

# Perennial Grain and Oilseed Crops

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## Keywords

intermediate wheatgrass, domestication, perennial food quality, perennial management

## Abstract

Historically, agroecosystems have been designed to produce food. Modern societies now demand more from food systems—not only food, fuel, and fiber, but also a variety of ecosystem services. And although today's farming practices are producing unprecedented yields, they are also contributing to ecosystem problems such as soil erosion, greenhouse gas emissions, and water pollution. This review highlights the potential benefits of perennial grains and oilseeds and discusses recent progress in their development. Because of perennials' extended growing season and deep root systems, they may require less fertilizer, help prevent runoff, and be more drought tolerant than annuals. Their production is expected to reduce tillage, which could positively affect biodiversity. End-use possibilities involve food, feed, fuel, and nonfood bioproducts. Fostering multidisciplinary collaborations will be essential for the successful integration of perennials into commercial cropping and food-processing systems.

## Contents

INTRODUCTION .....	704
Phenotypic Changes Under Domestication .....	707
Are High-Yielding Perennials Achievable? .....	707
THE CURRENT STATUS OF PERENNIAL CEREAL AND OILSEED GENETICS .....	707
Breeding Goals .....	708
Lessons from the Domestication Syndrome .....	708
Breeding Methods and Technologies .....	708
Creating Initial Breeding Populations .....	709
Improving Breeding Populations .....	709
Developing Perennial Grain Cultivars .....	711
GENOMIC TOOLS AND TECHNOLOGIES FOR PERENNIAL GRAIN DEVELOPMENT .....	712
Opportunities and Challenges in Exploring the Genomes of Perennial Grain Crops .....	712
Integration of New Technologies in the Improvement of Perennial Grain Crops .....	713
AGROECOLOGICAL EFFECTS OF PERENNIAL GRAIN CROPS .....	714
Water Quality and Quantity .....	714
Greenhouse Gas Emissions .....	715
Pests and Beneficial Organisms .....	716
FOOD USE .....	718
COORDINATED DEVELOPMENT METHODS .....	722

## INTRODUCTION

Society's conception of agroecosystems is constantly evolving. Throughout history, various crops and agricultural systems have been discovered, abandoned, and rediscovered. The study of these changing landscapes provides insights into the ever-changing human ethos of food and the environment. In ancient times, farmers utilized many grain and oilseed production systems and may have selected for perennial habit during the initial stages of rice domestication. However, annual production was eventually adopted to increase production (62). Green Revolution technologies have dramatically enhanced crop yields (11, 47) but have reduced ecosystem service outputs (136). Predictions regarding changes in global population (42, 114), declining natural capital (69), and diminished ecosystem service delivery (137) have renewed interest in systematically developing a wide range of perennial crops.

The use of perennial grains is generally folded into the concepts of sustainable intensification and creative land management. For nearly 100 years, the development of perennial cereal grains has been explored in many localities, with much of the initial effort attributable to Nikolai Vavilov (64, 141) (**Table 1**). Although the concept has been appealing to many, there have been few sustained efforts in perennial grain development. Recent advances in genetics, agronomy, and food chemistry allow a reevaluation of the feasibility of perennial production and of the overall concept of domestication for any species of interest. This review documents the history of perennial grain research, the different breeding methods that have been used in perennial grains, the current

**Table 1** Species and hybrids that have been explored as possible perennial crops

Species	Common name	Mating system	Haploid genome size	Chromosome number	Ploidy	Length of time bred	Strategy	Nearest crop/model relative
<i>Helianthus annuus</i> × <i>Helianthus tuberosus</i>	Perennial sunflower	Outcrossing	9.5 pg	$2n = 4x = 68$	Tetraploid	10 years	Modified domestication	<i>Helianthus annuus</i>
<i>Thinopyrum intermedium</i>	Intermediate wheatgrass	Outcrossing	13.1 pg	$2n = 6x = 42$	Hexaploid	30 years	Direct domestication	<i>Triticum aestivum</i>
<i>Helianthus maximiliani</i>	Maximilian sunflower	Outcrossing	Unknown	$2n = 2x = 34$	Diploid	15 years	Direct domestication	<i>Helianthus annuus</i>
<i>Helianthus divaricatus</i> × <i>Helianthus annuus</i>	Diploid perennial sunflower	Outcrossing	Unknown	$2n = 2x = 34$	Diploid	1 year	Modified domestication	<i>Helianthus annuus</i>
<i>Helianthus divaricatus</i>	Woodland sunflower	Outcrossing	8.45 pg	$2n = 2x = 34$	Diploid	1 year	Direct domestication	<i>Helianthus annuus</i>
<i>Triticum aestivum</i> × <i>Thinopyrum intermedium</i>	Perennial wheat	Selfing	Unknown	$2n = 6x = 42-56$	Amphiploid	90 years	Interspecific hybridization	<i>Triticum aestivum</i>
<i>Oryza sativa</i> × <i>Oryza longistaminata</i>	Perennial rice	Selfing	Unknown	$2n = 2x = 24$	Diploid	25 years	Interspecific hybridization	<i>Oryza sativa</i>
<i>Cajanus cajan</i>	Pigeon pea	Outcrossing	0.88 pg	$2n = 2x = 22$	Diploid	90 years	Perennial grown as an annual, with the goal of changing agricultural systems to perennial cultivation	<i>Cajanus cajan</i>
<i>Secale cereale</i> × <i>Secale montanum</i>	Perennial rye	Outcrossing	9.45 pg	$2n = 2x = 14$	Diploid	40 years	Interspecific hybridization	<i>Secale cereale</i>

(Continued)

**Table 1 (Continued)**

Species	Common name	Mating system	Haploid genome size	Chromosome number	Ploidy	Length of time bred	Strategy	Nearest crop/model relative
<i>Zea mays</i> × <i>Tripsacum dactyloides</i>	Perennial maize	Outcrossing	Unknown	Unknown	Amphiploid	40 years	Interspecific hybridization	<i>Zea mays</i>
<i>Zea diploperennis</i>	Perennial maize	Outcrossing	2.65 pg	$2n = 2x = 20$	Diploid	20 years	Direct domestication	<i>Zea mays</i>
<i>Avena sativa</i> × <i>Avena macrostachya</i>	Perennial oat	Selfing	13.23 pg	$2n = 6x = 42$	Hexaploid	20 years	Interspecific hybridization	<i>Avena sativa</i>
<i>Sorghum bicolor</i> × <i>Sorghum halepense</i>	Perennial sorghum	Outcrossing	Unknown	Unknown	Mixaploid	20 years	Interspecific hybridization	<i>Sorghum bicolor</i>
<i>Microdena stipoides</i>	Weeping rice grass	Outcrossing	0.92 pg	$2n = 4x = 48$	Tetraploid	15 years	Direct domestication	<i>Oryza sativa</i>
<i>Hordeum vulgare</i> × <i>Hordeum jubatum</i>	Perennial barley	Outcrossing	Unknown	$2n = 3x = 21$	Amphiploid	90 years	Interspecific hybridization	<i>Hordeum vulgare</i>
<i>Hordeum bulbosum</i>	Perennial barley	Outcrossing	5.50 pg	$2n = 2x = 14$	Diploid	90 years	Direct domestication	<i>Hordeum vulgare</i>
<i>Desmanthus illinoensis</i>	Illinois bundleflower	Selfing	Unknown	$2n = 2x = 28$	Diploid	25 years	Direct domestication	NA
<i>Silphium integrifolium</i>	Rosin weed	Outcrossing	Unknown	$2n = 2x = 14$	Diploid	10 years	Direct domestication	NA
<i>Silphium laciniatum</i>	Compass plant	Outcrossing	8.31 pg	$2n = 2x = 14$	Diploid	10 years	Direct domestication	NA

Abbreviation: NA, not applicable.

status of perennial cereal and oilseed genetics, the environmental benefits of different perennial cropping systems, the potential food uses of perennials, and coordinated developments that have been used to better fit crops to the landscape. Throughout this review, we use the example of intermediate wheatgrass (IWG, *Thinopyrum intermedium*) to illustrate the principles of perennial grain development.

### Phenotypic Changes Under Domestication

Domestication of a plant species involves selecting and modifying its wild progenitor to meet human needs. The grass family, Poaceae, is the most important plant family in terms of human caloric intake and crop production (3) and has been central to our understanding of domestication (34, 80, 81, 118, 132). As a consequence of the domestication syndrome, many grain crops share crucial traits such as reduced seed dispersal (shattering), minimized seed dormancy, and free threshing (i.e., where the glumes break and expose the naked grain) (55). Improvement traits after domestication include large seed size, high grain yield, superior grain quality, high fertility, uniform flowering and seed maturation, reduced branching, lodging resistance, resistance to biotic and abiotic stresses, and reduced toxicity. Agriculture has shifted toward mechanization, requiring modern crop cultivars to be more uniform (11). The combination of highly productive varieties and labor-saving cropping methods may have led plant breeders to overlook potentially promising crop phenotypes, particularly if modern definitions of productivity were expanded to include ecological, economic, and production sustainability (42, 51, 75, 137). Furthermore, investigations into perennial fruit crops have revealed that the phenotypes of domestication traits in perennial species differ from those in annual species, which implies that the plant form selected for must be carefully thought out (94). These differences have led to a rethinking of the ideal plant phenotype (ideotype) in grain crops and suggest that the domestication syndrome phenotype is the most productive ideotype in more complex agroecosystems (51). Recent work on the genetics of domestication and improved breeding technologies may provide an opportunity to identify new plant forms with agriculturally useful properties (51, 125, 132).

### Are High-Yielding Perennials Achievable?

New ideotypes have been developed and new thoughts on the nature of domestication have been postulated, yet there are lingering criticisms of high-yielding perennial grains. The major criticism revolves around the fact that this plant type has not been found in nature and will likely not exist based on predictions of trade-offs between longevity and seed production (33). The primary question is whether it is physiologically possible for a plant to allocate resources to both sexual and asexual production in a way that would allow for yields comparable to those of annual grains. However, a framework has been developed in which the longer growing period of perennial plants captures more photosynthate, which could be allocated to both sexual and asexual reproduction (25, 29, 35). Additionally, in a controlled agroecosystem it may be possible to develop new life history strategies. There has been little effort to understand how perennial plants allocate resources in response to selection in managed environments, the potential for initial gains from selection, and the relationship between production environments and perennial habit.

## THE CURRENT STATUS OF PERENNIAL CEREAL AND OILSEED GENETICS

Two major strategies are being used to develop perennial grain crops: interspecific hybridization and direct domestication (26). Interspecific hybridization involves crossing an annual cultivated crop with related perennial species, then using subsequent breeding strategies to retain the

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**Domestication syndrome:** the group of shared traits related to domestication, such as reduced seed dispersal (shattering), minimized seed dormancy, and free threshing

**Ideotype:** the ideal plant phenotype

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perennial habit along with genes controlling large seed size, shattering resistance, free threshing, and end-use quality. However, obtaining chromosomal stability and perenniality while preserving the domestication traits is challenging. Direct domestication of wild perennial species has the benefit of retaining perenniality, but substantial time is needed to improve shattering resistance, threshing ability, seed size, grain yield, and other domestication traits.

## Breeding Goals

All the perennial grain crops listed in **Table 1** were developed from wild species or are directly related to wild species. For example, IWG was developed from a wild perennial grass, and perennial wheat is being developed from the hybridization between annual wheat and wild wheatgrass. Many staple food crops were also domesticated from wild grasses, including wheat, rice, maize, barley, sorghum, oats, and millets (119). The development of perennial grain crops also requires improvements of the major determinants of grain yield, i.e., seed size, floret fertility, and head (ear or spike) weight. Wild perennial species usually produce tillers throughout the growing season. Some are nonreproductive tillers but increase the density of the population and reduce the light availability to reproductive tillers, which results in lodging. To improve lodging resistance, the plant architecture should be optimized; desirable traits include medium plant height, moderate tillering capacity, and erect leaves. Heading date, resistance to biotic stresses, tolerance to abiotic stresses, food quality, and nutrient use efficiency should also be considered during the breeding of perennial grain crops.

