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Commentary

Gourmet grasslands: Harvesting a perennial future

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The global food system is highly dependent on grains, the production of which requires annual biomass turnover, which reduces soil health and undermines sustainability. Investments in diverse perennial grain-producing crops that produce abundant biomass while enhancing ecosystem services are needed to sustain global food production and growing biomass demands.

Putting the brakes on runaway biomass cycling

Humanity depends directly upon the biomass production of Planet Earth for food, fuel, and fiber. Indirectly, we also rely upon the biomass of the planet for continual provision of ecosystem services such as soil formation, nutrient cycling, climate stability, and fresh water. However, as human appropriation of the earth's biomass increases, provision of ecosystem services has declined. We hypothesize that these trends are connected by global food production, specifically the displacement of deep-rooted, long-lived plant communities by fast-growing, short-lived crops whose biomass is completely removed, killed, or plowed under each year. The solution to this problem is not simply research to increase the production of biomass, but R&D toward crops that can grow rapidly and be harvested frequently while investing in some durable, long-lived biomass. The bioenergy community has done exactly this in moving from biomass crops such as maize (annual) toward perennial grass and tree bioenergy crops. Here we argue that a similar investment is needed for food crops.

Changes in biomass turnover time help explain human-driven changes to the global carbon cycle and corresponding degradations of ecosystem services. Forests and grassland have a biomass turnover time of about 14 years.[1] These plant communities represent the mid to late stages of ecological succession, a slow process that often terminates in ancient forests. Although biodiverse and productive, these communities produce little biomass that is digestible to humans. Therefore, humans have cleared the perennial plant communities, replaced them with edible crops, and maintained croplands in a state of early ecological succession through frequent disturbance. Currently, humans appropriate roughly 20%–28% of the potential net primary productivity (NPP) of the planet and may be appropriating up to 35% of potential NPP by 2050.[2] Under crop production, lands that once hosted perennial forests and grasslands now experience complete biomass turnover annually. The results of this conversion have been catastrophic, frequently beginning with severe soil erosion following land denudation. Even after revegetation with short-lived crops, with few living roots in the soil much of the year due to annual biomass turnover, average soil erosion on cropland is 12.7 Mg ha^{-1} year^{-1}, far surpassing rates of soil formation.[3]

The situation persists, in part, due to demand and unsustainable practices. Roughly 70% of human calories are provided by annual grain agriculture.[4] Tillage and herbicides are regularly used to eliminate competing species prior to establishing popular crops like maize, rice, wheat, and beans annually from seed, creating ecosystems trapped in an early-successional state.[5] This system allows large harvests of human-edible grains in the short term but comes at the cost of decreased soil fertility, reduced water-holding capacity, and exacerbation of human-driven climate change. These ecosystem dis-services are produced by the disturbances that accelerate biomass turnover and by the loss of mature, living plant structures that protect soil. Compared with mid-succession soils, early-succession soils are depleted in nutrient- and water-retaining organic matter and show elevated gaseous and leaching losses of nitrogen.

Adopting practices that shift agricultural production toward a mid-successional steady state[5] would increase carbon storage in plant biomass and soil organic matter, partially combating climate change by reducing atmospheric CO_2 and mitigating some of its deleterious effects by improving soil health via increased organic matter. Mid-successional agricultural systems are dominated by plants living for several seasons, with infrequent soil disturbance. Slowly cycling plant biomass, particularly belowground, permits the assembly of biodiverse communities depending on mature plant structures that cannot tolerate frequent physical disruption. Mid-succession communities achieve an intermediate biomass cycling rate that may optimally balance high productivity with high ecosystem services.[5] Regular harvest, burning, or grazing and occasional replanting prevent the system from moving into later successional stages that may have reduced productivity.

Hitting this ecological succession "sweet spot" is not only desirable but viable, as demonstrated by highly productive and sustainable forage and bioenergy production systems.[6] For example, alfalfa is a deep-rooted, nitrogen-fixing perennial that can be repeatedly mowed for hay. Switchgrass and miscanthus are hardy perennial grasses that build soil while allowing annual harvest of high-energy-content biomass.[7] Short-rotation tree crops similarly produce woody roots and trunks but permit regular harvesting of younger branches to maintain the stand in a highly productive state.

Harvested perennial grasslands have provided an excellent benchmark for sustainable biomass production from

