crop. If flavor and functional attributes approximate an existing grain, the new crop will be able to substitute for the other grain in recipes without need for modification or a training period to adjust consumer taste preferences as has been necessary with whole grains (Marquart et al., 2003). Conversely, unique flavors or functionality may contribute to the development of a high-value product (see the next point). An ideal new crop would be easy to substitute in existing recipes while having some features that increase its value.

6. **High-Value Product.** The development of a new crop will be aided—particularly from a funding standpoint—if the harvested material can be developed into a product of particularly high value. Examples include suitability for special diets (e.g., gluten free or low glycemic index), presence of compounds believed to provide health benefits (e.g., antioxidants, omega-3 fatty acids, soluble fiber), or

perceived benefits of the crop to areas such as sustainability or wildlife conservation. If the harvested product is visually distinct from other existing grains or produce, identity preservation in postharvest marketing will be considerably easier.

7. **High Nutrition and Quality Attributes.** A new food crop will most easily enter the market if consumers are confident that the food is safe for consumption. New crops with no known toxic intrageneric relatives are more likely to be safe than those related to highly toxic species. Likewise, if the crop has been historically eaten or is a close relative of a widely consumed crop, the likelihood of the grain being safe to eat is dramatically higher (Smartt, 1990), and if the species has been used in wide hybridization with current crops (Wulff and Moscou, 2014), companies will be more confident in marketing products containing the new grain without fear of liability from toxicity. Many current crops require processing to render them edible, but a new crop will be more profitable and will easily enter the market if special processing is not necessary. Crops such as rapeseed (*Brassica napus* L.) (Bell, 1982) were initially unpalatable for human and animal consumption but were made edible through selection for canola-quality oil. Although toxins may be bred out of most plants, breeding for edibility can be expensive. The cost of developing canola from rapeseed was about $95 million in 2014 US dollars (Bell, 1982). If necessary, a potential route may be first the adoption of candidate species as industrial or feed crops to build breeding resources, and second, funding for the development of food quality grain as happened with canola (McVetty and Scarth, 2002).

8. **Available Genetic Resources**. Abundant germplasm collections will facilitate the domestication of a species. Easily accessible wild populations can also be a good resource, but populations present primarily in inaccessible regions because of political reasons would be difficult. The size of the secondary gene pool (number and accessibility of closely related species) should be considered along with any factors that make it difficult to exploit genetic resources such as apomixis or lack of genomic stability. The low cost of whole-genome sequencing enables one to identify the complete gene space of any organism and make predictions about which genes might be targets for future improvement. If the species is a diploid with low gene redundancy, mutation breeding approaches can be used to identify beneficial mutations in the target genes (Sedbrook et al., 2014). These approaches will be especially amenable if the candidate species propagate primarily through self-fertilization. If there is a closely related species with significant genomic resources, genetic work with the target species will be greatly facilitated. For instance, work with either grasses or members of the Brassicaceae is enhanced by the extensive information available in rice (*Oryza sativa* L.), barley (*Hordeum vulgare* L.), and *Brachypodium distachyon* (L.) Beauv. and in *Arabidopsis thaliana* (L.) Heynh., respectively.

9. **Broadly Adapted or Adaptable.** To justify the investment in domestication and commodity development, a new crop should have the potential to be grown on hundreds of thousands to millions of hectares. Adequately testing the potential range is likely to be difficult if a non-native species is perceived as having the potential to become invasive or if it contains regulated psychoactive chemicals. Species already widely used for other economic purposes are particularly attractive, since genetic resources, information about range, reproductive biology, plant nutrition, pathology, and an international history of noninvasiveness are likely to be available. Ecogeographical approaches (e.g., Li et al., 2013) could be useful to identify potential regions of adaptation for new domesticates. When considering climate change, species that will be more resilient to uncertain weather patterns may be preferred.

10. **Low Input Requirements.** New crops that can be grown with minimal pesticide, irrigation, tillage, fertilizer, and weed control will be attractive to farmers for economic and conservation reasons. While any productive crop will require adequate moisture and fertility, there is particular need for crops that can tolerate periodic water shortages, use resources more efficiently, fix N symbiotically, access stored soil moisture, and remain free of pests and diseases through resistance or competitive ability. Low input requirements open the possibility of marketing new crops as specialty organic crops, which could potentially allow organic premiums to balance out lower initial yields.

11. **Enhanced Ecosystem Services.** Crops that can provide ecosystem services are more likely to attract funding for development, and their adoption may be facilitated by value placed on ecosystem services either by consumer choice or government support. Examples of ecosystem services that may be provided by new crops include soil C sequestration, habitat for wildlife (including pollinators), biocontrol of pests through habitat for natural enemies, and clean water by the prevention of runoff and nutrient leaching. As support for multifunctional agriculture increases and valuation methodology matures, crops that provide enhanced ecosystem services beyond provisioning grain will have an advantage.

12. **Culturally Tenable.** Traditional indigenous territories encompass up to 22% of the world's land surface and coincide with areas that hold 80% of the planet's biodiversity (Sobrevila, 2008). Despite this, the benefits of this biodiversity are disproportionately realized by the wealthy: 97% of patents worldwide are held by individuals and companies in industrialized countries (United Nations, 1999). Careful attention should be paid to equity and cultural issues when selecting candidate crops. Specifically, wild species that are important to a people group should not be domesticated without the express consent and collaboration of those people. For further discussion of this topic, see the case study on wild rice, below.

13. **Knowledge of the Candidate's Disease and Pest Risk.** Knowledge of a species' major diseases and insect pests will help to accelerate a domestication program because basic research to understand major limiting biotic factors can be a costly and lengthy endeavor before the species can be grown successfully in breeding nurseries. Potential of the species to become invasive in a particular region is a critical consideration. Relatives of existing crops or species grown widely for horticultural purposes will likely have a wealth of existing biological information. In contrast, obscure species from genera with no currently used plants will present a greater challenge.

