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Invited Expert Review

Toward the Domestication of Lignocellulosic Energy Crops: Learning from Food Crop Domestication

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Abstract

Domestication of cereal crops has provided a stable source of food for thousands of years. The extent to which lignocellulosic crops will contribute to the world's renewable energy depends largely on how the new crops will be domesticated. Growing miscanthus as biofuel feedstocks on marginal and degraded land in northern and northwestern China offers an example for developing theoretical framework and practical strategies for energy crop domestication. The domestication should incorporate the highest possible genetic diversity from wild species, focus on the improvement of drought and cold tolerance especially in the stage of crop establishment, increase the efficiencies of water and nutrient uses and photosynthesis, adjust vegetative growing season according to local temperature and precipitation, and reduce or prevent seed production. Positive ecological effects on soil conservation, landscape restoration, carbon sequestration, and hydrological cycles should be maximized, while negative impact on biodiversity needs to be minimized. With the development of other sources of renewable energy, the role of lignocellulosic crops may evolve from primarily energy production to increasingly ecological restoration and biomaterial development. The integration of this new cropping system into the existing agriculture may open a new avenue to the long-term sustainability of our society.

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Introduction

Food crop domestication that began approximately 10 000 years ago marked one of the most dramatic evolutionary events in human history (Diamond 2002). It relieved a large proportion of the population from food production to perform diverse social activities, which laid the foundation of civilization. The majority of food crops were domesticated from wild grasses, including wheat, rice, maize, barley, sorghum, oats, and millets, collectively known as cereals. It seems coincidental that domestication of major cereal crops started in different continents within a relatively short period of time: wheat and barley in Middle East ~10 000 years ago, rice in China ~8 000 years ago, and maize in Central America ~7 000–9 000 ago (Doebley et al. 2006).

Although it is still unclear what exactly drove these independent domestications, one common factor considered in various hypotheses is the climate change following the last glacial maximum (Sage 1995; Richerson et al. 2001; Cunniff et al. 2008). The changes of climates and subsequently global vegetation either provided opportunities for humans to explore the expanding grassland for food or forced them to develop a more reliable food source to feed the growing populations facing increasingly limited food available through hunting and gathering. In any event, it seems likely that humans' intrinsic needs combined with climate changes at the time triggered the massive domestication of various plant species that in turn led to the unprecedented evolution of the human society.

Equally dramatic was the impact of food crop domestication on Earth's land surface (Kareiva et al. 2007). Approximately

1.4 billion hectares or ∼10% of the terrestrial ecosystems have been converted to cropland. Cereal crops are currently produced on about half or ∼0.7 billion hectares of the cropland, of which the three top food crops, maize, rice, and wheat, take ∼0.55 billion hectares (http://faostat.fao.org).

Another event that more recently transformed human society was the Industrial Revolution, starting in the later part of the 18th century. It fundamentally changed the way energy is used. Previously, people relied exclusively on fuel wood, crop residues, and forage for cooking, heating, and transportation. Afterward fossil fuels quickly became the dominant energy source. Following two centuries of rapid consumption of fossil fuels, we are now facing the depletion of fossil energy and consequently an anthropogenic climate change. This leaves us with no choice but to switch to renewable sources of energy that do not add greenhouse gas (GHG) to the atmosphere.

Of the various types of renewable energy, the potential of bioenergy has been the subject of continuous debate, especially concerning net energy generation, GHG mitigation, and food security (Rajagopal et al. 2007; Fargione et al. 2008; Heaton et al. 2008a; Robertson et al. 2008; Schmer et al. 2008; Searchinger et al. 2008; Henry 2010). For the most part, this is because we have not come to a consensus on the performance of energy crops. In fact, we do not yet have a fully domesticated crop dedicated to energy production. If the magnitude of impact of energy crop domestication can be anywhere near that of food crop domestication, this new round of domestication will hold enormous potential to meet our energy and environment needs. Whereas the earliest framers could have never imagined the impact of food crop domestication, we are now in a much better position to project and control the processes of energy crop domestication.