## Lessons from the Domestication Syndrome

Perennial grain crops are relatives of domesticated annual crops (**Table 1**). In the domesticated annual species, many important traits have been characterized for genetic control. Many major genes that control domestication traits and improvements in annual crops have been identified (78, 92, 118). Many traits are controlled by a few genes of large effect and can be improved efficiently in perennial grain crops once the relevant genes are identified, as there are many known orthologous genes from other species. For example, shattering is controlled by *qSH1* in rice (81), *SH1* in sorghum, rice, and maize (86), and *qPDH1* in soybean (44); plant height is controlled by *Rht-1* in wheat (101), *GA20ox-2* in rice and barley (6, 67), and *dw3* or *d2* in sorghum and pearl millet (95, 100); grain size is controlled by *GS3* in corn and *GS3* and *GS5* in rice (83, 84, 88); threshing ability is controlled by *Q* and *Nud* (39, 131); flowering time is controlled by *VRN1* in barley, wheat, and ryegrass (7); grain weight is controlled by *GW2* in rice (82), wheat, and corn (83, 118, 127, 129); and glutinous grains are controlled by *GBSSI* or *Waxy* in rice, wheat, corn, foxtail millet, barley, and sorghum (78). Many domestication and improvement traits are conferred by mutations in regulatory genes, such as transcription factors (92), which likely accounts for their large phenotypic effects. Loss of function and alteration of gene expression are by far the most common types of mutations observed in domestication traits of annual grain crops; however, large sequence alterations in the genome (e.g., copy-number variants and large chromosomal rearrangements) are less commonly observed (92). Mutagens that can introduce loss-of-function mutations or putative *cis*-regulatory changes can be used to improve agronomic traits during perennial grain crop domestication.

## Breeding Methods and Technologies

The domestication or development of perennial grain crops takes considerable time. The process comprises four stages: stage I, evaluating wild perennial species and determining the candidate

species; stage II, initiating breeding populations by selecting the best genotypes from the available germplasm and making crosses; stage III, improving the breeding germplasm by fixing the genes or loci for domestication traits and integrating superior alleles for agronomic traits; and stage IV, breeding for the release of cultivars of perennial grain crops (**Figure 1**). Stage I represents species selection criteria; after stage I, many perennial species have been evaluated and selected as the candidates for perennial grain crops (**Table 1**). The development of these perennial grain crops ranges from infancy (stage II, e.g., perennial maize, perennial sunflower, and weeping rice grass), to intermediate (stage III, e.g., perennial wheat and IWG), to approaching reality (stage IV, e.g., perennial sorghum, perennial rice, and pigeon pea) (10). Here, we focus mainly on practical breeding methods for developing perennial grain crops at stages II, III, and IV.

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**Linkage disequilibrium:** the nonindependence of alleles

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## Creating Initial Breeding Populations

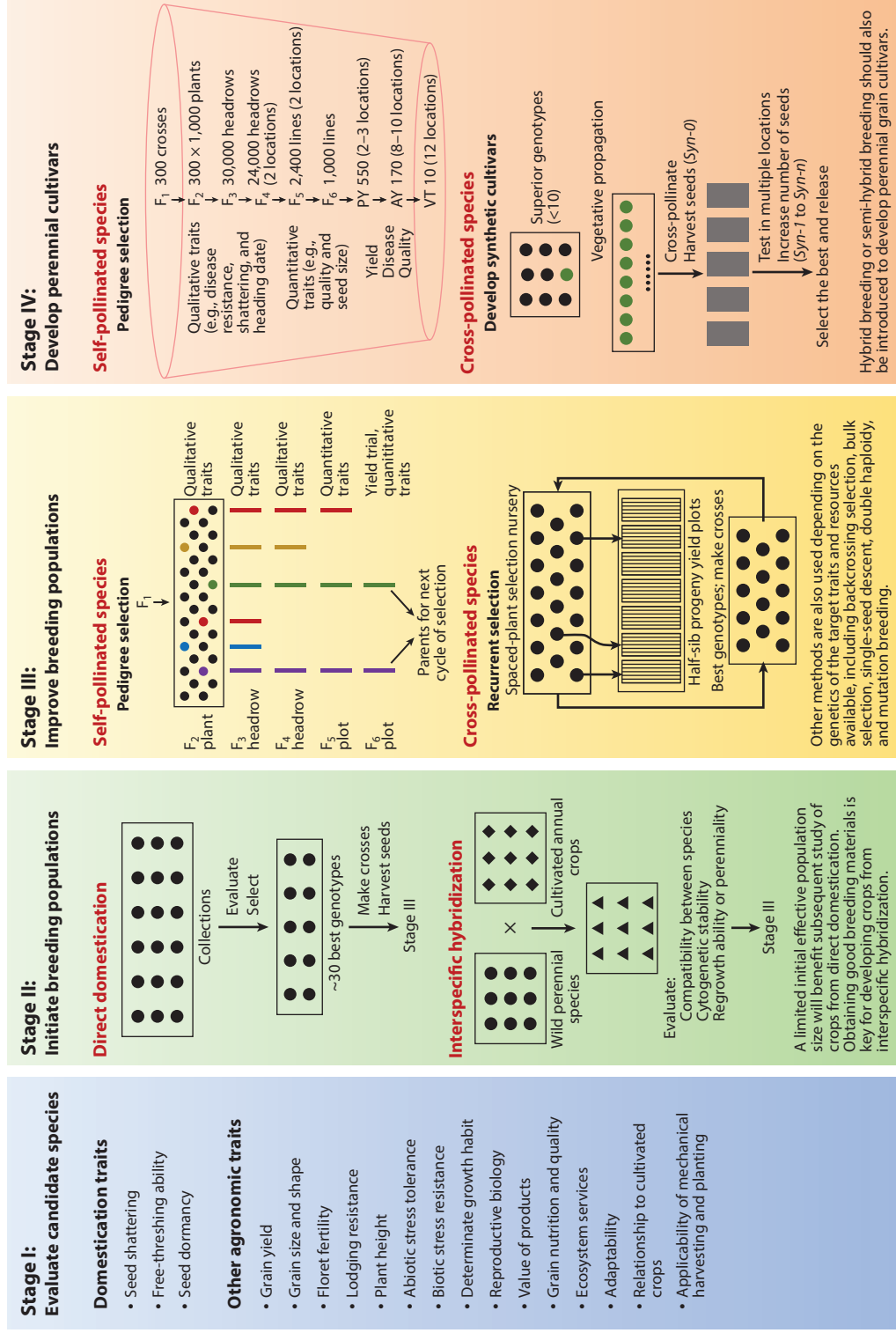
Global germplasm should be evaluated in multiple environments before a breeding program begins. Based on the most important traits, approximately 30 of the best genotypes are selected and become the initial breeding population for domestication. The moderate size of initial breeding populations may limit genetic diversity and contribute to a limited effective population size of the subsequent breeding population. The benefit of moderate effective population size is that it leads to a relatively low rate of linkage disequilibrium decay in the breeding population, and therefore only a small number of markers are required to capture the variations throughout the genome. Thus, selecting a limited number of genotypes from the initial collections will benefit the subsequent genetic analysis and breeding. For example, in the initial breeding of IWG, only 20 genotypes were selected from a collection of 300 genotypes that exhibited both significant variation and low linkage disequilibrium decay. Two thousand single-nucleotide-polymorphism markers were adequate to capture the genomic variation and obtain high predictive ability when applying genomic selection (155).

Obtaining good initial breeding materials is the key step (stage II) for the development of perennial grain crops through interspecific hybridization. Perennial habit can segregate in different ways depending on the parental genotypes and species used (115–117). Among the *Oryza* species suitable as donors of perenniality to annual rice, *O. longistaminata* is well adapted to upland conditions or rain-fed production, can form large monocultures in the wild, and has an AA genome similar to that of *O. sativa*. Thus, *O. longistaminata* was predominantly used as the source of genes to improve the regrowth ability of domesticated rice via introgression (116, 117). During the development of perennial wheat, the perennial progenies of interspecific hybridization generally contained seven or more pairs of chromosomes from perennial parents (58). Thus, Larkin & Newell (74) proposed that a perennial wheat-like grain crop should be a full or partial amphiploid, containing the wheat genome of tetraploid (AABB) or hexaploid (AABBDD) wheat plus one genome (XX) from the donor of perenniality.

## Improving Breeding Populations

In general, wild species have performed poorly for some domestication traits, including shattering, seeds with hulls, seed dormancy, and floret fertility. These traits should be enhanced or promoted during stage III to improve breeding populations. Potential breeding procedures and techniques include pedigree selection, backcrossing, bulk selection, single-seed descent, recurrent selection, double haploidy, mutation breeding, and marker-assisted selection (**Table 2**). The application of these methods depends on factors such as modes of reproduction, strategies of perennial crop development, the genetics of the traits to be improved, and the resources available. As new perennial





**Figure 1**

Breeding strategy used for intermediate wheatgrass, which we use in this review as an example of perennial grains. Abbreviations: AY, advance yield trial; PY, preliminary yield trial; VT, variety trial.



**Table 2** Differences among selection procedures for developing perennial grain and oilseed crops

Method	Description	Advantages	Disadvantages
Pedigree selection	Evaluates the performance of parents and progeny from early to advanced generations	Works well for both genetically simple and complex traits	Time and labor intensive Requires off-season nurseries to speed up the breeding process
Recurrent selection	Consists of recurrent cycles of selection for desirable genotypes, including mass selection, half-sib selection, and full-sib selection	Easy to apply in cross-pollinated species Increases the frequency of favorable alleles for complex traits	Difficult in self-pollinated species Requires several generations to complete a cycle
Marker-assisted selection	Uses linked markers to indirectly select desirable genotypes for a trait of interest	Early-generation selection Saves time, labor, and resources Single-plant-based selection	Polymorphic markers linked to the target traits are not available for new species
Genomic selection	A form of marker-assisted selection in which genome-wide markers combined with statistical tools are used to associate marker variation with phenotypic variation	Early-generation selection Saves time, labor, and resources Single-plant-based selection Accelerates the breeding process	Requires effort to train and validate the prediction models A high-throughput and cheap genotyping platform (<\$5 per sample) is still not available
Mutation breeding	Exposes seeds to chemical mutagens or ionizing radiation to generate mutant populations for selection of desirable genotypes	Creates novel and favorable genetic variation that was not present in the existing breeding population	Can induce undesired variations in the selected population Not very successful for complex quantitative traits
Bulk selection	Inbreeds a segregating population to achieve the desired level of homozygosity for further selection	Simple Tolerant to the traits that are inconsistent in natural occurrence, such as disease and abiotic stresses	Based on natural selection Plants must be planted in special environments Not suited to off-season nurseries

grain crops largely lack genetic information and resources, recurrent selection is a good choice for cross-pollinated species, and pedigree selection should work well for self-pollinated species to improve the performance of breeding populations. Mutation breeding should also be considered to improve the domestication traits controlled by major genes if no variation is present in the germplasm collections.

The performance of breeding populations can be effectively improved by using phenotypic data to select the best genotypes from the best families during recurrent selection (143). After two cycles of selection in Kansas, the seed yield of IWG increased by 77%, and seed size increased by approximately 23% (30). For the improvement of the self-pollinated progenies from interspecific hybridization, crosses or backcrosses should be made to develop segregating populations. In early-generation selection ( $F_2$  to  $F_4$ ), the traits controlled by a limited number of genes or loci (e.g., semidwarf stature, minimal shattering, and disease resistance) should be emphasized. For amphiploid populations (plants without a multiple of the basic chromosome number of the species), stable chromosome counts should also be prioritized. The later-generation selection should focus on quantitative traits, such as grain yield, seed size, floret fertility, grain quality, persistence of grain yield across seasons, and lodging resistance.