14. **Low Potential to Become Invasive or Contaminate the Gene Pool of a Native Species.** Invasiveness is a concern primarily with exotic species being domesticated for use outside their native range. Conversely, domestication of native species could increase the frequency of rare domestication alleles, which could then flow into the wild populations. Although domestication for use as a grain will likely reduce invasiveness by reducing seed dormancy, dispersal, and plant height (Nentwig, 2007), potential for invasiveness could limit early work with the species. Species projected to become invasive by predictive approaches (e.g., Mack, 1996; Pheloung et al., 1999) should not be introduced for domestication. Partially domesticated species may pose the greatest risk of invasiveness because early selections may increase vigor and seed production before fixation of traits, such as nonshattering, that will reduce invasive risk. During this period of semidomestication, the populations should be closely monitored for invasive potential and grown in limited locations. When domesticating a native species, genetic pollution of remnant populations may be reduced by not growing the domestic plant forms near critical remnant populations.

## RESEARCH PHASE II: WILD SPECIES TO NEW CROP

Every candidate for domestication will have a unique blend of strengths and weaknesses, but here, we suggest three primary strategies. For each candidate, a custom set of domestication milestones should be defined based on one, or a combination, of the three strategies below. Failure to meet the initial goals should trigger a thorough reevaluation of the candidate or shifting of resources to other candidates. We will describe each of these strategies in turn and provide examples of their use in the case studies that follow.

1. **Address the Primary Limitations.** Potential domesticates often have traits that limit viability of the crop or hinder breeding progress. These traits have been termed crucial domestication traits (Abbo et al., 2014). Among these are severe shattering, a seed coat that is impermeable to water (hard seed), very difficult threshing, severe lodging, and presence of toxins, or antiquality factors. Less obvious traits include complex germination requirements and poor seedling vigor, invasive spreading, or extreme height and plasticity. These restraints may need to be solved quickly because they make large-scale experiments or use as food almost impossible. The first step in addressing these limiting factors may be to obtain numerous collections and search for rare individuals with allelic variation to overcome the limitations. There is the possibility of conducting forward genetic screens if variability is not apparent in wild collections, with programs in mutagenesis, TILLING (Targeting Induced Local Lesions IN Genomes), ecoTILLING, or rapid cycling of strict selection cycles for the critical traits could be initiated (Till et al., 2006). Alternately, severe limitations such as difficult establishment, lodging, or stand decline in perennials may be readily overcome through physiological or agronomic studies. Perhaps the plant will be poorly adapted for grain production in the first test region but may succeed in other environments. If primary limitations cannot be overcome after making a substantial effort, resources could more wisely be directed toward other candidate species.

2. **Build on Strengths.** If the target species has particular strengths, as revealed in the evaluation above, these should be exploited to attract funding and research support to develop the crop. If the species has potential as a specialty crop, this aspect could be highlighted through product development and small-scale production to create market pull. If the grain has properties similar to existing commodities, then food science research to highlight the large potential market should be prioritized and initiated. When there is a close relative with extensive genomic resources, reverse genetic approaches

facilitated by sequencing the species may be an obvious choice to attract additional research support as was done with pennycress (*Thlaspi arvense* L.) (Dorn et al., 2015). In the case of crops with potential to provide expanded ecosystem services, documenting those services could be an important early research objective, as has been done with intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey] (Culman et al., 2013). Another strategy may be to develop a by-product market, such as forage or biofuel, to expand market potential, garner research support for the crop, and develop transition strategies into new markets.

3. **Breed to Improve Quantitative Traits.** In the absence of clearly limiting factors or obvious strengths to build on, primary attention should be given to important traits with quantitative control. In many cases, low grain yield (and its components) is the quantitative trait that should receive primary attention. Grain yield in current domestic grains has risen steadily over many decades, with the highest rates of increase in the United States of $\leq$2.4% yr$^{-1}$ (Ray et al., 2013). Harvestable yield may quickly increase through the use of a particular mutation as seen in strategy number one above. But in general, high yield will be attained through an incremental process of evaluation and selection that will result in small but steady increases. If yields have to increase by two- to fivefold for a wild plant to become viable domestic grain, at least a decade or more of breeding work will generally be required. In this case, breeding can proceed for many years to increase yield before beginning commercialization or utilization research. In the case of perennial grain crops, genomic selection may be particularly useful for accelerating progress (Heffner et al., 2010).

## PHASE III: FROM NEW CROP TO COMMODITY CROP

For those species passing the second phase and progressing to a full new-crop domestication program, aspects of all three strategies will eventually be integrated. In Phase III, recurrent selection for yield and other quantitative traits will be necessary to develop a broadly grown crop. However, we predict that most domestication candidates would also benefit from a regular reassessment along the lines of Strategies 1 and 2 (Phase II, above). Having made progress on the most serious limitation, it is critical to determine the next single most-limiting trait. Perhaps an intense effort is necessary to overcome that limitation and then to introgress the improvement into the elite lines or populations from the yield improvement program. Likewise, it will be helpful to periodically engage key stakeholders to ensure that germplasm development is coordinated with enterprise development (Runck et al., 2014).

## Case Studies: Lessons Learned

### *Illinois Bundleflower: Severe Primary Limitations*

For several decades, the Land Institute and other institutions have studied and worked toward the domestication of the herbaceous perennial legume Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. and Fernald]. This species attracted attention as a potential grain because of its soil-conserving perennial root system, symbiotic N fixing ability (Beyhaut et al., 2006), and high seed production relative to other perennial herbaceous species (DeHaan et al., 2003; Kulakow et al., 1990). Researchers identified abundant genetic variation for traits, such as seed size and yield (DeHaan et al., 2003), and even found a genetic solution to shattering. However, work with this species has been frustrating for a number of reasons. First, it is a difficult species to breed as a result of its small flower parts, partial selfing, challenging emasculation, and difficulty growing in standard greenhouse conditions. Second, the seed has an objectionable flavor, and safety for use as a human food has been difficult to demonstrate. Finally, the roots of Illinois bundleflower contain the regulated substance N,N-dimethyltryptamine (Halpern, 2004), raising questions about the legal regulations surrounding seed production and sale of this species. Work with Illinois bundleflower has mostly been placed on hold because these primary limiting factors were never addressed adequately. Before renewing domestication efforts with this species, the primary limitations listed here must be addressed. Learning from work with Illinois bundleflower, domestication programs should attempt to remedy severe primary limitations before advancing to other efforts. If the primary limitations cannot be solved quickly or efficiently, then resources would be better allocated to other species.