In this article, I attempt to develop a conceptual framework for energy crop domestication, especially through a comparison with food crop domestication. I will emphasize herbaceous perennials that are from the same grass family, Poaceae, as cereals. I will begin by depicting the desirable characteristics of energy crops, and then compare domestication traits and processes between energy and food crops. With these established, the environmental impact and sustainability of energy crop domestication will be discussed. I will take miscanthus as a primary example and consider its domestication in China where native *Miscanthus* species are most abundant and energy consumption and GHG emission have increased rapidly.

Lignocellulosic Energy Crops

Here energy crops are defined as domesticated plants that are grown for energy production. Two major categories of energy crops have been recognized. First-generation energy crops are those that were previously domesticated for food, sugar or vegetable oil, but are now grown for making liquid biofuels such as bioethanol and biodiesel. The most common first-generation energy crops include maize, sugarcane, soybean, and rapeseed.

While the use of first-generation energy crops takes advantage of well-developed biorefinery technologies, a growing body of evidence indicates that these crops cannot provide a sustainable solution to energy shortage or climate change. This is because the annual crops require high energy input for tillage, planting, irrigation, and fertilization, resulting in relatively low net energy output and a weak ability of GHG mitigation. Additionally, diverting these crops for energy production requires more cropland to compensate food, sugar, and vegetable oil supplies. Expanding cropland by converting from productive natural ecosystems will turn carbon sinks to sources and worsen soil erosion and GHG emission (Fargione et al. 2008; Robertson et al. 2008; Searchinger et al. 2008).

Because the existing crops cannot meet the goal of sustainable bioenergy production, new energy crops have been explored. To overcome the problems mentioned above, the new crops should be grown on marginal land unsuitable for food production. They should have a high biomass yield with relatively little irrigation or fertilization. Energy input involving tillage, planting, harvest, storage, and transportation should be minimized. These crops, domesticated specifically for energy production, are referred to as second-generation energy crops (Heaton et al. 2008b; Karp and Shield 2008; Oliver et al. 2009). Lignocellulosic crops, which provide biomass as feedstock for bioelectricity or bioethanol production, are a predominant type of second-generation energy crops.

Miscanthus has emerged as one of the most promising candidates for lignocellulosic energy crops in the temperate regions (Long 1987; Lewandowski et al. 2000; Somerville et al. 2010). This perennial grass has C4 photosynthesis and high water and nutrient use efficiencies. It has a high biomass yield under a wide range of climatic conditions, especially in cool temperate regions where productive C4 plants are rare but marginal and low-productivity land can be abundant (Boehmel et al. 2008; Wang et al. 2008; Dohleman and Long 2009; Sang and Zhu 2010). Once established, above-ground biomass of miscanthus is harvested annually as biofuel feedstock for up to 20 years (Zub and Brancourt-Hulmel 2010). Shoots are harvested following senescence, which allows nutrients to be translocated to rhizomes where they are stored for supporting the next-year growth.

Miscanthus × *giganteus* is a naturally occurring triploid hybrid between *M. sinensis* and *M. sacchariflorus* originated in Japan (Hodkinson et al. 2002). Field trials in the US suggested that on cropland, *M.* × *giganteus* could reach a dry biomass yield of more than 30 tons/hectare with little fertilization (Heaton et al. 2008a). If this yield level is widely achieved in the country, less than half of the 14.2 million hectares of the US cropland that is currently set aside for conservation could produce enough biomass for making 132 billion liters of ethanol (Somerville et al. 2010). This would offset 20% of the US gasoline use and 30% of US CO_2 emission from petroleum in 2008 (Heaton et al. 2008a).

However, this miscanthus production model does not fit other regions of the world where there is no surplus cropland that has been put into conservation. For example, China has less than 9% of the world's cropland that supports more than 20% of the world's population. The already stressed cropland has continued to lose to urbanization and soil salinization. Therefore, in China and other places alike, the criteria for second-generation energy crops have to be adopted more strictly, particularly by limiting their production on non-cropland.

Of approximately 14 *Miscanthus* species found in Asia and Africa (Clifton-Brown et al. 2008), China hosts about seven, including four high-biomass species, *M. floridulus*, *M. lutarioriparius*, *M. sacchariflorus*, and *M. sinensis* (Chen and Renvoize 2006). Miscanthus was suggested to be the most suitable energy crop to grow in the vast area of marginal and degraded land in northern and northwestern China (Sang and Zhu 2010). In these regions, however, climatic and soil conditions are much less favorable than those suited for the wild *Miscanthus* species and *M.* × *giganteus*. Domestication is necessary to make this possible.