### Developing Perennial Grain Cultivars

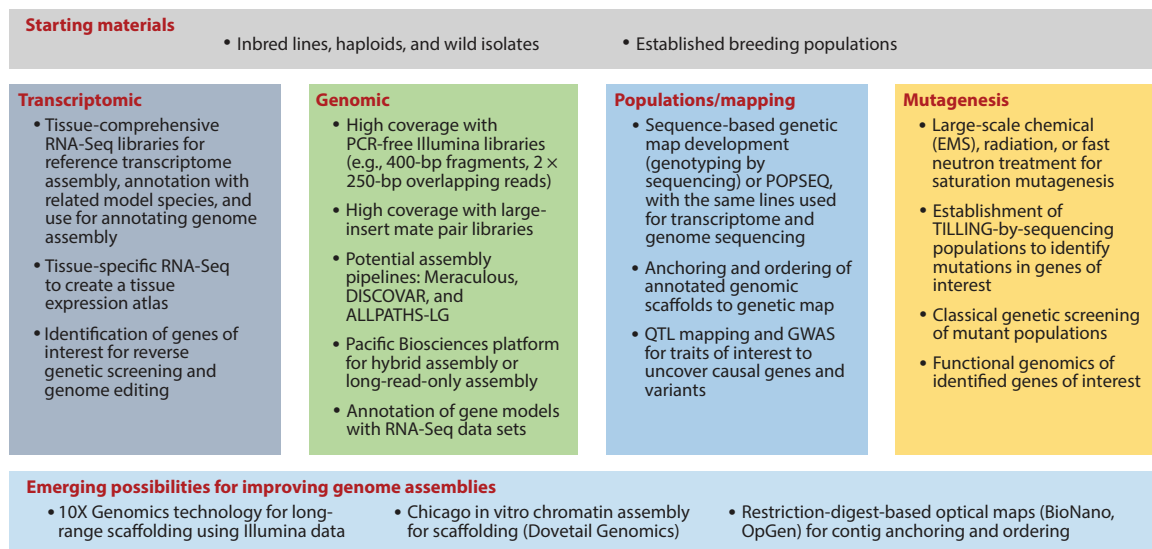
From the improved populations, advanced lines with superior traits, such as high regrowth ability, large seed size, minimal shattering, and low seed dormancy (to establish populations and explore genetics), can be used to develop perennial cultivars. Pedigree selection has been widely used

in self-pollinated species, whereas synthetic cultivars have been widely used in cross-pollinated species. A synthetic cultivar is produced by intermating genotypes and planting the resulting seeds as the cultivar (40). Cross-pollinated species generally have high hybrid vigor, but synthetic cultivars retain progressively lower amounts of hybrid vigor as additional generations of cross-pollination are performed. In the long term, methods to develop hybrids are worthy of exploration. Self-incompatibility and inbred depression should be investigated, and cytoplasmic male sterility lines should be developed or created.

## GENOMIC TOOLS AND TECHNOLOGIES FOR PERENNIAL GRAIN DEVELOPMENT

### Opportunities and Challenges in Exploring the Genomes of Perennial Grain Crops

The wide-scale adoption of next-generation sequencing technologies has revolutionized the plant sciences. These technologies include the massively parallel short-read sequencing of the Illumina platform and single-molecule sequencing technologies from companies such as Pacific Biosciences and Oxford Nanopore. Next-generation sequencing has been used to generate high-quality reference genomes and transcriptomes. The availability of genomic resources (sequence-based genetic maps and genome and transcriptome sequences) opens up vast possibilities for accelerating the breeding process of perennial grain species (125) (**Figure 2**). However, the adoption of these technologies has thus far been limited because of technical limitations, high costs, and the large, complex genomes of candidate perennial grain species (**Table 1**). With the current technologies, assembling large, heterozygous, polyploid genomes can be difficult, especially in light of the highly



**Figure 2**

Strategies for generating genomic resources to improve new perennial grain species. Abbreviations: bp, base pair; Chicago, cell-free Hi-C for assembly and genome organization; EMS, ethyl methanesulfonate; GWAS, genome-wide association study; PCR, polymerase chain reaction; POPSEQ, population sequencing; QTL, quantitative trait locus; RNA-Seq, RNA sequencing; TILLING, targeting induced local lesions in genomes.

repetitive nature of many plant genomes. To date, these challenges have made many large-scale sequencing projects cost prohibitive. Previous efforts have generated genomic resources for plant species with large genomes using exclusively next-generation sequencing technologies, as opposed to first-generation efforts that included expensive and time-intensive chromosome-sorted sequencing libraries and bacterial artificial chromosome libraries. New methods have been developed to deal with large, complex genomes (both diploid and polyploid) based on more affordable sequencing and increased computing power.

These groundbreaking approaches were developed in species with highly developed germplasm resources and populations, and parallel techniques are being used in the development of new perennial grain species such as IWG. IWG is an allohexaploid ( $2n = 6x = 42$ ) with a predicted 1C genome size of 13.1 pg (12.6 Gb) and a large repeat content (80–90%). It is primarily an outcrossing species with a high level of polymorphism. An anchored IWG genome will allow for reference-based genotyping-by-sequencing pipelines and the targeting of functional variation in known genes responsible for domestication traits, production of vegetative biomass (hereafter referred to simply as biomass), cellulosic conversion, and grain end-use traits.

There have also been significant gene discovery and functional genomics efforts within the IWG community. In the absence of a genome sequence for IWG, the cloning and characterization of candidate gene homologs rely on the sequences of distant relatives, which significantly impedes progress. Current efforts are focused on developing a draft genome assembly for IWG, along with generating reference transcriptome data sets that will be used for annotating gene models of the genome assembly, developing ultra-high-density genetic maps from genotyping by sequencing, and anchoring/ordering genomic scaffolds using population sequencing (POPSEQ) (Figure 2). In light of the quickly evolving DNA sequencing tools and related technologies for optical mapping and long-range scaffolding information [cell-free Hi-C for assembly and genome organization (Chicago), 10X Genomics], the initial draft assemblies developed from these efforts will improve as technologies mature.

## Integration of New Technologies in the Improvement of Perennial Grain Crops

Recent advances in sequencing-based marker technologies are dramatically reducing the cost of genome-wide marker discovery, and these marker technologies can be used with any species, even those without previous genomic resources (27). Genotyping by sequencing is one of the most powerful marker technologies because it is easy to operate and suitable for species without reference genomes (38, 87, 105). It was effective in identifying genome-wide markers in IWG, where 3,436 single-nucleotide-polymorphism markers were discovered from a biparental population and ordered in a genetic map (155). Markers can be used to create linkage maps in order to identify quantitative trait loci (QTLs) for agronomic traits in structured populations and to perform association mapping in order to map QTLs in a diverse population and better understand the genetic architecture of agronomic traits. Once major QTLs are identified using linkage mapping and association mapping, the corresponding traits can be improved in the breeding population within several cycles of selection.

Genome-wide markers combined with statistical tools to associate marker variation with phenotypic variation have the potential to revolutionize plant breeding and domestication. Genomic selection can improve the effectiveness of breeding programs in many animal and plant species (57, 65). This method could improve the efficiency of breeding programs by increasing selection accuracy and reducing breeding-cycle time compared with phenotypic selection. Genomic selection was established and optimized in the University of Minnesota IWG breeding program, and

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**Reference based:**  
based on a comparison of sequence data to a reference genome in order to identify molecular markers

**Genotyping by sequencing:**  
a reduced representation method of developing molecular markers

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high prediction ability ( $r > 0.5$ ) was obtained for several traits (e.g., grain yield, seed size, and free threshing), accelerating the improvement of IWG (155).

Mutation breeding is potentially useful for the development of new perennial grain crops. Large-scale mutagenesis is conducted on an inbred population (or on a population that is as genetically homogeneous as possible) of a perennial grain to develop novel genetic diversity. Genetic screens can be useful in identifying novel phenotypes and genotypes in these populations. This approach is of particular interest if there is a closely related annual species from which basic information on gene function can be translated, enabling a targeted reverse genetics approach to screen these mutant populations. Targeting induced local lesions in genomes (TILLING) and deletion TILLING (deTILLING) of mutagenized populations allows the identification of novel genes, especially those that may be difficult to phenotype or may be masked by homologous copies in subgenomes, as in the case of polyploids. With a sequenced genome, a TILLING-by-sequencing approach can be used to screen and identify an arbitrarily large number of candidate genes that would be difficult or impossible to identify by phenotype alone. Recent advances in genome editing technologies, such as CRISPR/Cas9 and transcription activator-like effector nucleases (TALENs), would be useful to improve agronomic traits that are controlled by genes of large effect if the genes are known (109, 124). However, the use of genome editing may create plant products that are viewed as genetically modified organisms, and therefore perennial grains produced by these techniques may be objectionable to some stakeholders (144). Field-based high-throughput phenotyping platforms could increase phenotyping ability and produce accurate data to dissect the genetics of agronomic traits (5) and thereby improve the efficiency of the domestication and improvement of perennial grain crops.

## AGROECOLOGICAL EFFECTS OF PERENNIAL GRAIN CROPS

### Water Quality and Quantity

Perennial crop development is pursued in part as a potential means to reduce the detrimental impacts of annual agriculture on the environment. However, the importance of high grain yields continues to increase as the growing population demands more grain-intensive foods like meat (137). Moreover, the effort to reduce the transition of native grassland and forest habitat to agricultural lands in order to protect biodiversity, maintain terrestrial carbon sinks, and conserve water resources increases the pressure to maximize yields on current agricultural lands (153). Perennial grains should result in fewer environmental impacts than annual production owing to the unique morphological and phenological characteristics of perennials.

Grain production affects water quality and quantity worldwide. In the upper Mississippi River basin, a portion of the fertilizers applied in crop production are lost via tile drainage and surface runoff and are transported from surface waters to marine communities in the Gulf of Mexico, where they are causing hypoxia (128). Buffers of perennial herbaceous vegetation placed within and along edges of annual crop fields reduce and filter surface runoff. Growth from perennial plants begins earlier than growth from major warm-season annual grain crops such as maize. Earlier growth and soil cover is important because spring is when the majority of precipitation occurs and nitrogen fertilizer is applied. The ability of perennial grain crops to utilize water early in the growing season can limit runoff to surface waters during spring precipitation events and thereby reduce stream bank erosion and the subsequent sediment and nutrient loads that occur (122). The deep root systems of perennial grain crops can also filter water of nutrients before it enters groundwater, which is a characteristic that is also essential for grain filling (149).

Reduced tillage is an inherent component of perennial cropping systems and can lead to reduced runoff and associated nutrient pollution (130). Residue management, however, is an important

component of perennial grain systems that can affect profitability, future grain yields, and runoff. Because perennials do not require annual replanting, a larger fraction of plant litter can be retained and used to reduce runoff. In a field of a perennial grain like IWG, up to 17 Mg per hectare (ha) of vegetative biomass can be present at the time of grain harvest. To effectively harvest the vegetative biomass and ensure a grain crop with uniform maturity and quality, the field can be cut and left to dry prior to combining. This may be the optimal harvest method because residue can be harvested and marketed as straw or feedstock for bioenergy to improve profitability. Decisions on cutting height and biomass removal can affect runoff prevention the following spring.

Reducing nutrient inputs such as nitrogen, phosphorus, and potassium fertilizers can prevent agriculturally derived water pollution. Annual and perennial plants have different rooting characteristics (112), which can lead to differences in nutrient acquisition, use efficiency, and agronomic requirements. Once established, perennial crops produce deep, dense root systems that can acquire more nutrients in a growing season compared with annual crops. Annual grain crops (winter wheat) can produce up to 6 Mg ha<sup>-1</sup> of roots during a year of growth (152), whereas perennial forage grass root biomass ranges from 5 to 10 Mg ha<sup>-1</sup> after the establishment year and twice that by the third year. Large root systems reduce the amount of nitrogen fertilizer needed to maximize grain yields. In Minnesota, IWG grain yields peaked at 79 kg ha<sup>-1</sup> of fertilizer, whereas corn grain yields peaked at 187 kg ha<sup>-1</sup> (D.L. Wyse, unpublished data). Underground biomass also prevents leaching; for example, IWG fields had at least 15% less nitrate leaching than annual wheat fields.

Alternative management techniques can be tested and used to improve perennial crop grain yields while maintaining their environmental benefits. Agronomic methods to optimize the production of roots and seeds are needed to maximize profitability and sustainability. Controlling factors such as plant density, disturbance, and fertility will affect the allocation of energy to roots and seeds, but more research is needed to evaluate how these factors can be controlled to optimize grain and ecosystem service production in a perennial grain cropping system. Perennial systems have considerable potential value to help mitigate climate change, create potential alternative systems to facilitate adaptation, and help with resilience strategies in cereal production.