### *Maximilian Sunflower: Target Environment Mismatch*

Decades of research have also been directed toward the herbaceous perennial sunflower (*Helianthus maximiliani* Schrad), which is native to most of North America. The species has high yield potential and genetic variation for seed size and head size (compared with other wild perennials). As a perennial grain, the species was expected to provide edible vegetable oils and reduce erosion, runoff, and input costs. With conventional breeding, selection for yield and seed size has been successful. A breeding population in 2012 has seeds that are on average 2.4 times larger than the unselected germplasm evaluated in 2002 (Van Tassel et al., 2014). Mechanical harvest is difficult because heads are produced at multiple heights and stalks are tall and tough, requiring very slow ground speed when harvesting mechanically. Populations with apical flowering have been developed to address ease of harvest and synchronicity of maturation (Van Tassel et al., 2014); however, reducing the number of heads per stalk reduces the yield and large increases in head size will be required to compensate.

Yield decline and drought sensitivity have been found to limit production and complicate selection for yield potential in central Kansas (D.L. Van Tassel, unpublished observations). So far, we have not been able to identify a rapid selection protocol or management tool to overcome these limitations. However, this species is amenable to greenhouse cultivation (D.J. Cattani, S.R. Asselin, unpublished observations) and is a member of a genus with rich genomic resources, suggesting that genomic assisted methods could perhaps overcome these obstacles in the future. In retrospect, it was a mistake to assume that the target agricultural range overlapped the full native range of the species; it tolerates dry periods through wilting, leaf abscission, and reduced growth and flowering responses that ensure survival but not reliable seed yield in the species' southern range. Targeted initial studies with this species should have identified yield stability in southern locations as a major limitation. The next step should have been identifying climatic conditions or management strategies that overcome or avoid this limitation. Unless simple, inexpensive management solutions had been quickly identified, the kind of recurrent candidate ranking proposed here would likely have deprioritized the domestication of this species for unirrigated, drought-prone environments because redesigning a species' drought response is a formidable additional breeding objectives that can only slow breeding progress for yield. However, in Manitoba, yield declines and summer drought stress have not been observed (D.J. Cattani, S.R. Asselin, unpublished observations). These observations illustrate the importance of matching the target agricultural environment with the strengths and limitations of the domestication candidate.

### *Weeping Rice Grass: Weak Support for Agricultural Target*

The native Australian weeping rice grass [*Microlaena stipoides* (Labill.) R. Br.] has been under consideration and experimentation for use as a resource-conserving perennial grain for more than a decade (Davies et al., 2005). Davies et al. (2005) suggested that determining the edibility of weeping rice grass would be an important step toward its use as a perennial grain crop. The authors also stressed the importance of yield. However, there is no indication that projects were ever initiated to breed for yield or determine whether antinutritional factors are present in the grain. Indeed, 9 yr later, low yield remained a primary limitation to using weeping rice grass as a grain (Malory, 2014). We interpret the initial lack of progress as evidence that the species was proposed as a domestication candidate without adequate support for the agricultural target in mind, that is, improving sustainability by developing a perennial grain. Thus, Strategy 1—solving the issue of edibility—and aggressively breeding for increased yield (Strategy 3) were left unfunded. Recent work with weeping rice grass took advantage of the genomic information available in rice, a related species. Mutagenesis combined with sequencing and genomic comparison to rice has been used to identify candidate alleles to be used in domestication (Shapter et al., 2013). Whether this advancement strategy can be used to develop high-yielding varieties remains uncertain.

### *Perennial Chickpeas: Target Environment Mismatch*

Several perennial *Cicer* spp. have been collected and are available from the USDA–ARS. Data on potential for domestication has been collected on 23 accessions from eight species (Watt et al., 2005). The relatively large seeds of some accessions suggested potential for domestication as a perennial pulse crop (i.e., grain legume). All of the accessions evaluated had seed shattering and pod shedding. These traits, along with soft seededness, would be among the first to address if a domestication program were initiated. When perennial *Cicer* spp. were evaluated in Kansas, indeterminate flowering and low survival (possibly as a result of disease) made the plants challenging to evaluate, and a breeding program was never initiated (L.R. DeHaan, unpublished observations). In other words, this group of species was screened out for use in the central United States primarily on the basis of high mortality and difficult harvest in the target environment. If a program were initiated with this species, disease resistance, seed shattering, and pod shedding are major limitations that should receive primary attention.

## Case Studies: Successes and Current Efforts

### *American Wild Rice: Building on Consumer Demand, Displacing an Indigenous Economy*

Since prehistoric times, the wild annual grass manoomin (wild rice; *Zizania palustris* L.) has been harvested from naturally occurring stands by Native Americans. Domestication of wild rice began in the first half of the twentieth century, with initial investigation done by European–American farmers who later asked the University of Minnesota to domesticate the species. University of Minnesota involvement led to genetic and agronomic advances, with manoomin eventually becoming an established crop (Oelke, 1993). The major genetic change that allowed increased cultivation of paddy rice was shatter resistance, first discovered in 1963, which resulted in an immediate 10-fold increase in harvestable wild rice yield in paddy rice systems and led to a 100-fold increase in Minnesota on-farm production over the next 20 yr (Oelke, 1993).

However, from the perspective of the Anishinaabe nations of Minnesota, the scientific investigation of manoomin (wild rice) was done in an exclusionary manner. It was noted that, "virtually all wild rice research emerging from the University of Minnesota has reflected the goals and desires of non-Indians with little regard for Native American concerns, perspectives, or the considerable store of traditional knowledge of manoomin" (Andow et al., 2011). The research has been labelled *biopiracy* because germplasm was taken from tribal nations with little or no consultation, was developed into a commercial product with little or no tribal nation involvement, and resulted in little or no revenue from the resultant crop to tribal nations.

Manoomin is vital to the perpetuation of Anishinaabe culture and identity, with this connection having developed over thousands of years of coexistence with the plant. Their domestication paradigm differs radically from the Western one and is derived from a different knowledge system, that is, harvesting the plant should domesticate people rather than people domesticating the plant. The tribes perceive their role as keen observers and active agents in responding to the conditions of the plant rather than changing those conditions.

Anishinaabe communities are deeply concerned about the labeling of marketed manoomin to distinguish between traditional grain produced in its native habitat and domesticated grain produced commercially in paddies. Tribal natural resource departments are interested in collaborative research that would benefit their community and preserve wild rice in its natural habitat. Without participation, research is viewed by the minority community as disrespectful, exploitative, a form of colonization, and a violation of treaty rights. However, strides have been made in this regard, with three large-scale meetings between Anishinaabe and the University of Minnesota held over the last 6 yr. Progress has been made toward a memorandum of understanding regarding research on wild rice (Nibi and Manoomin: Bridging Worldviews Committee, 2014).