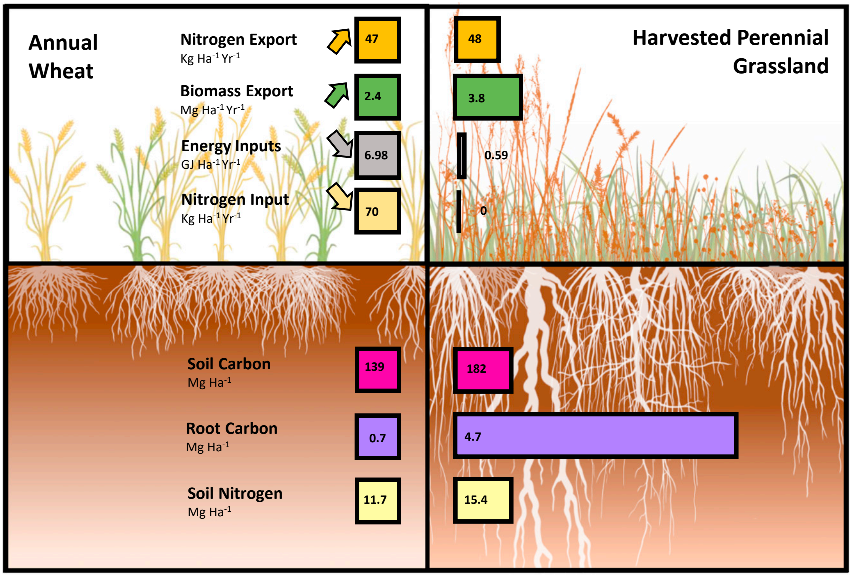

Figure 1. Energy and material flows and standing stocks in annual wheat and perennial hay systems over 75 years

Top panels represent flows into and out of the systems, while the bottom panels represent standing stocks in the systems. Rectangle size in the right panels represents size of the flow or stock relative to the wheat system at left. Note that root carbon in the wheat system turns over annually, so for some portions of the year standing stock of live root biomass is zero.

mid-successional systems (Figure 1). Glover et al. compared paired sites with annual wheat production fields adjacent to native perennial grasslands from which the aboveground biomass was harvested as hay annually.[8] Over 75 years, grassland harvest resulted in nitrogen removal similar to harvest of wheat. Despite similar nitrogen export and no fertilizer, the grassland system maintained 4 Mg ha^{-1} more total soil nitrogen. Furthermore, the grassland system maintained 43 Mg ha^{-1} more soil organic carbon than annual wheat production. Wheat production required 11.75 times the energy input of the grassland production system, with 60% of in-field energy use in wheat due to nitrogen fertilizer. The root biomass, 6.7 times greater than wheat and present year-round in the grassland, is likely the driving force behind the efficient carbon and nitrogen cycling in the grassland system.

The profound conservation benefits resulting from perennial cover were used to justify policy establishing the US Conservation Reserve Program in 1985 and sustaining it to the present day. In 2007, the program paid for non-harvested vegetative cover (mostly perennial species) on 14.9 million hectares in the USA.[6] Is this story too good to be true? Biodiverse grasslands from which humans can perpetually extract huge quantities of protein and carbohydrate without seeming to reduce their ability to produce these goods in the future? What's the catch?

The catch is that humans cannot efficiently consume hay, even though it is a rich source of plant protein, and we cannot digest or metabolize the most abundant carbohydrates in hay. Ruminant mammals can digest cellulose, but they also metabolize a large proportion of the energy before humans get a chance to obtain energy from meat or dairy products. Mid-successional systems that meet human demand and requirements for food remain an outstanding challenge.

Human food from novel mid-successional agro-ecosystems

Humans are consummately adaptable. We do not foresee our species giving up on a promising new opportunity simply because we inherited teeth, alimentary canal, and digestive enzymes that are poorly adapted to eating grass and forbs. Indeed, several innovative new crops and technologies have been proposed to permit the production of abundant food from mid-successional systems (Table 1). Given adequate research investment, any one or a combination of these approaches could one day largely replace annual grains as the primary source of human calories.

The biorefinery

The "biorefinery" has been proposed to convert mid-successional biomass into a form that is directly edible for humans.[9] The biochemical and engineering challenges are daunting: anti-nutritive factors must be eliminated, proteins concentrated, and abundant indigestible molecules such as cellulose must be converted into digestible starches and sugars, with the outcome palatable. Conceptually, we could view this option as the evolution of an artificial rumen that enables humans to become leaf-eaters. Therefore, we know that it is biophysically possible for mammals (and their microbiome) to subsist on leaves. The chemical pathways are known and enzyme manipulation is standard practice in biotechnology, but to be ecologically and economically viable, biorefined food from perennial biomass would need to be produced at lower energetic and environmental cost than naturally grown food. Furthermore, the healthfulness and acceptability of such food in society remains an open question. However, the enthusiasm currently developing around plant-based and lab-cultured meat products does provide some indication that biorefined foods have potential for broad acceptance. Clark and Fabien proposed that processing in biorefineries could be simplified by developing plant strains that produce a greater proportion of desirable feedstock.[9] The next approach takes this recommendation to its logical conclusion.