## Greenhouse Gas Emissions

Agriculture contributes substantially to annual global greenhouse gas (GHG) emissions (61, 138). Agricultural GHGs include CO<sub>2</sub> from farm machinery, fertilizer and pesticide production, and decomposition following tillage; CH<sub>4</sub> from inundated soils and livestock; and N<sub>2</sub>O during nitrification of fertilizers. As a result, a conventionally managed corn-soybean-wheat rotation can emit 98 g of CO<sub>2</sub> equivalents per hectare per year of greenhouse forcing (50). Removing tillage can improve the GHG footprint so that the system is CO<sub>2</sub>-equivalent neutral (2, 50). Replacing the annuals with perennial grain crops not only reduces tillage and fossil fuel usage associated with annual planting, but also results in more carbon storage in roots and soil compared with annuals.

Although perennial crops efficiently acquire soil nitrogen (77), fossil fuel-based nitrogen fertilizers can still increase grain yields (D.L. Wyse, unpublished data). The seed yields of perennial turf and forage grasses increase with nitrogen fertilizer (54, 72). Increased productivity from nitrogen fertilization does not occur equally in all biomass components (66), which is important when roots, shoots, and seeds are all critical biomass components for achieving a system that provides marketable products and GHG mitigation potential. Although the production of nitrogen fertilizer results in GHG emissions, increased root productivity and biomass yields for bioenergy from nitrogen fertilization could more than offset the GHG emissions related to nitrogen production and application (50). Therefore, it is important to determine the optimum nitrogen fertilization rate at which plant traits that lead to GHG mitigation are no longer improved. Estimating nitrogen fertilizer rates that maximize grain yields and profit is also imperative.

Another way in which perennial crops mitigate GHGs lies in their capacity to sequester carbon belowground. Root biomass is a relatively large belowground carbon sink in perennial ecosystems, and measurements of up to  $7 \text{ Mg ha}^{-1}$  have been reported for IWG in the top 20 cm of soil (98). Root biomass, and subsequently carbon storage in roots, can increase for up to 12 years after establishment in grasslands (8). Other belowground carbon sinks include mineral soil carbon, which can build for decades but does so at very slow rates compared with biomass carbon accumulation (4). To the best of our knowledge, the relative contributions of these two GHG mitigation pathways—conversion of aboveground biomass to bioenergy and belowground carbon storage in soil and roots—have not been determined for perennial cropping systems.

The United States has mandated an annual production of 21 billion gallons of renewable transportation fuel by 2022, two-thirds of which is anticipated to come from cellulosic sources such as perennial grass crops. The production of cellulosic ethanol is an emerging technology that offers an end-use market for perennial grasses such as IWG. Biomass yields can reach  $10 \text{ Mg ha}^{-1}$  for forage varieties of IWG (146); however, the concentration of fermentable carbohydrates in IWG, and thus ethanol conversion potential, has not been evaluated.

### **Pests and Beneficial Organisms**

Changes in management practices resulting from growing perennial grains in areas that have historically produced annual grains will have a variety of effects on both pests and beneficial organisms. Perennial bioenergy crops, for example, support higher biodiversity, higher biological control of pest insects, and greater pollinator services than annual grains such as corn (150), although it is not clear whether these differences are due to perenniality or to other features of the cropping system. One important change resulting from perennialization will be a reduction in the amount of disturbance because of reduced cultivation and longer growing times. Although strategies to increase seed yield include cultivation between perennial crop rows, these approaches leave undisturbed soil around the plants. Another significant disturbance factor likely to change is pesticide regimes, possibly reducing pesticide inputs—in particular the use of herbicides. Increased land area in perennial grain production may also increase crop diversity at the landscape level, which may have a variety of effects on animal communities.

Tillage regimes of perennial crops differ from conventional agriculture in several ways that could affect natural enemy, pollinator, and pest populations. Although perennial crops, like conventional systems, will be harvested annually, we expect reduced tillage, an extended growing season with greater early-season cover, and greater persistence of stubble and leaf litter layers. Reduced tillage may have effects on natural enemy populations, as highlighted by findings in no-till annual systems. No-till agriculture increases the densities of beneficial organisms, including seed-eating ground beetles (16, 73, 93) and harvester ants (9), entomopathogenic fungi (99), predatory ground beetles (124) and ants (102), and overwintering parasitoids (110). Ward et al. (147) showed that the number of days since the last disturbance event (mowing of summer cover crop or cultivation) positively correlated with the active density of weed-seed-eating carabids in a soybean system with a variety of summer cover crops. Changes in soil disturbance could also benefit pollinator populations. Ground-nesting bees can overwinter in fields, and reduced tillage may enhance these pollinator populations (93, 125a).

A more persistent habitat may have differential effects on specialist versus generalist natural enemies (106). Generalists (i.e., species that can consume a broad taxonomic range of organisms) often benefit from a diversity of nonpest prey (such as springtails) that may be present even when pest densities are low (102). Generalists may increase in perennial systems owing to increased duration of prey availability, which could result in improved pest control via apparent competition



(63). Winter cover crops decrease pest pressure in annual cropping systems (71), and although the mechanisms for this effect are not clear, it is potentially due to an increase in generalist predator populations in the cover crop, with these predators subsequently attacking pests in the annual crop. Although increased densities of generalists can increase intraguild predation of specialists (126), perennial systems are expected to have extended plant cover through time and more leaf litter, which could increase the complexity of agroecosystems compared with annual crops and thereby minimize such intraguild predation (41). Perennial crops provide an interesting context to investigate basic ecological questions on the interactions between generalist and specialist natural enemies and the effects of disturbance on pests and beneficial organisms.

More persistent agricultural habitats may favor different natural enemy species with different dispersal or life history strategies. For example, aphid parasitoids persist in periodically disturbed alfalfa fields because they remain protected in the host and stay in the field to suppress aphid populations during the subsequent alfalfa growing cycle (106). Perennial crops could also serve as a reservoir of natural enemies (or pests) that could colonize highly disturbed conventional agriculture systems, as has occurred on perennial borders of annual crops (76, 134). This idea is bolstered by the observation that predator arrival time is critical in mediating pest population outbreaks (133). Dispersal is a critical feature determining the ability of natural enemies to colonize and maintain a population in new areas (60). For insect pests, decreased tillage has unclear effects (24, 102, 110). Crop rotation can reduce pest populations in sunflower fields, yet pest species such as the banded sunflower moth (*Cochylis hospes*) can overwinter in these fields and therefore may increase under a perennial system. The persistence of pest populations could also enhance parasitoid population stability; e.g., several parasitoids of *C. hospes* exist, and less disturbance may enhance biological control of this pest. The broad diversity of pests on annual sunflowers suggests a high potential for significant pest pressure on perennial sunflowers (111).

In addition to changes in insect pests and natural enemies, changes to plant pathogen population dynamics may occur. Increases in *Pseudomonas* spp. under no-till conditions could increase the generation of extracellular protease activity and the soil concentration of hydrogen cyanide, which could reduce plant pathogens (40a). How breeding of perenniality would affect host plant resistance is unclear. Schrottenboer et al. (121) investigated five switchgrass populations (including near-wild-type populations and highly selected cultivars) and found that populations with higher potential biomass accumulation rates were more susceptible to barley and cereal yellow dwarf viruses.

Breeding strategies for perennial grains have not involved transformation of traits for herbicide resistance. The lack of regular, multispectrum (e.g., glyphosate) herbicide applications could increase the prevalence of floral resources and weeds. Increases in weeds may supplement pollinator diets (108) and provide larval hosts for species in decline (104). Many weeds are flowering at the time of herbicide applications, which can have adverse indirect effects on pollinators, so the indirect benefits of reduced herbicide use may be substantial for pollinators in decline (97). Decreased herbicide use and subsequent small increases in weed densities enhance biological control as well (14).

Over the stand life of a perennial grain cropping system, fewer herbicides may be needed compared with annual grain crops. However, during the establishment year of perennial crops, the use of herbicides may be equal to or higher than it is with annuals because perennials typically have a slower relative growth rate and thus are less competitive with annual weeds. Spring weed competition could be reduced by planting perennial grain crops in the fall, as observed for cover cropping systems (15, 85, 152). Although fall planting could reduce adverse competitive effects from weeds in the following spring, high mortality (e.g., resulting from winterkill) can lead to reduced spring stand density and thus greater weed growth (13). More research on planting date and weed suppression in perennial cropping systems is needed.



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**Fatty acid profile:**

the ratio of saturated, monounsaturated, and polyunsaturated fatty acids in an oil; this profile determines the oil's possible applications and nutritional value

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Insecticides, if applied while pollinators are foraging in the field on crops or noncrop resources, could cause inadvertent harm to these beneficial organisms. Broad-spectrum insecticides have harmful impacts on natural enemies, so a conservation biological control strategy of using insecticides less harmful to biological control agents (43) could become more valuable. Because the increased stability of perennial systems can favor both pests and their natural enemies, it is not easy to predict whether pest populations will increase or decrease in a perennial cropping system. However, perenniality favors biological control interventions such as importation biological control (19, 53, 56), and these strategies may become more prominent or successful with increased perennial cropping.

Perennial crops may replace annual crops with no net change in crop diversity; however, there are many promising opportunities for increasing diversity at the field (e.g., intercropping) or landscape level, and such changes could have beneficial impacts on pollinator, natural enemy, and pest populations. Ecosystem services (such as biological control of pest insects) increase with both field-level (79) and landscape-level plant diversity (46). However, the effects of agricultural diversification on ecosystem services are not straightforward (139). In some cases, spillover of pests onto perennial bioenergy crops has occurred across the interface of seminatural habitat and annual crops (37), suggesting that landscape-level diversity could enhance the impacts of some pest populations on perennial crops. The effects of diversification activities at the farm scale depend on the available diversity in the landscape; local diversification benefits are often greatest at intermediate landscape diversity (68, 139, 140). Impacts stemming from a diverse landscape incorporating perennial grains will open up many opportunities for study at different scales. Although perennialized cropping systems may have lower pest pressure owing to diversification, continuous living cover, and reduced disturbance, this expectation may not be realized in all contexts. As discussed above, perennial cropping systems can influence multiple trophic levels, leading to direct and indirect effects on natural enemies and pests that could have complex consequences for the sustainability of perennialized cropping systems.

## FOOD USE

When considering the use of perennial plants in food products as alternatives to their more established annual counterparts, a crucial question arises: Do the perennials possess the necessary functionality to compete? For example, can they provide manufacturers with ingredients that meet consumers' demands in terms of taste, texture, and shelf life? And if they display shortfalls that cannot feasibly be altered by breeding, can processing compensate for these issues? Continuous cooperation between breeders and food scientists will be essential to successfully integrate perennials into food production systems. This section focuses on food-use outcomes of breeding efforts involving barley, sunflower, and IWG.

Hybridization between the perennial wild barley (*Hordeum bulbosum*) and cultivated annual barley (*Hordeum vulgare*) has been performed since the 1970s, with the goal of producing doubled haploids and introgressing disease resistance in barley. Use of *H. bulbosum* facilitated the production of annual malting barley lines with improved disease resistance as well as suitable brewing characteristics. These characteristics include appropriate diastatic power, which enables estimates of fermentable sugar formation; high soluble nitrogen contents, indicating sufficient cell wall breakdown; and low levels of  $\beta$ -glucans, to limit haziness in chilled beer (45, 96, 103).

Breeding programs with annual and perennial wild sunflower species evaluated their oil concentrations and profiles in comparison with commercially cultivated hybrids. A study of wild Canadian sunflowers found that annuals and perennials had similar oil concentrations and fatty acid profiles (123). In both annual and perennial sunflowers, warmer temperatures were positively

**Table 3 Challenges and impacts of incorporating the perennial grain intermediate wheatgrass into food**

Challenge	Impact	Potential strategy	
		Breeding	Processing
Deficiency in high-molecular-weight glutenin	Lack of a gas-holding network, which limits doughs formation	Increase glutenin content	Add wheat or vital wheat gluten to doughs Add binders such as egg whites or gums to batters Use strategies developed for gluten-free products such as transglutaminases for the formation of a protein network
Low starch content	Different texture than other grain-based products Potential impact on flavor development if lower amounts of reducing sugars are formed	Increase endosperm (and seed) size	Add starch to recipes
High dietary fiber content	Impaired gluten network formation caused by arabinoxylans competing for water	Increase endosperm (and seed) size	Remove bran through milling, if endosperm size is sufficiently large Add water to recipes Use xylanases
Higher fat content compared with whole wheat	Decreased shelf life caused by lipid oxidation	Develop lipoxygenase-reduced lines if these enzymes result in off flavors	Add antioxidants Use steam treatments and optimum storage conditions to inhibit lipases

correlated with oleic acid content and negatively correlated with linoleic acid content (28). Higher contents of polyunsaturated linoleic acid increase sunflower oil's vulnerability to lipid oxidation (148). In sunflower oils with similar linoleic acid contents, higher levels of antioxidants, particularly  $\gamma$ - and  $\delta$ -tocopherol, may attenuate this effect (32, 148). Therefore, future breeding efforts focused on improving perennial sunflowers for food use could target increased tocopherol content.