Domestication Traits

Domesticating a crop to meet our immediate needs is a new challenge. Fortunately, we have learned a great deal about food crop domestication, on which we can rely for guidance. During the domestication, a combination of physiological and morphological traits was modified under human selection. When a domestication process was completed, it usually gave rise to a new species that formed at least partial reproductive isolation with its wild progenitor.

Cereal crops underwent a suite of phenotypic transitions from wild grasses, known as domestication syndrome (Harland 1992). The most important is probably the loss of grain shattering and seed dormancy, which allowed effective harvesting and planting. Other domestication-related traits include synchronization of flowering time and grain maturation, reduction in tiller number, increase in tiller erectness, enlarged panicles and grains, and the loss of grain covers and coloration that protect them from seed predation. These changes were selected consciously or unconsciously by early farmers to improve grain yield and quality.

Domestication began near the natural habitats of wild progenitors from which plants were brought for cultivation. Crops later experienced changes in climates and field conditions as they spread along with human migration. For example, maize, rice, and wheat, which were domesticated in warm climates, are now grown at much colder high latitudes. This indicates that the crops were capable of adapting to drastic habitat changes through artificial selection and breeding.

For energy crops, habitat change is likely to be one of the early steps of domestication. For miscanthus, cold winter combined with dry spring may be the toughest climatic condition for initial crop establishment in northern and northwestern China. It was reported that miscanthus seedlings and young plants in the first one and two years of planting were relatively susceptible to freezing and drought (Clifton-Brown and Lewandowski 2000a, 2000b). Once fully established, they should have much enhanced cold and drought tolerance and can be produced for many years with abiotic stresses less of a concern.

After establishment, the annual yield is the next important factor to consider. Only with sufficiently high yield will it effectively provide feedstock for bioelectricity generation at a power plant or bioethanol production at a biorefinery. The lower the yield, the larger radius of crop field is needed to support a power plant or refinery. This consequently increases transportation cost and energy input. Irrigation and fertilization can improve yield, but require substantial energy input. Thus successful crops will have to rely on rainfall and minimal fertilization to reach the expected yield level.

In those regions of northern and northwestern China, annual precipitation is usually lower than 500 mm. For most of these areas such as the Loess Plateau, annual precipitation is unevenly distributed, with the majority of it occurring between May and October. Heavy summer rains have been a major cause of serious erosion and even disastrous debris flow. On the encouraging side, however, the raining season overlaps well with the growing season of miscanthus. Thus the ability to utilize most, e.g., $>$80%, of annual precipitation serves as a key factor for realizing the yield potential of miscanthus. After shoot senescence, rhizomes go dormant and require little water to get a through dry winter.

With the above discussion, miscanthus energy crops suited for marginal land in cold and dry climates begin to take shape. Newly established crops, especially seedlings and second-year plants, should have strong drought and cold resistance. Sprouting and flowering times should match closely the beginning and end of the warm and wet season so that the crops can have the maximal duration of vegetative growth. They should have the highest possible photosynthetic rates under the optimal growing conditions. The crops should have the highest possible water and nutrient use efficiencies. Rhizomes should suffer from the least drought or freezing damage over winter.

Additionally, seed production not only takes resources away from continuing growth of vegetative biomass harvested as biofuel feedstock, but also reduces the amount of nutrients returned annually to the rhizomes (Heaton et al. 2008b). Although miscanthus seeds are small and light, minimizing seed production should still help improve feedstock yield. In this regard, a sterile hybrid like *M.* × *giganteus* is advantageous. However, total sterility has its own drawback as being unable to breed with other varieties for further crop improvement. To balance these aspects, an ideal crop probably should be either male or female sterile but not both. Varieties with few seed production through inbreeding seem also acceptable as long as they are isolated from each other in the field. These features will help prevent the crops from becoming invasive when they are grown in exotic regions.