Early commercial paddy production of wild rice succeeded because of one particular strength—willing buyers. Consumer demand has been strong based on its flavor, texture, and nutritional benefits (Cho and Kays, 2013). Wild rice illustrates how early production can use a strength (in this case consumer demand) to attract the research required to overcome a primary limitation (in this case seed shattering). In contrast, shattering was a characteristic valued by Indigenous communities in traditional wild rice production systems for reseeding and maintenance of genetic diversity. This domestication case study reveals domestication breeding as a sharp but double-edged sword capable of rapidly transforming a wild species to create a new crop and at the same time undermining a preexisting culture and economy based on the harvesting of wild populations. In the future, wild species that are economically important to a people group should not be considered as candidates for domestication without the express consent and collaboration of those people.

### Sweet White Lupin: Target Environment Match

Lupin production in Australia is based primarily on the annual leguminous species *Lupinus angustifolius* L., which was developed as a new crop in the 1960s. The crop's genetic history has been recorded by Cowling and Gladstones (2000), and we will summarize their work below. As reported, other lupin species were considered for domestication in Australia, but they suffered from drought stress, poor adaptation to local soils, late maturity, or susceptibility to disease and insects. *Lupinus angustifolius* was selected based on its vigorous growth and the presence of critical mutant types. Semidomesticated forms (each possessing some domestication traits but lacking others) were introduced from Europe, but fully domesticated plants were developed by identifying and stacking several rare alleles for early flowering, shatter resistance, soft seed, white flowers and seed, and low alkaloid content. In the early years of lupin production, the diseases grey leaf spot [*Stemphylium vesicarium* (Wallr.) E.G. Simmons] and Phomopsis stem blight (*Diaporthe toxica* P.M. Will.) severely limited production. Discovery of resistance genes and the release of resistant cultivars were critical to the expansion of lupin production.

Marsh et al. (2000) have reported on the factors influencing lupin production and expansion in Western Australia, and we will summarize their work here. The first fully domesticated cultivars resulted in rapid adoption, with 120,000 ha planted in 1973. Droughts and poor management practices caused declining yields, and planted area had fallen to 40,000 ha in 1978. In 1979, a new higher-yielding variety was released, and a major extension effort was initiated to demonstrate that successful cropping of lupin was possible. The new agronomic package of improved varieties, higher planting density, earlier planting, and effective weed control was successful. By 1987, planted area peaked at 877,000 ha. In summary, the decision to invest in lupin was based on its ability to fix N and produce high-protein animal feed in an environment where fully domesticated grain legumes had been unadapted because of the Mediterranean climate and poor soils. Success of lupin as a crop depended on breeding for key domestication traits followed by agronomic research and extension to help producers grow the crop successfully.

A postscript to this story is that lupin production in Australia has been declining in recent years. Marketed as an animal feed, the export price is lower than soybean [*Glycine max* (L.) Merr.], which produces both feed and oil. Many farmers have replaced lupin with canola in their rotation because of better weed control options and fewer fungal diseases. New disease- and herbicide-resistant lupin lines are being developed. Perhaps somewhat belatedly, building on evidence of health benefits, Western Australia is investing in food product development to increase the value of lupin grain (Peterson and Wilkinson, 2014). This example suggests that developing high-value end uses may be a strategic investment to ensure long-term new-crop viability.

### Field Pennycress: Excellent Primary Characteristics

Pennycress (*Thlaspi arvense* L.) is a potential winter annual oilseed crop being developed in the US Midwest for use as a cover crop and biodiesel feedstock. Domestication of this species is an example of building on strengths within a wild species. The first strength is derived from the plant's phenology. Its exceptionally short lifecycle and cold tolerance allows it to be grown successfully over the winter within the corn–soybean rotation. Although a pennycress cover crop has been shown to reduce soybean yield, the combined pennycress and soybean yield has been greater than soybean alone (Johnson et al., 2015). Not only does the crop have potential to increase farmer incomes through increased total oilseed yield, a pennycress cover crop could also improve soil and water quality, although this remains to be shown experimentally.

The second strength that pennycress has comes from its small genome and close relationship to the model species *A. thaliana* (Sedbrook et al., 2014). With modern sequencing techniques, the transcriptome of several pennycress tissues and a draft genome have been assembled (Dorn et al., 2013, 2015). Comparative analysis with *A. thaliana* allowed identification of orthologs that may control critical traits such as flowering time and glucosinolate metabolism. With these genomic tools, breeding of more adapted types of pennycress with seed suitable for animal or human consumption should be possible (Dorn et al., 2015).

### Silphium: Good Agricultural Target, Overcoming Primary Limitations

The herbaceous perennial species *Silphium integrifolium* Michx. is native throughout the central United States. Efforts to domesticate this species as a perennial grain crop are ongoing, and are described by Van Tassel et al. (2014). Two strengths made the species particularly attractive: large seed and drought tolerance. Seed mass of 21 mg has been reported (Kowalski and Wiercinski, 2004), and *S. intergrifolium* is among the most drought-tolerant plants found in the North American prairie (Weaver et al., 1935). *Silphium integrifolium* was selected for domestication over its relative, *S. laciniatum*, because the latter develops more slowly and may not flower until the third year after planting.

The most obvious breeding target to raise grain yield in *S. integrifolium* was to increase the number of ray florets (the only florets that produce a seed) per head. Selection on this easily measured trait was expected to induce a more rapid response in yield potential at lower cost than complex yield measures (DeHaan and Van Tassel, 2014). More than 10,000 individuals were evaluated for ray floret number in 2006. The average number of ligules per head (a proxy for ray florets per head) was estimated to be 28 to 30, and 83 plants with 38 or more ligules were selected for intermating. Polycross progeny were established the next year, and the selection procedure was repeated for two more cycles. In 2012, the average number of ray florets per head was 52, and some plants had >100 ray florets. One plant had >150 ray florets per head (Van Tassel et al., 2014). Having addressed the problem of low seed number per head, the program at the Land Institute has since moved on to additional germplasm collection and evaluation and selecting for yield per stalk, mass per seed, and fatty acid profile. *Silphium integrifolium* provides an excellent example of using cost-effective recurrent selection for several years to solve a major limiting factor in a potential domesticate (Strategy 1) before moving on to broader-scale work with the species.