In terms of food use, IWG has been the subject of more research than other perennial grains. The following discussion highlights the functional demands that a perennial grain must meet in order to compete with other grains, mainly wheat (*Triticum aestivum* L.), which serves as the gold standard for most grain-based food products and can be incorporated into an unsurpassed array of foods (Table 3).

What makes wheat so unique among grains? Grains find significant use as flours that form the base of batters and doughs. For batters, nongrain ingredients such as eggs determine functionality, whereas for dough formation, grain characteristics are crucial. The best doughs are made of refined wheat flour, because this flour type contains a unique array of proteins capable of forming gluten, a network that holds gas and gives rise to the pleasant texture of baked goods. If a grain does not contain gluten-forming proteins and is thus unable to form a gas-holding network, then it can be used only in breads together with either wheat or vital wheat gluten, or its use is restricted to batters, flakes, and whole kernels. Consequently, the end use of wheat varieties is determined largely by their protein content (31).

Currently, IWG has only marginal dough-forming capabilities. As shown in Figure 3, although its total protein content is considerably larger than those of wheat and other cereal grains (12, 90), it is deficient in gluten-forming proteins. Specifically, IWG does not contain the same high-molecular-weight glutenin subunits (HMW-GSs) that provide elasticity to wheat doughs

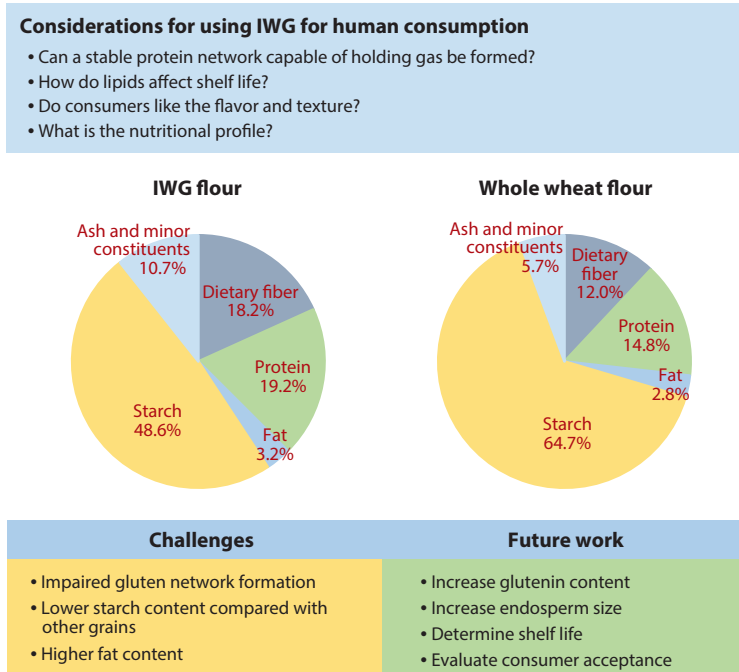
#### Lipid oxidation:

a reaction cascade in lipids that results in a shorter shelf life; lipids with more double bonds are more susceptible to it

#### Antioxidants:

compounds that delay the onset or slow the progression of lipid oxidation; examples in plants include tocopherols, carotenoids, and hydroxycinnamic acids

**Gluten:** a protein network formed by glutenins and gliadins that is capable of holding gas in doughs; starch and other minor compounds are embedded in this network



**Figure 3**

Challenges and opportunities for the development of intermediate wheatgrass (IWG) as a food ingredient.

(90). However, IWG is not completely devoid of gluten-forming proteins; it contains gliadins and a small amount of low-molecular-weight glutenins. From a marketing viewpoint, this creates the challenging situation of a grain that cannot be used for gluten-free products yet suffers from inadequate functionality. Proper dough development requires associations between glutenins and gliadins, which are made possible only by specific protein secondary structures, as discussed further below.

Research on IWG-wheat addition lines indicates that breeding could potentially overcome glutenin deficiency. Cao et al. (21) identified and characterized unique high-molecular-weight glutenin subunits in such lines with interesting structural features, including an unusually small size and two cysteine residues in the repetitive region not found in wheat HMW-GSs. This is relevant because gluten network formation depends on the presence of accessible cysteines to link subunits via disulfide bonding (151). The hybrid HMW-GS was inherited from IWG (21), and subsequent studies confirmed the presence of a protein with similar molecular weight in other IWG samples (20) and, in some cases, with additional cysteines in the repetitive region (155). Perennial wheat breeding lines have also been reported to possess small HMW-GSs (49). IWG's broad genotype pool and the high degree of diversity among its genomes suggest that it could be bred with sufficient HMW-GS contents for adequate dough formation.

How does IWG's current protein profile translate to its dough properties? Marti et al. (89) tested dough made of bread wheat and IWG flours in varying ratios, ranging from 0% to 100% IWG flour. The most striking influence of IWG addition on protein secondary structures was the reduction of  $\beta$ -sheets. This finding is important because  $\beta$ -sheets provide doughs with elasticity

**Glutenin:** a group of proteins classified into low- and high-molecular-weight subunits; cysteine residues can connect these subunits through covalent linkages

**Protein secondary structure:** the three-dimensional structure of protein segments, determined by noncovalent interactions between amino acids; examples include  $\alpha$ -helices,  $\beta$ -sheets, and  $\beta$ -turns

and stability and facilitate formation of disulfide linkages (91). However, dough from composite flour did not differ from the wheat control dough in the number of  $\beta$ -turns (89), structures that enhance gas bubble formation and dough volume (17). When measuring the ability of proteins to aggregate, dough containing IWG flour was capable of forming a weak but measurable protein network (90), which represented an improvement over earlier reports in which no gluten formation was observed (12). However, IWG doughs are currently no real match for pure wheat doughs, and the use of processing strategies could therefore assist in the formation of a protein network. Enzymes such as transglutaminases have become a popular choice for this purpose (31) and could be studied in future projects.

Another factor with a negative impact on the baking quality of current IWG breeding populations is their lower starch contents compared with wheat. Values for IWG are <45% starch on a wet basis (90), whereas typical starch contents in whole wheat flour range from 55% to 65%. In addition, its starch granule characteristics were shown to be notably different from those of wheat: IWG's starch granules are clustered and show a lower affinity to iodine staining (90). In addition, the starch gelatinization temperatures of IWG flour are higher than those of wheat, an effect that was attributed solely to the starch in IWG and not to other factors, such as dietary fiber (90).

Perennials generally produce smaller seeds than annuals because their vegetative structures contribute more to their evolutionary fitness than seed size (24). Consequently, current IWG breeding populations have comparatively smaller endosperms, resulting in a higher proportion of bran at the expense of starch. This relationship is also present in perennial wheat lines (49). The small seed size is the reason that previous work on IWG has been conducted only on flours from the whole kernel, not refined flour. In whole grain flour, bran components can interfere with gluten network formation. Like wheat bran, IWG is rich in nonstarch polysaccharides (especially arabinoxylans), which influence the dough characteristics (e.g., by increasing the amount of water needed) (145). IWG arabinoxylans display some similar characteristics to wheat and rye arabinoxylans, especially a low xylan backbone substitution rate (120). The overall effect of arabinoxylans on dough structure strongly depends on their water extractability and molecular weight. Addition of xylanase enzymes to dough is a processing tool for enhancing the positive effects of arabinoxylans by solubilizing water-unextractable arabinoxylans (36) that has not yet been tested in IWG-based breads but may improve their texture. In the case of bread made from rye flour, whose ability to form a strong gluten network is marginal compared with wheat, water-extractable arabinoxylans are essential for gas retention and loaf formation during baking (142).

At approximately 3%, the amount of fat in IWG grain is higher than that in most reports for whole wheat (12), and for both cereals, linoleic acid constitutes the main fatty acid (B. Ismail, M. Bunzel, D.G. Peterson, E.C. Shin, R.R. Schendel, et al., manuscript in preparation). Higher levels of unsaturation make a fat more prone to lipid oxidation. On the other hand, IWG is richer in certain antioxidants, notably carotenoids and hydroxycinnamic acids (B. Ismail, M. Bunzel, D.G. Peterson, E.C. Shin, R.R. Schendel, et al., manuscript in preparation). These findings point to the importance of future studies of IWG shelf life to determine whether measures against oxidation should be at the forefront of future breeding and processing operations.

In addition to functional considerations, the nutritional profiles of grains are also important for novel breeds, particularly owing to grains' role as staple foods in many cultures. IWG contains equal or higher amounts of essential amino acids compared with wheat (12), and an evaluation of antinutrient factors in uncooked IWG found lower levels of trypsin inhibitor than in whole wheat and equal nutritional values for both (12). Thus, IWG provides protein of good nutritional quality while potentially being less resource intensive than proteins from annual grains.

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**Repetitive region:**

one of three structural domains in high-molecular-weight glutenin subunits; cysteine linkages between subunits originate from this region

**Starch gelatinization:**

the process of heating starch in the presence of water, which leads to irreversible structural changes in starch granules

**Dietary fiber:**

indigestible polysaccharides and associated components, such as cutin or lignin; common cereal fibers include cellulose, arabinoxylans, and  $\beta$ -glucans

**Arabinoxylans:**

a nonstarch polysaccharide type commonly found in grain cell walls; depending on their structure, arabinoxylans can be water soluble or water insoluble

**Antinutrient factors:**

compounds that prevent the full utilization of nutrients

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Another key difference of nutritional importance is IWG's high content in dietary fiber, particularly insoluble dietary fiber. Dietary fiber makes up 16–17% of IWG grains, representing approximately 13% insoluble and 3% soluble fiber (90). The health effects of dietary fiber depend on its type and characteristics, such as gut viscosity and fermentability. Higher intakes of cereal fiber have repeatedly been associated with reduced risk for a wide range of chronic diseases, including type 2 diabetes (154) and stroke (135).

Although IWG provides less tocopherols than wheat, it contains more carotenoids, especially lutein and zeaxanthin (B. Ismail, M. Bunzel, D.G. Peterson, E.C. Shin, R.R. Schendel, et al., manuscript in preparation). In addition to protecting food against lipid oxidation through antioxidant action, these compounds are involved in maintaining human health; for instance, carotenoids (especially lutein and zeaxanthin) can positively affect eye health (1). Although IWG's carotenoid content is lower than that of some green leafy or yellow-orange vegetables, grains are often consumed in larger amounts than vegetables, and IWG could thus contribute to a better supply of these compounds.

In summary, perennials offer encouraging possibilities for breeding future food ingredients. Hybridization of barley with *H. bulbosum* is an established technique that has been routinely employed to create malting barley lines with superior disease resistance and competitive brewing performance. To the best of our knowledge, a systematic evaluation of perennial sunflower oil, including work on different applications and shelf life, has not been conducted. Such research would reveal breeding priorities, such as modifying fatty acid profiles or increasing antioxidant content. Although neither IWG nor any other perennial or annual grain is likely to replace wheat, IWG may soon provide a valuable addition to the range of grains for food use, particularly for health- and environmentally-conscious consumers. For perennial grains to become successful players in the marketplace, their ability to form doughs will be their most important functional attribute. In addition, starch, dietary fiber, lipids, and phytochemicals are important in terms of both nutrition and impact on product properties and shelf life.

## COORDINATED DEVELOPMENT METHODS

In addition to the traditional products of food, feed, fiber, and fuel, agriculture is increasingly called on to provide nontraditional ecosystem services, such as carbon sequestration and soil, water, and biodiversity conservation (59). Perennial grains offer one potential strategy for delivering these additional benefits (51). The reflective plant breeding paradigm (113) offers a conceptual framework for perennial grain breeding that couples plant development and commercialization aimed at generating multiple ecosystem services from agricultural landscapes. The framework brings together scientists, growers and other stakeholders, supply chain managers, and end users within boundary organizations (23, 70), institutions that enable the codevelopment of crop species by integrating and coordinating resources from multiple sectors (18).