Strategies and Processes of Domestication

With recent advances in grass genomics, considerable progress has been made toward characterizing the genetic basis and processes of cereal domestication (Salamini et al. 2002; Glémin and Bataillon 2009; Sang 2009). Population dynamics of domestication in general is better understood at both genetic and genomic levels (Gepts 2004; Doebley et al. 2006; Ross-Ibarra et al. 2007; Burger et al. 2008; Purugganan and Fuller 2009; Sang 2009; Gross and Olsen 2010; Tang et al. 2010). This growing body of knowledge gained from analyzing the previous domestication is invaluable for directing and accelerating energy crop domestication.

Domestication started from selection on one or multiple populations of wild species at a single or multiple locations. Cereal crops derived from the wild progenitors went through a genetic bottleneck leading to severe reduction in genetic diversity (Buckler et al. 2001; Zhu et al. 2007). The ability to utilize a broad genetic variation, especially by accessing to the wild progenitors, can substantially enhance the chance of crop improvement (Tanksley and McCouch 1997; Kovach and McCouch 2008).

The maintenance of a high genetic diversity is of particular importance for a lignocellulosic energy crop because adequate biotic resistance is necessary for the production of a perennial crop with minimal pesticide input. Thus, it is essential that the domestication begins with the broadest possible genetic basis. Moreover, as we learned from rice domestication, genetic diversity could be increased during domestication through crossing between independently domesticated cultivars and/or between newly domesticated crops and the wild progenitors (Sang and Ge 2007a, 2007b). Phylogenetic and population genetic analyses of wild progenitors will be necessary in assisting effective population sampling and cross design during energy crop domestication.

For cereals, a critical domestication trait, such as grain shattering in rice, could be quickly modified through strong selection on a mutation of large phenotypic effect (Li et al. 2006; Zhang et al. 2009), while the entire process of optimizing a trait might have taken much longer (Fuller et al. 2009). Whereas food crop domestication could have proceeded in the field similar to the habitats of wild progenitors, energy crop domestication would have to be carried out under different climatic and soil conditions where the crops are intended to be grown. In this case, selection should be strong as individuals incapable of surviving will die and most likely a small fraction of the tested populations will be purposely selected for further field trials and breeding.

As long as we begin with populations with high genetic diversity, domestication can proceed quickly as genes of large effect become the targets of strong selection. The process can be further accelerated through designed experimental crosses, molecular breeding, and gene transformation. This requires characterization and sequencing of energy crop genomes and genetic studies of important domestication traits, especially those related to abiotic stress resistance and efficiencies of photosynthesis and water and nutrient uses.

As for the further improvement of feedstock quality, such as optimization of plant cell wall compounds and digestibility for making bioethanol, genetic engineering will play an important role (Pauly and Keegstra 2008). This seems analogous to the part of rice domestication processes that modified grain qualities for more effective food processing and storage (Sweeney et al. 2007; Yu et al. 2008). But a major distinction between these two domestication practices is that the previous grain modifications were done primarily under unconscious selection, whereas the biofuel feedstock improvement would be achieved through designed breeding and genetic engineering based on extensive studies of natural variation and biosynthesis of cell wall components (Somerville et al. 2004; Hodgson et al. 2010).

Another difference between food and energy crops is the relation between yield and input. For food crops, yield is the primary concern. To ensure the yield, people have been willing to increase the input of water, fertilizer, labor, and machinery. For energy crops, not only because these resources are likely unavailable but because any increased input will be at the cost of net energy output, the crops would have to grow under tougher conditions with relatively little help from farmers. Will energy crops then be fully domesticated and rely on humans for survival?

If it becomes widely accepted that energy crops should be at least partially sterile, they will have to rely on breeding programs for sexual reproduction. This would also limit their ability to disperse from the field. Another important reliance on humans would be the initial establishment. The survival of seedlings and young plants in unfavorable habitats will require the right planting time, weed control, and at least some irrigation in certain areas. These processes tend to produce fully domesticated crops with considerable modification in a suite of physiological traits but perhaps to a lesser degree in morphological features.