Perennial grain systems

Many of the annual grain crops that feed humanity have perennial relatives that live for numerous years and are at home in mid-successional ecosystems. For example, wheat, sorghum, and sunflower can be hybridized with hardy perennial relatives. For nearly a century, the idea has been circulating among plant breeders and geneticists to use wide hybridization or even more advanced methods to combine the long-lived perennial nature of these wild relatives with the high capacity of domestic grain crops to produce human-edible food. Early efforts, such as developing perennial wheat beginning in the 1920s, ended in frustration, perhaps due to the unavailability of modern tools to study the complex interactions that occur between the chromosomes and

Table 1. Relative strengths and weaknesses of annual grain crop production compared to alternative approaches using perennial species

	Annual grain crops	Annuals and perennial ground covers	Perennial grain crops	Biomass crops and biorefineries	Tree staple crops
Ecological succession	early	mid	mid	mid	mid to late
R&D status	many cultivars, globally adopted	promising on-farm trials	early commercial production	conceptual, futuristic	constrained to specialty crops
Minimum time to widespread adoption	none	years	decades	many decades	many decades
Harvest technology	standard	standard	standard	standard	expensive
Need for dietary change	none	none	little	extreme	large
Crop establishment period	short	short	short to medium	short to medium	long
New research investment required	none	$	$$$	$$$$	$$$$
System biodiversity	–	+	++	+++	++
Soil carbon/soil health	–	+	+++	+++	+++
Efficient nutrient cycling	–	+	+++	+++	+++

With sufficient investment, any of these techniques could fill the current role of annual grains in the human diet.

genes of different species when they are intermated . Sterility has been common, and plants with longevity and high grain yield were elusive, suggesting to some that the energetic cost of reserving resources for perennial regrowth may preclude simultaneous abundant grain production.

However, in a recent breakthrough, perennial rice, developed by hybridizing annual rice with the perennial relative *Oryza longistaminata*, yielded grain equivalent to annual rice in quality and quantity while surviving for multiple harvests.[10] Regrowing perennial rice can save farmers about half the usual cost of purchased inputs in the regrowing seasons, in part due to reduced tillage and fertilizer. Therefore, this perennial grain has shown potential to reduce tillage and other inputs derived from fossil fuels while maintaining similar output of food. And this system is appealing to farmers because it has enhanced profitability. It is striking to find an agricultural practice that greatly enhances both profitability and sustainability without requiring government subsidies or specialty pricing.

In addition to rice, programs are underway to develop perennial grains via wide hybridization with wheat and grain sorghum, and others are possible.[4] Another approach to developing perennial grain crops is to domesticate wild perennials, and programs in the legume, sunflower, and grass families are ongoing. Modern genetic tools are particularly relevant to these efforts, potentially achieving in a decade or two what took our ancestors centuries to accomplish. Genomic selection uses statistical predictions based on abundant genetic markers to allow selection at the seedling stage, eliminating the drawback of long time frames for breeding perennials.[11] Continued innovation in DNA sequencing and phenomic technologies is making new domestication projects more affordable. Genome editing techniques may be even more powerful, producing plants with domestic phenotypes in just a few years by editing corresponding genes in wild perennials to obtain the function of known domestication genes in annual crops.[12] As knowledge of genes controlling perenniality and domestication traits builds, numerous perennial species may be rapidly domesticated for a wide array of production environments and human uses.

Perennials intercropped with annual grains

One approach to bring the benefits of perennials to annual crop production systems in the near term is to grow perennial species alongside annual grain crops. Growing strips of perennial herbaceous plants within crop fields provides numerous benefits to water quality, soil conservation, and wildlife habitat. Woody perennials also have been successfully integrated for conservation purposes. However, these methods require the farmer to remove roughly 10% of each field from direct production of human-edible crops.

A technique that is rapidly gaining attention and research investment is to establish dense stands of long-lived low-growing species within grain-producing fields to enhance soil quality and regenerate water, carbon, and nutrient cycles.[13] These perennial ground covers can also contribute economically through nitrogen fixation (with legumes) or the production of forage for livestock. However, the system will require fine-tuning to prevent yield loss through competitive growth of the perennial cover crop, and it remains to be seen if the short-rooted perennial grasses and legumes currently favored for this purpose produce sufficient mature below-ground biomass to perform a full range of ecosystem services, including carbon storage.

Expanded tree cropping

Numerous tree species produce fruits and nuts that are nutritious and flavorful.

Although tree crops currently provide less than 10% of human caloric needs on a global scale, this status is by no means fixed. Molnar et al. have argued that tree crops are underutilized due to limited investment in breeding them for enhanced production and broad adaptation.[14] So far, even highly productive nut crops produce food that remains a specialty item, rather than a human staple, due to high cost. The high cost may in part be explained by the expense of labor and special machinery involved in nut production. Transforming nuts into easily managed staple crops would require a radical genetic reshaping of the plant, or perhaps a revolution in robotic harvest technology. Either approach would likely require a long-term investment in research and development.

Conclusion

Human appropriation of planetary biomass is threatening to undermine the ecosystem services upon which humanity and much of the biosphere depend. Among the available solutions to this growing crisis, we believe perennial grain crops are the most elegant potential pathway to long-term global food security.[15] Perennial grain agroecosystems would provide ecosystem services similar to natural grasslands. Grasslands, while less iconic than mountains and forests in the popular imagination, have a long history of resilience to human use and can be species-rich, serving as important biodiversity refuges. Only in the last decade have biological tools and understanding matured to the point where perennial grain crops can be developed in reasonable timescales. Since proof of concept has been recently demonstrated with perennial rice and progress achieved with other species, now is the time to expand work to develop perennial grain crops worldwide.

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