The rationale for coordination is simple. By having growers, supply chain managers, and potential end users define the ideal phenotypes, the resulting perennial grain species are more closely aligned with user needs and, therefore, more likely to be adopted. Additionally, by including a diversity of stakeholders with multiple interests—ranging from phenotypic fit for existing machinery to storability and final product quality to environmental and social sustainability—a single crop can advance multiple economic, social, and environmental objectives simultaneously, which is a key component of sustainable development and intensification of agriculture (48, 52, 59). To maximize the phenotypic fit for growers, the reflective plant breeding paradigm involves both centralized and decentralized plant breeding (22).

## SUMMARY POINTS

1. Integrated programs that evaluate perennials throughout their life cycles, from field to fork, will help new plant materials realize their full potential.
2. Perennial grains are well poised to assist in feeding a worldwide population of more than 9 billion while preserving natural resources, including wildlife habitats, water, and soil health; however, they are at an early stage of development.
3. Biomass crops are an important adjunct to perennial grain crops in the perennialization of agriculture, which may produce additional value.
4. Many nonfood products are derived from perennials, including nonfood bioproducts, medicine, and organic herbicides.
5. Modern breeding tools based on an understanding of the domestication and improvement process make the development of perennials with favorable agronomic traits an achievable goal.
6. Breeding efforts have already succeeded in identifying promising crops, creating improved breeding populations, and beginning to integrate molecular technologies in new crops.
7. Expansive root systems in perennials combat environmental challenges ranging from nitrogen leaching to soil erosion.
8. Perennial plants have the ability to produce more habitat for pollinators and extend the food resources for all beneficial insects.
9. The impact that perennials will exert on agriculture in the twenty-first century will depend on breeding outcomes that satisfy end users' consciences as well as their palates.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## LITERATURE CITED

1. Abdel-Aal EM, Akhtar H, Zaheer K, Ali R. 2013. Dietary sources of lutein and zeaxanthin carotenoids and their role in eye health. *Nutrients* 5:1169–85
2. Adler P, Del Grasso S, Parton W. 2007. Life-cycle assessment of net greenhouse-gas flux for bioenergy cropping systems. *Ecol. Appl.* 17:675–91
3. Alston JM, Beddow JM, Pardey PG. 2009. Agricultural research, productivity, and food prices in the long run. *Science* 325:1209–10
4. Anderson-Teixeira KJ, Davis SC, Masters MD, Delucia EH. 2009. Changes in soil organic carbon under biofuel crops. *Glob. Change Biol. Bioenergy* 1:75–96
5. Araus JL, Cairns JE. 2014. Field high-throughput phenotyping: the new crop breeding frontier. *Trends Plant Sci.* 19:52–61
6. Asano K, Yamasaki M, Takuno S, Miura K, Katagiri S, et al. 2011. Artificial selection for a green revolution gene during *japonica* rice domestication. *PNAS* 108:11034–39
7. Asp T, Byrne S, Gundlach H, Bruggmann R, Mayer KFX, et al. 2011. Comparative sequence analysis of *VRN1* alleles of *Lolium perenne* with the co-linear regions in barley, wheat, and rice. *Mol. Genet. Genom.* 286:433–47



8. Baer SG, Kitchen DJ, Blair JM, Rice CW. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecol. Appl.* 12:1688–701
9. Baraibar B, Torra J, Westerman PR. 2011. Harvester ant (*Messor barbarus* (L.)) density as related to soil properties, topography and management in semi-arid cereals. *Appl. Soil Ecol.* 51:60–65
10. Batello C, Wade L, Cox S, Pogna N, Bozzini A, Choptiany J, eds. 2014. *Perennial Crops for Food Security: Proceedings of the FAO Expert Workshop*. Rome: Food Agric. Organ. UN
11. Baulcombe D, Crute I, Davies B, Dunwell J, Gale M, et al. 2009. *Reaping the Benefits: Science and the Sustainable Intensification of Global Agriculture*. London: R. Soc.
12. Becker R, Wagoner P, Hanners GD, Saunders RM. 1991. Compositional, nutritional and functional evaluation of intermediate wheatgrass (*Thinopyrum intermedium*). *J. Food Process. Preservat.* 15:63–77
13. Beres BL, Harker KN, Clayton GW, Bremer E, Blackshaw RE, Graf RJ. 2010. Weed-competitive ability of spring and winter cereals in the northern great plains. *Weed Technol.* 24:108–16
14. Bigler F, Albajes R. 2011. Indirect effects of genetically modified herbicide tolerant crops on biodiversity and ecosystem services: the biological control example. *J. Verbr. Lebensm.* 6:79–84
15. Björkman T, Lowry C, Shail JW, Brainard DC, Anderson DS, Masiunas JB. 2015. Mustard cover crops for biomass production and weed suppression in the great lakes region. *Agron. J.* 107:1235–49
16. Blubaugh CK, Kaplan I. 2015. Tillage compromises weed seed predator activity across developmental stages. *Biol. Control* 81:76–82
17. Bock JE, Damodaran S. 2013. Bran-induced changes in water structure and gluten conformation in model gluten dough studied by Fourier transform infrared spectroscopy. *Food Hydrocolloids* 31:146–55
18. Bos B, Koerkmap PG, Gosselink J, Bokma S. 2009. Reflexive interactive design and its application in a project on sustainable dairy husbandry systems. *Outlook Agric.* 38:137–45
19. Cameron PJ, Hill RL, Bain J, Thomas WP. 1993. Analysis of importations for biological control of insect pests and weeds in New Zealand. *Biocontrol Sci. Technol.* 3:387–404
20. Cao S, Li Z, Gong C, Xu H, Yang X, et al. 2014. Identification and characterization of high-molecular weight glutenin subunits from *Agropyron intermedium*. *PLOS ONE* 9:e87477
21. Cao S, Xu H, Li Z, Wang X, Wang D, et al. 2007. Identification and characterization of a novel *Ag. intermedium* HMW-GS gene from *T. aestivum*-*Ag. intermedium* addition lines TAI-I series. *J. Cereal Sci.* 54:293–301
22. Ceccarelli S. 2015. Efficiency of plant breeding. *Crop Sci.* 55:87
23. Clark WC, Tomich TP, van Noordwijk M, Guston D, Catacutan D, et al. 2011. Boundary work for sustainable development: natural resource management at the Consultative Group on International Agricultural Research (CGIAR). *PNAS*. In press. doi: 10.1073/pnas.0900231108
24. Clement SL, Elberson LR, Youssef N, Young FL, Evans AA. 2004. Cereal aphid and natural enemy populations in cereal production systems in eastern Washington. *J. Kans. Entomol. Soc.* 77:165–73
25. Cox TS, Bender M, Picone C, Van Tassel DL, Holland JB, et al. 2002. Breeding perennial grain crops. *Crit. Rev. Plant Sci.* 21:59–91
26. Cox TS, Glover JD, Van Tassel DL, Cox CM, DeHaan LR. 2006. Prospects for developing perennial-grain crops. *BioScience* 56:649–59
27. Davey JW, Hohenlohe PA, Etter PD, Boone JQ, Catchen JM, et al. 2011. Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nat. Rev. Genet.* 12:499–510
28. De Haro A, Fernandez-Martinez J. 1991. Evaluation of wild sunflower (*Helianthus*) species for high content and stability of linoleic acid in the seed oil. *J. Agric. Sci.* 116:359–67
29. DeHaan LR, Van Tassel DL, Cox TS. 2005. Perennial grain crops: a synthesis of ecology and plant breeding. *Renew. Agric. Food Syst.* 20:5–14
30. DeHaan LR, Wang S, Larson S, Cattani D, Zhang X, Kantarski T. 2014. Current efforts to develop perennial wheat and domesticate *Thinopyrum intermedium* as a perennial grain. See Ref. 10, pp. 72–89
31. Delcour JA, Joye I, Pareyt B, Wilderjans E, Brijs K, Lagrain B. 2012. Wheat gluten functionality as a quality determinant in cereal-based food products. *Annu. Rev. Food Sci. Technol.* 3:469–92
32. Demurin Y, Skorid D, Karlovic D. 1996. Genetic variability of tocopherol composition in sunflower seeds as a basis of breeding for improved oil quality. *Plant Breed.* 115:33–36
33. Denison RF. 2012. *Darwinian Agriculture: How Understanding Evolution Can Improve Agriculture*. Princeton, NJ: Princeton Univ. Press



34. Doebley J, Stec A. 1991. Genetic analysis of the morphological differences between maize and teosinte. *Genetics* 129:285–95
35. Dohleman FG, Long SP. 2009. More productive than maize in the Midwest: How does *Miscanthus* do it? *Plant Physiol.* 150:2104–15
36. Dornez E, Verjans P, Aranaut F, Delcour JA, Courtin CM. 2011. Use of psychrophilic xylanases provides insight into the xylanase functionality in bread making. *J. Food Agric. Chem.* 59:9553–62
37. Eckberg JO, Johnson GA, Pain RE, Wyse DL, Heimpel GE. 2015. Spillover of tent caterpillar (*Malacosoma americanum*) herbivory onto willow bioenergy crops in an agricultural landscape. *Ann. Appl. Biol.* 167:178–85
38. Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K, et al. 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLOS ONE* 6:e19379
39. Faris JD, Fellers JP, Brooks SA, Gill BS. 2003. A bacterial artificial chromosome contig spanning the major domestication locus *Q* in wheat and identification of a candidate gene. *Genetics* 164:311–21
40. Fehr WR. 1987. *Principles of Cultivar Development*, Vol. 1: *Theory and Technique*. New York: Macmillan
- 40a. Fernandez L, Agaras B, Zalba P, Wall LG, Valverde C. 2012. *Pseudomonas* spp. isolates with high phosphate-mobilizing potential and root colonization properties from agricultural bulk soils under no-till management. *Biol. Fertil. Soils* 48:763–73
41. Finke DL, Denno RF. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643–52
42. Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, et al. 2011. Solutions for a cultivated planet. *Nature* 478:337–42
43. Frewin AJ, Schaafsma AW, Hallett RH. 2012. Susceptibility of *Aphelinus certus* to foliar-applied insecticides currently or potentially registered for soybean aphid control. *Pest Manag. Sci.* 68:202–8
44. Funatsuki H, Hajika M, Hagihara S, Yamada T, Tanaka Y, et al. 2008. Confirmation of the location and the effects of a major QTL controlling pod dehiscence, *qPDH1*, in soybean. *Breed. Sci.* 58:63–69
45. Furusho M, Baba T, Yamaguchi O, Yoshida T, Hamachi Y, et al. 1999. Breeding of a new malting barley cultivar *Housbun* by the *bulbosum* method. *Breed. Sci.* 49:281–84
46. Gardiner MM, Landis DA, Gratton C, DiFonzo CD, O’Neal M, et al. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19:143–54
47. Garnett T, Appleby MC, Balmford A, Bateman IJ, Benton TG, et al. 2013. Sustainable intensification in agriculture: premises and policies. *Science* 341:33–34
48. Garrity DP, Akinnifesi FK, Ajayi OC, Weldesemayat SG, Mowo JG, et al. 2010. Evergreen agriculture: a robust approach to sustainable food security in Africa. *Food Secur.* 2:197–214
49. Gazza L, Galassi E, Ciccoritti R, Cacciatori P, Pogna NE. 2016. Qualitative traits of perennial wheat lines derived from different *Thinopyrum* species. *Genet. Resour. Crop. Evol.* 63:209–19
50. Gelfand I, Sahajpal R, Zhang X, Izaurrealde RC, Gross KL, Robertson GP. 2013. Sustainable bioenergy production from marginal lands in the US Midwest. *Nature* 493:514–17
51. Glover JD, Reganold JP, Bell LW, Borevitz J, Brummer EC, et al. 2010. Increased food and ecosystem security via perennial grains. *Science* 328:1638–39
52. Griggs D, Stafford Smith M, Rockström J, Öhman MC, Gaffney O, et al. 2014. An integrated framework for sustainable development goals. *Ecol. Soc.* 19:art49
53. Hall RW, Ehler LE. 1979. Rate of establishment of natural enemies in classical biological control. *Bull. Entomol. Soc. Am.* 25:280–82
54. Han Y, Hu T, Wang X, Hannaway DB, Li J, et al. 2014. Effects of seeding rate and nitrogen application on tall fescue seed production. *Agron. J.* 106:119
55. Harlan JR, De Wet JMJ, Price EG. 1973. Comparative evolution of cereals. *Evolution* 27:311–25
56. Hawkins BA, Mills NJ, Jervis MA, Price PW. 1999. Is the biological control of insects a natural phenomenon? *Oikos* 86:493–506
57. Hayes BJ, Bowman PJ, Chamberlain AJ, Goddard ME. 2009. Genomic selection in dairy cattle: progress and challenges. *J. Dairy Sci.* 92:433–43
58. Hayes RC, Newell MT, DeHaan LR, Murphy KM, Crane S, et al. 2012. Perennial cereal crops: an initial evaluation of wheat derivatives. *Field Crops Res.* 133:68–89