To provide a significant source of renewable energy and to mitigate climate change with lignocellulosic crops, we do not have the luxury of centuries or millennia to experiment with domestication as early farmers did for food crops, but need to come up with reasonably productive crops within one to a few decades. Because we have learned so much from the previous domestication and are equipped with technologies of modern breeding and genetic engineering, this can be achievable. Unlike the largely unconscious and uncontrolled manners of the last domestication, this round of domestication will be performed with precise designs to meet our specific needs and monitored closely for its environmental impacts. While the previous domestication was driven primarily by people's need for a stable source of food under a changing environment, this one is driven by our need for a renewable source of energy that mitigates the anthropogenic climate change (**Table 1**).

Environmental Impact and Sustainability of Domestication

Food crop domestication had a dramatic impact on the terrestrial ecosystems, having turned an enormous area of forests, grassland, and wetland into agricultural fields. The conversion often occurred in regions with mild climates and ample fresh water resources. In China, for example, the vast majority 130 million hectares of cropland is located in southern and eastern portions of the country (Piao et al. 2010). Food production in today's scale comes with a variety of negative environmental effects and faces a growing concern of sustainability (Godfray et al. 2010). To mention just a few, these include the shortage of fresh water for irrigation, increasingly worsened soil erosion and salinization, and reduction in biodiversity. An appealing solution to these problems is to develop more sustainable crops

Table 1. Comparison between food and energy crop domestication from grasses

	Food crops	Energy crops[a]
Purpose of domestication	To provide a stable source of food	To ensure energy and environment security
Time of domestication	Began ~10 000 years ago	From now onward
Duration of domestication[b]	Centuries to millennia	Decades
Driving force of domestication	Climate change following the last glacial maximum, food shortage	Depletion of fossil energy, climatic change resulting from the use of fossil energy
Product of domestication	Grains for human calories	Aboveground biomass as feedstock for producing bioelectricity or liquid biofuels
Focus of domestication	Harvesting and planting efficiencies, grain yield, harvest index, grain processing	Vegetative biomass yield, crop establishment, net energy output, biorefining properties
Domestication transitions	Reduced grain shattering and seed dormancy, synchronized grain maturation, fewer tillers, increased panicle size and fertility, heavier grains, improved grain threshing and quality	Enhanced biotic and abiotic stress resistance, higher water and nutrient use efficiencies, higher photosynthetic rates, optimized growing season, reduced fertility, improved biorefining properties
Habitat change	Not initially required, but later occurred	Initially required for growing on marginal land under less favorable climatic conditions
Artificial selection	Conscious and unconscious selection for desirable domestication traits from large local populations	Purposing selection for domestication traits from genetically divergent populations at locations suitable for crop production
Hybridization	Played a significant role primarily through selection on naturally occurred hybrids	Important from the beginning, with designed crosses and subsequent selection for hybrids with desirable traits
Domestication practice	Simple cycles of growing, harvesting, and selection	Genetic and ecological evaluation of wild progenitors, field trials, experimental crosses, genetic and genomic analyses of domestication traits, molecular breeding, transgenic improvement, theoretical modeling
Consequence of domestication	Human population growth and civilization	Long-term sustainability of the human society

[a] Energy crops considered here are second-generation energy crops growing on marginal land unsuitable for food production.

[b] Duration is defined in a relatively narrow sense that a domestication is considered to be completed as long as the basic domestication related traits are selected.

that have stronger biotic and abiotic stress resistance and less demand for water and fertilizers (Zhang 2007; Godfray et al. 2010). Clearly, this is in alignment with the concept of next-generation energy crops.

Improving environmental sustainability is one of the essential goals of energy crop domestication. Whether it can be achieved depends on what kinds of crops will be domesticated. Taking an example of growing miscanthus crops in northern and northwestern China (Sang and Zhu 2010), converting marginal and degraded land with little vegetation covers would not release a large amount of CO_2 into the atmosphere. Conversely, rapidly developing roots and rhizomes of miscanthus will facilitate carbon sequestration (Clifton-Brown et al. 2007; Brandão et al. 2010). Thus, the land-use change is likely to turn these areas into bigger carbon sinks (Jansson et al. 2010). Along with their main function of mitigating CO_2 emission of fossil fuels, the energy crops should have a positive impact on carbon cycles.