### Intermediate Wheatgrass: Good Primary Characteristics, Early Market Potential

Researchers at the Rodale Institute selected the perennial intermediate wheatgrass *T. intermedium* as a target for domestication as a grain crop after evaluating nearly 100 species based on the following traits: vigorous perennial growth, good flavor, easy threshing, large seed, synchronous seed maturity, shatter resistance, lodging resistance, and ease of mechanical harvest (Wagoner, 1990). Vigorous perennial growth was considered an essential trait in this instance because the primary objective was to develop a plant that would provide the ecosystem service of erosion control. In collaboration with USDA–NRCS scientists at the Big Flats Plant Materials Center, two cycles of selection for a broad index of traits were performed. Because the species was partially domesticated through these efforts, no trait was seen as an outstanding strength or weakness when the Land Institute began work with the species in 2001.

Since 2003, phenotypic recurrent selection based mainly on yield and yield components (mass of seed per head and mass per seed) has been performed at the Land Institute. As reported by DeHaan et al. (2014), after two generations, seed mass had increased over the starting material by 23%, but yield per land area in solid seeded plots responded more quickly, increasing by 77%. If these gains continue in a linear fashion, yields similar to wheat (*Triticum aestivum* L.) currently grown in Kansas would require another 20 yr of breeding. Because seed mass is responding more slowly, about 110 yr would be required to achieve a seed mass of 30 mg seed$^{-1}$. To address mass per seed directly, mass selection was performed on individual seed weight for eight generations. Over this time, mass per seed increased by 0.52 mg seed$^{-1}$ generation$^{-1}$. If progress continues in a linear fashion, another 44 yr of selection will be required to achieve a seed mass of 30 mg seed$^{-1}$. These extended timescales underscore the importance of initiating large-scale selection programs to improve important quantitative traits in new domestication programs.

When improved intermediate wheatgrass germplasm is grown in northern environments, grain yields exceeding 150 g m$^{-2}$ can now be obtained on experimental plots (DeHaan et al., 2014; Culman et al., 2013). These promising yields have led to the first commercial plantings of the grain with small-scale marketing under the name Kernza. Yield and commercial interest have attracted support for additional work in important areas such as milling and baking quality (Zhang et al., 2014) and molecular genetics (DeHaan et al., 2014). Using genotyping-by-sequencing, genome-wide markers are available for intermediate wheatgrass. With maturity of the breeding program, genome-wide prediction is being introduced to accelerate the domestication of intermediate wheatgrass by increasing the selection efficiency and shortening the selection cycle (Zhang et al., 2016). While an all-around excellent target for domestication and improvement, the large polyploid genome (~13 Gb) makes the implementation of genomics-assisted breeding challenging. Breeding objectives are now being broadened to include traits such as lodging resistance, shatter resistance, and free threshing ability. Furthermore, agronomic studies are in progress to identify methods of enhancing and sustaining yield with low inputs and documenting potential ecosystem services from the crop (Culman et al., 2013).

In summary, the intermediate wheatgrass domestication effort provides a good example of starting with a generally promising species that provides valuable ecosystem services and using phenotypic selection sustained over a decade to increase yield (Strategy 3) to the point where the crop is worthy of additional research investment. More recent work has built on the strength of a grain with qualities somewhat similar to wheat and genetic variability that may allow development of varieties for specific types of products (e.g., bread, pancakes, beer) and blending with wheat (Strategy 2).

## CONCLUSIONS

Modern domestication is an economic and political activity as much as a biological one. In an era of fixed or contracting public investment in plant genetics, tradeoffs are inescapable; more time and field space devoted to one candidate likely means less allocated to others. Here, we have attempted to develop an economically rational approach to new domestications that (i) reduces the amount of research and development required to bring a new crop to full commercialization by prioritizing wild plants with fortuitous preadaptations (e.g., large seeds), (ii) reduces wasted effort by quickly screening out candidates with insurmountable risk factors, (iii) strategically allocates early investments to increase a project's appeal to additional investors and collaborators, and (iv) simultaneously lays the foundation for sustained gains in yield and marketability.

Plant domestication efforts should begin with an agricultural target in mind. That is to say, the domestication effort should be performed to meet a particular need or solve a problem in a unique way. Then, various species should be evaluated and experimented with to eventually develop at least one new crop species that addresses the perceived needs. This approach contrasts with efforts that begin with a particularly interesting species and seek to find ways to make that species useful or profitable.

The species ranking and screening process described in Phase I is partially a deductive and descriptive process. It may be possible to score plants for many of the attributes listed using herbarium specimens, species monographs, etc. Specialists accustomed to collecting and growing wild or partially domesticated plants, including indigenous communities, ornamental and forage breeders and dealers, native vegetation restorers, or botanical garden curators, can suggest candidates with agronomic growth form, high vigor, adaptation to a particular environment, etc. Preliminary empirical research is likely to be necessary, at least in some cases, to obtain estimates on traits such as seed dormancy, seedling vigor, seed nutrient content, or edibility. These studies should not only evaluate variation between species and populations, but also screen the diversity within populations and collections.

However, evaluation of candidates will never be completed by surveying species and their mean or range of values for various traits. Only by initiating selection programs will domesticators be able to fully evaluate the relative potential of various species. Once species are in the domestication pipeline, ranking species by their potential becomes feasible.

Phase II should be seen not only as an opportunity to strategically improve the candidate to make it easier to fund and work with, but also as an opportunity to test its ability to respond to intense directional selection. Even where this is not an explicit part of the strategically highest priority research, we suggest that some selection be initiated. For example, even in the cases where it makes sense to first focus resources on projects such as validating a food crop's reputed antioxidant content, on designing harvesting machinery, or on optimizing agronomic practices, single-trait recurrent selection experiments could be performed with minimal cost or labor requirements as described above for increased numbers of seeds in *S. integrifolium* heads and seed mass in intermediate wheatgrass. In addition to making progress on an important trait, the exercise is likely to result in innovations in protocols for growing, crossing, harvesting, phenotyping, etc. These practical insights will be needed for Phase III, when, funding-permitting, the domestication process will be scaled up.