59. Heaton EA, Schulte LA, Berti M, Langeveld H, Zegada-Lizarazu W, et al. 2013. Managing a second-generation crop portfolio through sustainable intensification: examples from the USA and the EU. *Biofuels Bioprod. Biorefin.* 7:702–14
60. Heimpel GE, Asplen MK. 2011. A “Goldilocks” hypothesis for dispersal of biological control agents. *BioControl* 56:441–50
61. Heimpel GE, Yang Y, Hill JD, Ragsdale DW. 2013. Environmental consequences of invasive species: greenhouse gas emissions of insecticide use and the role of biological control in reducing emissions. *PLOS ONE* 8:e72293
62. Hill RD. 2010. The cultivation of perennial rice, an early phase in southeast Asian agriculture? *J. Hist. Geogr.* 36:215–23
63. Holt RD, Lawton JH. 1994. The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* 25:495–520
64. Jackson W. 1980. *New Roots for Agriculture*. San Francisco: Friends of the Earth
65. Jannink JL, Lorenz AJ, Iwata H. 2010. Genomic selection in plant breeding: from theory to practice. *Brief. Funct. Genom.* 9:166–77
66. Jarchow ME, Liebman M, Rawat V, Anex RP. 2012. Functional group and fertilization affect the composition and bioenergy yields of prairie plants. *GCB Bioenergy* 4:671–79
67. Jia QJ, Zhang JJ, Westcott S, Zhang XQ, Bellgard M, et al. 2009. GA-20 oxidase as a candidate for the semidwarf gene *sdw1/denso* in barley. *Funct. Integr. Genom.* 9:255–62
68. Jonsson M, Straub CS, Didham RK, Buckley HL, Case BS, et al. 2015. Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *J. Appl. Ecol.* 52:1274–82
69. Jordan N, Boody G, Broussard W, Glover JD, Keeney D, et al. 2007. Sustainable development of the agricultural bio-economy. *Science* 316:1570
70. Jordan N, Schulte LA, Williams C, Mulla D, Pitt D, et al. 2013. Landlabs: an integrated approach to creating agricultural enterprises that meet the triple bottom line. *J. High. Educ. Outreach Engagem.* 17:175–200
71. Koch RL, Sezen Z, Porter PM, Ragsdale DW, Wyckhuys KAG, Heimpel GE. 2015. On-farm evaluation of a fall-seeded rye cover crop for suppression of soybean aphid (Hemiptera: Aphididae) on soybean. *Agric. For. Entomol.* 17:239–46
72. Koeritz EJ, Watkins E, Ehlke NJ. 2013. A split application approach to nitrogen and growth regulator management for perennial ryegrass seed production. *Crop Sci.* 53:1762
73. Lalonde O, Legere A, Stevenson FC, Roy M, Vanasse A. 2012. Carabid beetle communities after 18 years of conservation tillage and crop rotation in a cool humid climate. *Can. Entomol.* 144:645–57
74. Larkin PJ, Newell MT. 2014. Perennial wheat breeding: current germplasm and a way forward for breeding and global cooperation. See Ref. 10, pp. 39–49
75. Laurance WF, Sayer J, Cassman KG. 2014. Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* 29:107–16
76. Lee JC, Menalled FD, Landis DA. 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38:472–83
77. Lemus R, Parrish DJ, Abaye O. 2008. Nitrogen-use dynamics in switchgrass grown for biomass. *BioEnergy Res.* 1:153–62
78. Lenser T, Theissen G. 2013. Molecular mechanisms involved in convergent crop domestication. *Trends Plant Sci.* 18:704–14
79. Letourneau DK, Armbrrecht I, Rivera BS, Lerma JM, Carmona EJ, et al. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21:9–21
80. Li C, Zhou A, Sang T. 2006. Genetic analysis of rice domestication syndrome with the wild annual species, *Oryza nivara*. *New Phytol.* 170:185–94
81. Li C, Zhou A, Sang T. 2006. Rice domestication by reducing shattering. *Science* 311:1936–39
82. Li Q, Li L, Yang XH, Warburton ML, Bai GH, et al. 2010. Relationship, evolutionary fate and function of two maize co-orthologs of rice *GW2* associated with kernel size and weight. *BMC Plant Biol.* 10:143
83. Li Q, Yang XH, Bai GH, Warburton ML, Mahuku G, et al. 2010. Cloning and characterization of a putative *GS3* ortholog involved in maize kernel development. *Theor. Appl. Genet.* 120:753–63

84. Li YB, Fan CC, Xing YZ, Jiang YH, Luo LJ, et al. 2011. Natural variation in *GS5* plays an important role in regulating grain size and yield in rice. *Nat. Genet.* 43:1266–69
85. Liebl R, Simmons RW, Wax LM, Stoller EW. 1992. Effect of rye (*Secale cereale*) mulch on weed control and soil moisture in soybean (*Glycine max*). *Weed Technol.* 6:838–46
86. Lin ZW, Li XR, Shannon LM, Yeh CT, Wang ML, et al. 2012. Parallel domestication of the *Shattering1* genes in cereals. *Nat. Genet.* 44:720–24
87. Lu F, Lipka AE, Glaubitz J, Elshire R, Cherney JH, et al. 2013. Switchgrass genomic diversity, ploidy, and evolution: novel insights from a network-based SNP discovery protocol. *PLOS Genet.* 9:e1003215
88. Mao HL, Sun SY, Yao JL, Wang CR, Yu SB, et al. 2010. Linking differential domain functions of the *GS3* protein to natural variation of grain size in rice. *PNAS* 107:19579–84
89. Marti A, Bock JE, Pagani MA, Ismail B, Seetharaman K. 2015. Structural characterization of proteins in wheat flour doughs enriched with intermediate wheatgrass (*Thinopyrum intermedium*) flour. *Food. Chem.* 194:994–1002
90. Marti A, Qiu X, Schoenfuss TC, Seetharaman K. 2015. Characteristics of perennial wheatgrass (*Thinopyrum intermedium*) and refined wheat flour blends: impact on rheological properties. *Cereal Chem.* 92:434–40
91. Mejia CD, Mauer LJ, Hamaker BR. 2007. Similarities and differences in secondary structure of viscoelastic polymers of maize  $\alpha$ -zein and wheat gluten proteins. *J. Cereal Sci.* 45:353–59
92. Meyer RS, Purugganan MD. 2013. Evolution of crop species: genetics of domestication and diversification. *Nat. Rev. Genet.* 14:840–52
93. Meziere D, Colbach N, Dessaint F, Granger S. 2015. Which cropping systems to reconcile weed-related biodiversity and crop production in arable crops? An approach with simulation-based indicators. *Eur. J. Agron.* 68:22–37
94. Miller AJ, Gross BL. 2011. From forest to field: perennial fruit crop domestication. *Am. J. Bot.* 98:1389–414
95. Multani DS, Briggs SP, Chamberlin MA, Blakeslee JJ, Murphy AS, et al. 2003. Loss of an MDR transporter in compact stalks of maize *br2* and sorghum *dw3* mutants. *Science* 302:81–84
96. Nagamine T, Kato T. 2008. Recent advances and problems in malting barley breeding in Japan. *Jpn. Agric. Res. Q.* 42:237–43
97. Nicholls CI, Altieri MA. 2012. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agron. Sustain. Dev.* 33:257–74
98. Ogle D, St. John L, Tober D, Jensen K. 2011. *Intermediate wheatgrass: Thinopyrum intermedium (Host) Barkworth & D.R. Dewey*. Plant Guide, Ida. N.D. Plant Mater. Cent., Nat. Resour. Conserv. Serv., US Dep. Agric., Washington, DC. [http://plants.usda.gov/plantguide/pdf/pg\\_thin6.pdf](http://plants.usda.gov/plantguide/pdf/pg_thin6.pdf)
99. Oliveira I, Pereira JA, Quesada-Moraga E, Lino-Neto T, Bento A, et al. 2013. Effect of soil tillage on natural occurrence of fungal entomopathogens associated to *Prays oleae* Bern. *Sci. Hortic.* 159:190–96
100. Parvathaneni RK, Jakkula V, Padi FK, Faure S, Nagarajappa N, et al. 2013. Fine-mapping and identification of a candidate gene underlying the *d2* dwarfing phenotype in pearl millet, *Cenchrus americanus* (L.) Morrone. *G3* 3:563–72
101. Pearce S, Saville R, Vaughan SP, Chandler PM, Wilhelm EP, et al. 2011. Molecular characterization of *Rht-1* dwarfing genes in hexaploid wheat. *Plant Physiol.* 157:1820–31
102. Pereira JL, Picanço MC, Pereira EJG, Silva AA, Jakelaitis A, et al. 2010. Influence of crop management practices on bean foliage arthropods. *Bull. Entomol. Res.* 100:679–88
103. Pickering R, Niks R, Johnston P, Butler R. 2004. Importance of the secondary gene pool in barley genetics and breeding II. Disease resistance, agronomic performance and quality. *Czech J. Genet. Plant Breed.* 40:79–85
104. Pleasants JM, Oberhauser KS. 2013. Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conserv. Divers.* 6:135–44
105. Poland JA, Brown PJ, Sorrells ME, Jannink JL. 2012. Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. *PLOS ONE* 7:e32253
106. Rauwald KS, Ives AR. 2001. Biological control in disturbed agricultural systems and the rapid recovery of parasitoid populations. *Ecol. Appl.* 11:1224–34