Water availability is probably the most critical factor determining whether the energy crops can establish and how much biomass they can produce. Equally important is the impact of large-scale plantations on the local and regional hydrologic cycles. The marginal and degraded land in the Loess Plateau and northern grassland of China has poor soil quality and vegetation cover. Most precipitation gets away through quick drainage and surface runoff, which is responsible primarily for flood and debris flow following strong storms. Growing perennial energy crops such as miscanthus will significantly reduce surface runoff and slow down drainage (Vanloocke et al. 2010). Meanwhile, it will increase water loss to the atmosphere through transpiration. The long-term balance of these processes and its impact on hydrological cycles is critical not only to the sustainable production of energy crops but also the environmental security of these regions.

Ecological restoration in northern and northwestern China has been a challenging task. The previous efforts through afforestation were largely unsuccessful and possibly made certain situations worse (Chen et al. 2007; Cao 2008; Cao et al. 2009). Limited precipitation in the arid and semiarid regions has been unable to support evapotranspiration of the planted forests. In addition, the deep roots of some big trees such as poplars have drawn a considerable amount of underground water and might have caused underground water levels to drop (Wilske et al. 2009).

In these regions, re-establishment of natural vegetation and planting perennial herbaceous species may very well be the most suitable restoration strategies (Jiang et al. 2006; Zhou et al. 2007; Cao et al. 2010). Miscanthus with shallower but much more extensive root and rhizome systems is more effective than trees in preventing erosion and less likely to cause underground water depletion. As a C4 plant with high water-use efficiency, miscanthus is capable of producing a sufficient amount of biomass without having a negative impact on the hydrological cycles if the plantation is appropriately managed (Smeets et al. 2009; Vanloocke et al. 2010). It is the important task of domestication that further improves water-use efficiency and adjusts the growing season to more effectively utilize local precipitation, which is key to the development of sustainable crops in these regions.

For landscape such as the Loess Plateau, which has suffered from severe erosion, large-scale plantation of miscanthus crops can substantially improve water and soil conservation. Keeping more water in the local hydrological cycle with less risk of erosion would tremendously improve the ecological conditions of the region where limited and uneven precipitation has long been a major factor contributing to land degradation. In this regard, the energy crop could also be viewed as an ecological crop.

In comparison with food crops, miscanthus plantations require much less nitrogen fertilizer or pesticide and provide more stable habitats for wildlife (Clifton-Brown et al. 2008; Heaton et al. 2009; Smeets et al. 2009; Zub and Brancourt-Hulmel 2010). Taken together, the above comparisons suggest that energy crop domestication should have a much less destructive impact on the natural ecosystems than food crop domestication. Nevertheless, the question of how this large-scale land-use change in addition to the past cropland conversion and urbanization can be ultimately sustainable and at the least cost of biodiversity should be addressed through rigorous research (Rowe et al. 2009). During the process of domestication, all ecological effects need to be carefully considered, analyzed, and balanced to maximize the overall benefit for specific landscape dedicated for growing energy crops.

With the development of other sources of renewable energy, land area needed for bioenergy production may be allowed to fluctuate. Fields with soil quality improved through growing energy crops can be rotated for food production or restoration of natural vegetations. In turn, degraded cropland or pastures can be periodically converted for energy crop production that also serves as a function of soil conservation and land restoration. This way of integrating food and energy cropping systems could provide a long-term sustainable solution to agricultural and ecological problems that we have been encountering.

As technology advances, the role of energy crops is likely to evolve. If other sources of renewable energy become more dominant, we may no longer need energy crops in such a large scale. However, our reliance on lignocellulosic crops for providing renewable material is likely to increase (Nilolau et al. 2008). Advances in biotechnology and biochemical engineering will make biomass and other compounds from the lignocellulosic crops more amenable for biorefining and biosynthesis (Ragauskas et al. 2006; Börnke and Broer 2010). This could eventually replace fossil-carbon feedstocks and a large portion of forest products for material production.

With all of these potential roles considered, what we are setting out to domesticate is more likely an energy, material, and ecological crop combined. The growing knowledge about food crop domestication coupled with advances in breeding techniques and biotechnology can considerably accelerate and optimize energy crop domestication to meet our current and future needs. This may initiate another wave of domestications that opens a new avenue to the long-term sustainability of our society.

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