Even in cases for which it is necessary to drop candidates from the pipeline, efforts should be made to catalog and disseminate the efforts undertaken. Given the time and expense of development efforts, as well as the potential for the same or similar species to be independently reconsidered later, even negative results should be viewed as important findings.

Finally, to justify the large investment required to domesticate a wild plant species, there must be a reasonable chance for it to be successfully grown over extensive areas for many years. For that to happen, it must displace existing alternate crops on some landscapes. This requires the new crop to be more profitable, which implies both adequate yields and some advantage in grain quality, reduced inputs, coproduct values, or ecosystem services. Although many candidates could have this biological potential, few will have both traits that make them appealing to plant breeders and the potential for initial use as new specialty crops that will bootstrap their own later stages of domestication. Furthermore, even a promising species will require genetic or genomic resources to permit rapid deployment of new cultivars to adapt to changing climate, pests, and markets (Gur and Zamir, 2004; Hoisington et al., 1999; Varshney et al., 2012). For these reasons we have proposed criteria and strategies to help breeders dispassionately evaluate candidates at early stages in the domestication pipeline, advancing only the most promising candidates for additional investment.

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## References

Abbo, S., R.P. van-Oss, A. Gopher, Y. Saranga, I. Ofner, and Z. Peleg. 2014. Plant domestication versus crop evolution: A conceptual framework for cereals and grain legumes. Trends Plant Sci. 19:351–360. doi:10.1016/j.tplants.2013.12.002

Andow, D., T. Bauer, M. Belcourt, P. Bloom, B. Child, J. Doerfler, A. Eule-Nashoba, T. Heidel, A. Kokotovich, A. Lodge, J. LaGarde, K. Lorenz, L. Mendoza, E. Mohl, J. Osborne, K. Prescott, P. Schultz, D. Smith, S. Solarz, and R. Walker. 2011. Preserving the integrity of Manoomin in Minnesota. Wild Rice White Paper, Univ. of Minnesota, St. Paul. http://www.cfans.umn.edu/sites/cfans.umn.edu/files/WhitePaperFinal-Version2011.pdf (accessed 13 May 2015).

Bates, D.M. 1985. Plant utilization: Patterns and prospects. Econ. Bot. 39:241–265. doi:10.1007/BF02858794

Bell, J.M. 1982. From rapeseed to canola: A brief history of research for superior meal and edible oil. Poult. Sci. 61:613–622. doi:10.3382/ps.0610613

Bell, L.W., R.G. Bennett, M.H. Ryan, and H. Clarke. 2011. The potential of herbaceous native Australian legumes as grain crops: A review. Renew. Agric. Food Syst. 26:72–91. doi:10.1017/S1742170510000347

Beyhaut, E., L.R. DeHaan, J.L. Byun, C.C. Sheaffer, and P.H. Graham. 2006. Response to inoculation in Illinois bundleflower. Can. J. Plant Sci. 86:919–926. doi:10.4141/P05-097

Brummer, C.E., W.T. Barber, S.M. Collier, T.S. Cox, R. Johnson, and S.C. Murray. 2011. Plant breeding for harmony between agriculture and the environment. Front. Ecol. Environ 9:561–568. doi:10.1890/100225

Cho, S., and S.J. Kays. 2013. Aroma-active compounds of wild rice (*Zizania palustris* L.). Food Res. Int. 54:1463–1470. doi:10.1016/j.foodres.2013.09.042

Cowling, W.A., and J.S. Gladstones. 2000. Lupin breeding in Australia. In: R. Knight, editor, Linking research and marketing opportunities for pulses in the 21st century. Kluwer Academic Publishers, Dordrecht. p. 541–547.

Cox, T.S., J.D. Glover, D.L. Van Tassel, C.M. Cox, and L.R. DeHaan. 2006. Prospects for developing perennial grain crops. Biosci. 56:649–659. doi:10.1641/0006-3568(2006)56[649:PFDPGC]2.0.CO;2

Cox, T.S., D.L. Van Tassel, C.M. Cox, and L.R. DeHaan. 2010. Progress in breeding perennial grains. Crop Pasture Sci. 61:513–521. doi:10.1071/CP09201

Culman, S.W., S.S. Snapp, M. Ollenburger, B. Basso, and L.R. DeHaan. 2013. Soil and water quality rapidly responds to the perennial grain Kernza wheatgrass. Agron. J. 105:735–744. doi:10.2134/agronj2012.0273

Davies, C.L., D.L. Waugh, and E.C. Lefroy. 2005. Variation in seed yield and its components in the Australian native grass *Microlaena stipoides* as a guide to its potential as a perennial grain crop. Crop Pasture Sci. 56:309–316. doi:10.1071/AR04204

DeHaan, L.R., N.J. Ehlke, C.C. Sheaffer, R.L. DeHaan, and D.L. Wyse. 2003. Evaluation of diversity among and within accessions of Illinois bundleflower. Crop Sci. 43:1528–1537. doi:10.2135/cropsci2003.1528

DeHaan, L.R., and D.L. Van Tassel. 2014. Useful insights from evolutionary biology for developing perennial grain crops. Am. J. Bot. 101:1801–1819. doi:10.3732/ajb.1400084

DeHaan, L.R., S. Wang, S.R. Larson, D.J. Cattani, X. Zhang, and T. Kantarski. 2014. Current efforts to develop perennial wheat and domesticate *Thinopyrum intermedium* as a perennial grain. In: C. Batello, L. Wade, S. Cox, N. Pogna, A. Bozzini, and J. Choptiany, editors, Perennial crops for food security: Proc. of the FAO Expert Workshop, 28–30 Aug. 2013. FAO, Rome. p. 72–89.

Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418:700–707. doi:10.1038/nature01019

Doebley, J., and A. Stec. 1991. Genetic analysis of the morphological differences between maize and teosinte. Genetics 129:285–295.