107. Deleted in proof
108. Ricou C, Schneller C, Amiaud B, Plantureux S, Bockstaller C. 2014. A vegetation-based indicator to assess the pollination value of field margin flora. *Ecol. Indic.* 45:320–31
109. Rife TW, Wu SY, Bowden RL, Poland JA. 2015. Spiked GBS: a unified, open platform for single marker genotyping and whole-genome profiling. *BMC Genom.* 16:248
110. Roger-Estrade J, Anger C, Bertrand M, Richard G. 2010. Tillage and soil ecology: partners for sustainable agriculture. *Soil Tillage Res.* 111:33–40
111. Rogers CE. 1992. Insect pests and strategies for their management in cultivated sunflower. *Field Crops Res.* 30:301–32
112. Roumet C, Urceley C, Díaz S. 1997. Suites of root traits differ between annual and perennial species growing in the field. *New Phytol.* 170:357–68
113. Runck BC, Kantar MB, Jordan NR, Anderson JA, Wyse DL, et al. 2014. The reflective plant breeding paradigm: a robust system of germplasm development to support strategic diversification of agroecosystems. *Crop Sci.* 54:1939–48
114. Runge FC, Senauer B, Pardey PG, Rosegrant MW. 2003. *Ending Hunger in Our Lifetime: Food Security and Globalization*. Baltimore, MD: Johns Hopkins Univ. Press
115. Sacks EJ, Dhanapala MP, Cruz MTS, Sallan R. 2007. Clonal performance of perennial *Oryza sativa/O. rufipogon* selections and their combining ability with *O. sativa* cultivars for survival, stolon production and yield. *Field Crops Res.* 100:155–67
116. Sacks EJ, Dhanapala MP, Tao DY, Cruz MTS, Sallan R. 2006. Breeding for perennial growth and fertility in an *Oryza sativa/O. longistaminata* population. *Field Crops Res.* 95:39–48
117. Sacks EJ, Schmit V, McNally KL, Cruz MTS. 2006. Fertility in an interspecific rice population and its effect on selection for rhizome length. *Field Crops Res.* 95:30–38
118. Sang T. 2009. Genes and mutations underlying domestication transitions in grasses. *Plant Physiol.* 149:63–70
119. Sang T. 2011. Toward the domestication of lignocellulosic energy crops: learning from food crop domestication free access. *J. Integr. Plant Biol.* 53:96–104
120. Schendel RR, Becker A, Tyl C, Bunzel M. 2015. Isolation and characterization of feruloylated arabinoxylan oligosaccharides from the perennial cereal grain intermediate wheat grass (*Thinopyrum intermedium*). *Carbohydr. Res.* 407:16–25
121. Schrotenboer AC, Allen MS, Malmstrom CM. 2011. Modification of native grasses for biofuel production may increase virus susceptibility. *GCB Bioenergy* 3:360–74
122. Schultz RC, Isenhardt TM, Simpkins WW, Colletti JP. 2004. Riparian forest buffers in agroecosystems—lessons learned from the Bear Creek Watershed, central Iowa, USA. *Agrofor. Syst.* 61:35–50
123. Seiler GJ, Brothers ME. 1999. Oil concentration and fatty acid composition of achenes of *Helianthus* species (Asteraceae) from Canada. *Econ. Bot.* 53:273–80
124. Shan QW, Wang YP, Li J, Gao CX. 2014. Genome editing in rice and wheat using the CRISPR/Cas system. *Nat. Protoc.* 9:2395–410
125. Shapter FM, Cross M, Ablett G, Malory S, Chivers IH, et al. 2013. High throughput sequencing and mutagenesis to accelerate the domestication of *Microlaena stipoides* as a new food crop. *PLOS ONE* 8:e82641
- 125a. Shuler RE, Roulston TH, Farris GE. 2005. Farming practices influence wild pollinator populations on squash and pumpkin. *J. Econ. Entomol.* 98:790–95
126. Snyder WE, Ives AR. 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology* 82:705–16
127. Song XJ, Huang W, Shi M, Zhu MZ, Lin HX. 2007. A QTL for rice grain width and weight encodes a previously unknown RING-type E3 ubiquitin ligase. *Nat. Genet.* 39:623–30
128. Sprague LA, Hirsch RM, Aulenbach BT. 2011. Nitrate in the Mississippi River and its tributaries, 1980 to 2008: Are we making progress? *Environ. Sci. Technol.* 45:7209–16
129. Su ZQ, Hao CY, Wang LF, Dong YC, Zhang XY. 2011. Identification and development of a functional marker of TaGW2 associated with grain weight in bread wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.* 122:211–23

130. Sun KM, Li R, Li Y, Xin M, Xiao J, et al. 2015. Responses of *Ulva prolifera* to short-term nutrient enrichment under light and dark conditions. *Estuar. Coast. Shelf Sci.* 163:56–62
131. Taketa S, Amano S, Tsujino Y, Sato T, Saisho D, et al. 2008. Barley grain with adhering hulls is controlled by an ERF family transcription factor gene regulating a lipid biosynthesis pathway. *PNAS* 105:4062–67
132. Tang H, Cuevas HE, Das S, Sezen UU, Zhou C, et al. 2013. Seed shattering in a wild sorghum is conferred by a locus unrelated to domestication. *PNAS* 110:15824–29
133. Tenhumberg B, Poehling HM. 1995. Syrphids as natural enemies of cereal aphids in Germany: aspects of their biology and efficacy in different years and regions. *Agric. Ecosyst. Environ.* 52:39–43
134. Thies C, Tschamtk T. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893–95
135. Threapleton DE, Burley VJ, Greenwood DC, Cade JE. 2015. Dietary fibre intake and risk of ischaemic and haemorrhagic stroke in the UK Women's Cohort Study. *Eur. J. Clin. Nutr.* 69:467–74
136. Tilman D, Balzer C, Hill J, Belfort BL. 2011. Global food demand and the sustainable intensification of agriculture. *PNAS* 108:20260–64
137. Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S. 2002. Agricultural sustainability and intensive production practices. *Nature* 418:671–77
138. Tilman D, Clark M. 2014. Global diets link environmental sustainability and human health. *Nature* 515:518–22
139. Tschamtk T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8:857–74
140. Tschamtk T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, et al. 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. *Biol. Rev.* 87:661–85
141. Vavilov NI. 1926. *Origin and Geography of Cultivated Plants*. Cambridge, UK: Cambridge Univ. Press
142. Vinkx C, Delcour J, Verbruggen MA, Gruppen H. 1996. Rye (*Secale cereale* L.) arabinoxylans: a critical review. *J. Cereal Sci.* 24:1–14
143. Vogel KP. 2013. Comparison of two perennial grass breeding systems with switchgrass. *Crop Sci.* 53:863–70
144. Voytas DF, Gao C. 2014. Precision genome engineering and agriculture: opportunities and regulatory challenges. *PLoS Biol.* 12:e1001877
145. Wang M, van Vliet T, Hamer RJ. 2004. How gluten properties are affected by pentosans. *J. Cereal Sci.* 39:395–402
146. Wang RL, Stec A, Hey J, Lukens L, Doebley J. 1999. The limits of selection during maize domestication. *Nature* 398:236–39
147. Ward MJ, Ryan MR, Curran WS, Barbercheck ME, Mortensen DA. 2010. Cover crops and disturbance influence activity-density of weed seed predators *Amara aenea* and *Harpalus pensylvanicus* (Coleoptera: Carabidae). *Weed Sci.* 59:76–81
148. Warner K, Miller J, Demurin Y. 2008. Oxidative stability of crude mid-oleic sunflower oils from seeds with high  $\gamma$ - and  $\delta$ -tocopherol levels. *J. Am. Oil Chem. Soc.* 85:529–33
149. Wasson AP, Richards RA, Chatrath R, Misra SC, Prasad SS, et al. 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. *J. Exp. Bot.* 63:3485–98
150. Werling BP, Dickson TL, Isaacs R, Gaines H, Gratton C, et al. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *PNAS* 111:1652–57
151. Wieser H. 2007. Chemistry of gluten proteins. *Food Microbiol.* 24:115–19
152. Williams MM II, Mortensen DA, Doran JW. 1998. Assessment of weed and crop fitness in cover crop residues for integrated weed management. *Weed Sci.* 46:595–603
153. Wright CK, Wimberly MC. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *PNAS* 110:4134–39
154. Yao B, Fang H, Xu W, Yan Y, Xu H, et al. 2014. Dietary fiber intake and risk of type 2 diabetes: a dose-response analysis of prospective studies. *Eur. J. Epidemiol.* 29:79–88
155. Zhang X, DeHaan LR, Higgins LA, Markowski TW, Wyse DL, et al. 2014. New insights into high-molecular-weight glutenin subunits and sub-genomes of the perennial crop *Thinopyrum intermedium* (Triticeae). *J. Cereal Sci.* 59:203–10





# Contents

The Path to Thioredoxin and Redox Regulation in Chloroplasts <i>Bob B. Buchanan</i> .....	1
Learning the Languages of the Chloroplast: Retrograde Signaling and Beyond <i>Kai Xun Chan, Su Yin Phua, Peter Crisp, Ryan McQuinn, and Barry J. Pogson</i> .....	25
NDH-1 and NDH-2 Plastoquinone Reductases in Oxygenic Photosynthesis <i>Gilles Peltier, Eva-Mari Aro, and Toshibaru Shikanai</i> .....	55
Physiological Functions of Cyclic Electron Transport Around Photosystem I in Sustaining Photosynthesis and Plant Growth <i>Wataru Yamori and Toshibaru Shikanai</i> .....	81
The Costs of Photorespiration to Food Production Now and in the Future <i>Berkley J. Walker, Andy VanLooche, Carl J. Bernacchi, and Donald R. Ort</i> .....	107
Metabolite Damage and Metabolite Damage Control in Plants <i>Andrew D. Hanson, Christopher S. Henry, Oliver Fiehn,          and Valérie de Crécy-Lagard</i> .....	131
The Regulation of Essential Amino Acid Synthesis and Accumulation in Plants <i>Gad Galili, Rachel Amir, and Alisdair R. Fernie</i> .....	153
Triacylglycerol Metabolism, Function, and Accumulation in Plant Vegetative Tissues <i>Changcheng Xu and John Shanklin</i> .....	179
The Plant Polyester Cutin: Biosynthesis, Structure, and Biological Roles <i>Eric A. Fich, Nicholas A. Segerson, and Jocelyn K.C. Rose</i> .....	207
Biosynthesis of the Plant Cell Wall Matrix Polysaccharide Xyloglucan <i>Markus Pauly and Kenneth Keegstra</i> .....	235
TOR Signaling and Nutrient Sensing <i>Thomas Dobrenel, Camila Caldana, Johannes Hanson, Christophe Robaglia,          Michel Vincentz, Bruce Veit, and Christian Meyer</i> .....	261

Rapid, Long-Distance Electrical and Calcium Signaling in Plants <i>Won-Gyu Choi, Richard Hilleary, Sarah J. Swanson, Su-Hwa Kim, and Simon Gilroy</i> .....	287
Endocytosis and Endosomal Trafficking in Plants <i>Julio Paez Valencia, Kaija Goodman, and Marisa S. Otegui</i> .....	309
Staying Tight: Plasmodesmal Membrane Contact Sites and the Control of Cell-to-Cell Connectivity in Plants <i>Jens Tilsner, William Nicolas, Abel Rosado, and Emmanuelle M. Bayer</i> .....	337
Pre-Meiotic Anther Development: Cell Fate Specification and Differentiation <i>Virginia Walbot and Rachel L. Egger</i> .....	365
Plant Sex Chromosomes <i>Deborah Charlesworth</i> .....	397
Haploidization via Chromosome Elimination: Means and Mechanisms <i>Takayoshi Ishii, Rabeleh Karimi-Ashtiyani, and Andreas Houben</i> .....	421
Mechanisms Used by Plants to Cope with DNA Damage <i>Zhubing Hu, Toon Cools, and Lieven De Veylder</i> .....	439
The Conservation and Function of RNA Secondary Structure in Plants <i>Lee E. Vandivier, Stephen J. Anderson, Shawn W. Foley, and Brian D. Gregory</i> .....	463
Toxic Heavy Metal and Metalloid Accumulation in Crop Plants and Foods <i>Stephan Clemens and Jian Feng Ma</i> .....	489
Light-Mediated Hormonal Regulation of Plant Growth and Development <i>Mieke de Wit, Vinicius Costa Galvão, and Christian Fankhauser</i> .....	513
Transcriptional Responses to the Auxin Hormone <i>Dolf Weijers and Doris Wagner</i> .....	539
Mapping Transcriptional Networks in Plants: Data-Driven Discovery of Novel Biological Mechanisms <i>Allison Gaudinier and Siobhan M. Brady</i> .....	575
The Intracellular Dynamics of Circadian Clocks Reach for the Light of Ecology and Evolution <i>Andrew J. Millar</i> .....	595
Environmental Control of Root System Biology <i>Rubén Rellán-Álvarez, Guillaume Lobet, and José R. Dimmeny</i> .....	619
The Haustorium, a Specialized Invasive Organ in Parasitic Plants <i>Satoko Yoshida, Songkui Cui, Yasunori Ichihashi, and Ken Shirasu</i> .....	643



Antibody Production in Plants and Green Algae <i>Vidadi Yusibov, Natasha Kushnir, and Stephen J. Streatfield</i> .....	669
Perennial Grain and Oilseed Crops <i>Michael B. Kantar, Catrin E. Tyl, Kevin M. Dorn, Xiaofei Zhang, Jacob M. Jungers, Joe M. Kaser, Rachel R. Schendel, James O. Eckberg, Bryan C. Runck, Mirko Bunzel, Nick R. Jordan, Robert M. Stupar, M. David Marks, James A. Anderson, Gregg A. Johnson, Craig C. Sheaffer, Tonya C. Schoenfuss, Baraem Ismail, George E. Heimpel, and Donald L. Wyse</i> .....	703

## Errata

An online log of corrections to *Annual Review of Plant Biology* articles may be found at <http://www.annualreviews.org/errata/arplant>