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385–403. doi:10.1007/BF00056241

Donmez, E., R.G. Sears, J.P. Shroyer, and G.M. Paulsen. 2001. Genetic gain in yield attributes of winter wheat in the great plains. Crop Sci. 41:1412–1419. doi:10.2135/cropsci2001.4151412x

Dorn, K.M., J.D. Frankhauser, D.L. Wyse, and M.D. Marks. 2013. *De novo* assembly of the pennycress (*Thlaspi arvense*) transcriptome provides tools for the development of a winter cover crop and biofuel feedstock. Plant J. 75:1028–1038. doi:10.1111/tpj.12267

Dorn, K.M., J.D. Frankhauser, D.L. Wyse, and M.D. Marks. 2015. A draft genome of field pennycress (*Thlaspi arvense*) provides tools for the domestication of a new winter biofuel crop. DNA Res. 22:121–131. doi:10.1093/dnares/dsu045

Earle, F.R., and Q. Jones. 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16:221–250. doi:10.1007/BF02860181

Fuller, D.Q., R.G. Allaby, and C. Stevens. 2010. Domestication as innovation: The entanglement of techniques, technology and chance in the domestication of cereal crops. World Archaeol. 42:13–28. doi:10.1080/00438240903429680

Gepts, P. 2004. Crop domestication as a long-term selection experiment. Plant Breed. Rev. 24:1–44.

Glover, J.D., J.P. Reganold, L.W. Bell, J. Borevitz, E.C. Brummer, E.S. Buckler, et al. 2010. Increased food and ecosystem security via perennial grains. Science 328:1638–1639. doi:10.1126/science.1188761

Gur, A., and D. Zamir. 2004. Unused natural variation can lift yield barriers in plant breeding. PLoS Biol. 2:E245. doi:10.1371/journal.pbio.0020245

Halpern, J.H. 2004. Hallucinogens and dissociative agents naturally growing in the United States. Pharmacol. Ther. 102:131–138. doi:10.1016/j.pharmthera.2004.03.003

Hammer, K. 1984. Das domestikationssyndrom. Kulturpflanze 32:11–34. doi:10.1007/BF02098682

Heffner, E.L., A.J. Lorenz, J.L. Jannink, and M.E. Sorrells. 2010. Plant breeding with genomic selection: Gain per unit time and cost. Crop Sci. 50:1681–1690. doi:10.2135/cropsci2009.11.0662

Hoisington, D., M. Khairallah, T. Reeves, J. Ribaut, B. Skovmand, S. Taba, and M. Warburton. 1999. Plant genetic resources: What can they contribute toward increased crop productivity? Proc. Natl. Acad. Sci. USA 96:5937–5943. doi:10.1073/pnas.96.11.5937

Jaenicke, H., S. Franzel, and D.J. Boland. 1995. Towards a method to set priorities amongst species for tree improvement research: A case study from West Africa. J. Trop. For. Sci. 7:490–506.

Jain, S.K. 1983. Domestication and breeding of new crop plants. In: D.R. Wood, editor, Crop breeding. ASA and CSSA, Madison, WI. p. 177–197.

Janick, J., M.G. Blase, D.L. Johnson, G.D. Jolliff, and R.L. Myers. 1996. Diversifying U.S. crop production. CAST Issue Paper 6. Council of Agric. Sci. and Tech., Ames, Iowa.

Johnson, G.A., M.B. Kantar, K.J. Betts, and D.L. Wyse. 2015. Field pennycress production and weed control in a double crop system with soybean in Minnesota. Agron. J. 107:532–540. doi:10.2134/agronj14.0292

Jolliff, G.D. 1989. Strategic planning for new-crop development. J. Prod. Agric. 2:6–13. doi:10.2134/jpa1989.0006

Knowles, P.F. 1960. New crop establishment. Econ. Bot. 14:263–275. doi:10.1007/BF02908035

Kowalski, R., and J. Wiercinski. 2004. Evaluation of chemical composition of some *Silphium* L. species seeds as alternative foodstuff raw materials. Polish J. Food Nutr. Sci. 13:349–354.

Kulakow, P.A., L.L. Benson, and J.G. Vail. 1990. Prospects for domesticating Illinois bundleflower. In: J. Janick and J.E. Simon, editors, Advances in new crops. Timber Press, Portland, OR. p. 168–171.

Leakey, R.B. 2007. Domesticating and marketing novel crops. In: S.J. Scherr and J.A. McNeely, editors, Farming with nature: The science and practice of ecoagriculture. Island Press, Washington. p. 83–102.

Li, C., A. Zhou, and T. Sang. 2006a. Rice domestication by reducing shattering. Science 311:1936–1939. doi:10.1126/science.1123604

Li, C., A. Zhou, and T. Sang. 2006b. Genetic analysis of rice domestication syndrome with the wild annual species, *Oryza nivara*. New Phytol. 170:185–194. doi:10.1111/j.1469-8137.2005.01647.x

Li, L., R.J. Redden, X. Zong, J.D. Berger, and S.J. Bennett. 2013. Ecogeographic analysis of pea collection sites from China to determine potential sites with abiotic stresses. Genet. Resour. Crop Evol. 60:1801–1815. doi:10.1007/s10722-013-9955-6

Mack, R.N. 1996. Predicting the identity and fate of plant invaders: Emergent and emerging approaches. Biol. Conserv. 78:107–121. doi:10.1016/0006-3207(96)00021-3

Malory, S. 2014. Accelerated domestication of Australian native grass species using molecular tools. Ph.D. thesis, Southern Cross Univ., Lismore, NSW.

Marquart, L., K.L. Wiemer, J.M. Jones, and B. Jacob. 2003. Whole grain health claims in the USA and other efforts to increase whole-grain consumption. Proc. Nutr. Soc. 62:151–160. doi:10.1079/PNS2003242

Marsh, S.P., D.J. Pannell, and R.K. Lindner. 2000. The impact of agricultural extension on adoption and diffusion of lupins as a new crop in Western Australia. Aust. J. Exp. Agric. 40:571–583. doi:10.1071/EA99080

McKell, C.M. 1983. Genetic resources of unexploited native plants. Plant Mol. Biol. Rep. 1:89–94. doi:10.1007/BF02680304

McVetty, P.B.E., and R. Scarth. 2002. Breeding for improved oil quality in Brassica oilseed species. J. Crop Prod. 5:345–369. doi:10.1300/J144v05n01_14

Meyer, R.S., A.E. DuVal, and H.R. Jensen. 2012. Patterns and processes in crop domestication: An historical review and quantitative analysis of 203 global food crops. New Phytol. 196:29–48. doi:10.1111/j.1469-8137.2012.04253.x

Morrell, P.L., E.S. Buckler, and J. Ross-Ibarra. 2012. Crop genomics: Advances and applications. Nat. Rev. Genet. 13:85–96.

Nentwig, W., editor. 2007. Biological invasions. Vol. 193. Springer-Verlag, Berlin.

Nibi and Manoomin: Bridging Worldviews Committee. 2014. 2015 Nibi and Manoomin Symposium. http://www.cfans.umn.edu/wildrice (accessed 13 May 2015).

Oelke, E.A. 1993. Wild rice: Domestication of a native North American genus. In: J. Janick and J.E. Simon, editors, New crops. Wiley, New York. p. 235–243.

Payne, D.J., M.N. Gwynn, D.J. Holmes, and D.L. Pompliano. 2007. Drugs for bad bugs: Confronting the challenges of antibacterial discovery. Nat. Rev. Drug Discov. 6:29–40. doi:10.1038/nrd2201

Peterson, J., and I. Wilkinson. 2014. Western Australian lupin industry. Western Australia Department of Agriculture and Food, South Perth, Wales. https://www.agric.wa.gov.au/grains-research-development/western-australian-lupin-industry (accessed 14 Mar. 2015).

Pheloung, P.C., P.A. Williams, and S.R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. J. Environ. Manage. 57:239–251. doi:10.1006/jema.1999.0297

Ray, D.K., N.D. Mueller, P.C. West, and J.A. Foley. 2013. Yield trends are insufficient to double global crop production by 2050. PLoS ONE 8:e66428. doi:10.1371/journal.pone.0066428

Runck, B.C., M.B. Kantar, N.R. Jordan, J.A. Anderson, D.L. Wyse, J.O. Eckberg, R.J. Barnes, et al. 2014. The reflective plant breeding paradigm: A robust system of germplasm development to support strategic diversification of agroecosystems. Crop Sci. 54:1939–1948. doi:10.2135/cropsci2014.03.0195

Sang, T. 2011. Toward the domestication of lignocellulosic energy crops: Learning from food crop domestication. J. Integr. Plant Biol. 53:96–104. doi:10.1111/j.1744-7909.2010.01006.x

Sedbrook, J.C., W.B. Phippen, and M.D. Marks. 2014. New approaches to facilitate rapid domestication of a wild plant to an oilseed crop: Example pennycress (*Thlaspi arvense* L.). Plant Sci. 227:122–132. doi:10.1016/j.plantsci.2014.07.008

Shapter, F.M., M. Cross, G. Ablett, S. Malory, I.H. Chivers, G.J. King, and R.J. Henry. 2013. High-throughput sequencing and mutagenesis to accelerate the domestication of *Microlaena stipoides* as a new food crop. PLoS ONE 8:e82641. doi:10.1371/journal.pone.0082641

Singh, I.D., and N.C. Stoskopf. 1971. Harvest index in cereals. Agron. J. 63:224–226.

Smartt, J. 1990. 5. Vavilov's Law of Homologous Series and *de novo* crop plant domestication. Biol. J. Linn. Soc. Lond. 39:27–38. doi:10.1111/j.1095-8312.1990.tb01610.x

Smith, B.D. 2006. Eastern North America as an independent center of plant domestication. Proc. Natl. Acad. Sci. USA 103:12223–12228. doi:10.1073/pnas.0604335103

Smith, B.D., and R.A. Yarnell. 2009. Initial formation of an indigenous crop complex in eastern North America at 3800 BP. Proc. Natl. Acad. Sci. USA 106:6561–6566. doi:10.1073/pnas.0901846106

Sobrevila, C. 2008. The role of indigenous peoples in biodiversity conservation: The natural but often forgotten partners. World Bank, Washington, DC.

Till, B.J., T. Zerr, L. Comai, and S. Henikoff. 2006. A protocol for TILLING and Ecotilling in plants and animals. Nat. Protoc. 1:2465–2477. doi:10.1038/nprot.2006.329

Tollenaar, M. 1989. Genetic improvement in grain yield of commercial maize hybrids grown in Ontario from 1959 to 1988. Crop Sci. 29:1365–1371. doi:10.2135/cropsci1989.0011183X002900060007x

United Nations. 1999. Human development report 1999. Oxford Univ. Press, New York.

Van Tassel, D.L., S.R. Asselin, S.A. Cox, G. Sideli, and D.J. Cattani. 2014. Evaluating perennial candidates for domestication: Lessons from wild sunflower relatives. In: C. Batello, L. Wade, S. Cox, N. Pogna, A. Bozzini, and J. Choptiany, editors, Perennial crops for food security: Proc. of the FAO Expert Workshop, 28–30 Aug. 2013. FAO, Rome. p. 112–140.

Varshney, R.K., J. Ribaut, E.S. Buckler, R. Tuberosa, J.A. Rafalski, and P. Langridge. 2012. Can genomics boost productivity of orphan crops? Nat. Biotechnol. 30:1172–1176. doi:10.1038/nbt.2440

Wagoner, P. 1990. Perennial grain: New use for intermediate wheatgrass. J. Soil Water Conserv. 45:81–82.

Watt, C., S. Cox, and C.J. Coyne. 2005. Measurement of domestication traits in perennial Cicer species. ASA-CCSA-SSSA Int. Annu. Meetings. Salt Lake City, UT. ASA, CCSA, and SSSA, Madison, WI.

Weaver, J.E., L.A. Stoddart, and W.M. Noll. 1935. Response of the prairie to the great drought of 1934. Ecology 16:612–629. doi:10.2307/1932592

Wulff, B.B.H., and M.J. Moscou. 2014. Strategies for transferring resistance into wheat: From wide crosses to GM cassettes. Front. Plant Sci. 5. doi:10.3389/fpls.2014.00692

Zhang, X., L.R. DeHaan, L. Higgins, T.W. Markowski, D.L. Wyse, and J.A. Anderson. 2014. New insights into high-molecular-weight glutenin subunits and sub-genomes of the perennial crop *Thinopyrum intermedium* (Triticeae). J. Cereal Sci. 59:203–210. doi:10.1016/j.jcs.2014.01.008

Zhang, X., A. Sallam, L. Gao, T. Kantarski, J. Poland, L.R. DeHaan, D.L. Wyse, and J.A. Anderson. 2016. Establishment and optimization of genomic selection to accelerate the domestication and improvement of intermediate wheatgrass. Plant Genome 9. doi:10.3835/plantgenome2015.07.0059