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Authors
Moore, Virginia M
Peters, Tessa
Schlautman, Brandon
et al.

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Toward plant breeding for multicrop systems

Virginia M. Moore[a,1], Tessa Peters[b], Brandon Schlautman[b], and E. Charles Brummer[c]

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Increasing cropping system diversity has great potential to address environmental problems associated with modern agriculture, such as erosion, soil carbon loss, nutrient runoff, water pollution, and loss of biodiversity. As with other agricultural sciences, plant breeding has primarily been conducted in the context of dominant monoculture cropping systems, with little focus on multicrop systems. Multicrop systems have increased temporal and/or spatial diversity and include a diverse set of crops and practices. In order to support a transition to multicrop systems, plant breeders must shift their breeding programs and objectives to better represent more diverse systems, including diverse rotations, alternate-season crops, ecosystem service crops, and intercropping systems. The degree to which breeding methods need to change will depend on the cropping system context in question. Plant breeding alone, however, cannot drive adoption of multicrop systems. Alongside shifts in breeding approaches, changes are needed within broader research, private sector, and policy contexts. These changes include policies and investments that support a transition to multicrop systems, increased collaboration across disciplines to support cropping system development, and leadership from both the public and private sectors to develop and promote adoption of new cultivars.

plant breeding | cropping systems | crop diversity | sustainability

Agricultural research frequently focuses on increasing agricultural productivity to feed a growing world population. However, current US agricultural systems largely prioritize crop production goals at the expense of ecosystems, and often achieve these goals by reducing system diversity and complexity, reflected in long-term trends toward monoculture, mechanization, specialization, and higher input use (1–6). Agroecosystem diversity confers a wide range of benefits for both crop production and ecosystems, including increased crop productivity and yield stability; reduced pest, disease, and weed impacts; and improved soil health, carbon sequestration, and economic resilience (1, 7). Under the current dominant production practices, services that had been provided by agroecosystem diversity have been substituted with extensive field operations, external fertilizer and pesticide inputs, and regular soil disturbances. Along with changes in crop management, plant breeding has contributed enormously to yield increases in the major crops (8–11). While these systems have been enormously productive in terms of crop yield, they have been highly destructive to ecosystems, contributing to climate change and causing soil erosion (12), loss of soil organic carbon (13), nutrient runoff, surface/groundwater pollution (14), and biodiversity loss (15, 16) at scales that threaten not only future crop productivity (masked only by modern crop genetics and production technologies) (17) but, arguably, stable access to the most basic public goods such as clean air, pure water, and healthy food. There is long-term evidence that diversified cropping systems and other methods of ecological intensification can maintain crop productivity while addressing environmental challenges (18). These systems are productive despite limited investment in related research (19), which indicates the potential to further improve performance given adequate investment. We propose that a return to cropping system diversity will be necessary to address such environmental challenges and can support a more desirable balance between priorities associated with crop production (i.e., provisioning services) and other ecosystem services (e.g., regulating services such as clean water, erosion control, and carbon sequestration); see Box 1 for key terms used throughout this paper.

Increasing cropping system diversity may occur in time (e.g., through increased rotational diversity within a single year or over a long-term rotation) or space (e.g., through various forms of intercropping). Intercropping includes a range of practices, including crop mixtures, row intercropping (planting distinct rows of multiple crops), strip intercropping (growing strips of multiple crops wide enough for independent cultivation), and relay intercropping (planting a second crop while the first is in its reproductive stage) (20). We use the term multicrop systems to describe such temporally and/or spatially diverse cropping systems (Fig. 1). Within the US agricultural context, diverse multicrop systems were used more widely prior to 1940 (2), and such systems are still common in places where agricultural production systems are less dependent on input use to achieve crop production goals.

US agricultural policy has played a major role in driving the shift from multicrop to monoculture agriculture, for example, through direct subsidies and crop insurance (21). These programs are designed, in part, to mitigate production risk for farmers, but they also have implications for adoption of multicrop systems, as they incentivize production of a limited suite of crops supported by federal

Author affiliations: [a]Plant Breeding and Genetics Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853; [b]The Land Institute, Salina, KS 67401; and [c]Department of Plant Sciences, University of California, Davis, CA 95616

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[1]To whom correspondence may be addressed. Email: vm377@cornell.edu.

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Box 1. Definitions of key terms used in the manuscript
Alternate-season crop: crops grown when fields would otherwise be fallow in dominant cropping systems
Cash crop: harvested for their commercial value
Cover crop: a noncash crop planted for the purpose of improving soil or for other environmental benefits
Ecological intensification: the enhancement of ecosystem services to complement or substitute for the role of anthropogenic inputs in maintaining or increasing yields (18)
Ecosystem service crop: crops planted primarily for the ecosystem services they provide, in addition to crop yield (e.g., cover crops, companion plants, hedgerows)
General mixing ability (GMA): the average performance of a cultivar across all tested mixture combinations
Orphan crop: crops that receive little scientific focus or funding relative to their importance for food security (56)
Perennial groundcover: living mulch incorporated into annual cash crop systems
Provisioning ecosystem service: material benefits obtained from ecosystems (e.g., food, water)
Regulating ecosystem service: benefits associated with regulation of ecosystem processes
Relay intercropping: intercropping system in which the lifecycle of one crop overlaps with another
Row intercropping: intercropping of multiple crops in distinct rows
Specific mixing ability (SMA): the deviation of a mixture from the estimated performance of the pair based on the GMA of the mixture components
Strip intercropping: intercropping of multiple crops in strips wide enough to cultivate each crop separately
Thick legitimacy: authority that is woven into the knowledge-making of scientific and political institutions, and embedded in widely practiced social conventions (49)

programs and reduce incentives to use crop diversification as an alternative risk mitigation strategy (22, 23). Farmers may have limited willingness to adopt multicrop systems despite the resilience and reduced production risks they can provide in the context of a changing and unpredictable climate, because crop insurance decouples production and economic risks faced by farmers (24, 25).

As plant breeders, we are particularly concerned with the role of plant breeding in a transition to multicrop systems. Modern breeding and agronomic efforts have focused largely on adapting crops to the dominant monoculture systems rather than to multicrop systems. Given the larger policy drivers favoring the homogenization of dominant agricultural systems, plant breeders alone cannot drive the shift to multicrop systems. Plant breeders impact the agricultural landscape by developing and releasing cultivars which are adopted by farmers (26). Therefore, for cultivar development efforts to be effective, plant breeders need buy-in from both farmer and seed companies. When considering adoption not only of a new cultivar but of an entirely new crop or a major change in management practices, even more actors have roles to play, including agronomists, engineers, and, especially, policy makers. Given the role policy has played in reducing diversity in the agricultural landscape, policy changes will be needed to make adoption of alternative systems more feasible and desirable. If and when policy incentives and markets align with multicrop systems, then plant breeding programs will be necessary to optimize those systems. Breeding programs can shift their orientation by adapting breeding methods, adding crops, and reprioritizing traits of interest, to better address the needs of multicrop systems. In this paper, we describe the methods and approaches needed to breed for multicrop systems and identify the major breeding targets that will support widespread adoption of multicrop systems in US field crop production. We also identify opportunities for plant breeders to work alongside other researchers, seed companies, farmers, and policy makers to chart a path toward increased breeding for, and adoption of, multicrop systems.

Multicrop Breeding Targets

Assuming that relevant market development and policy incentives are implemented to facilitate adoption of multicrop systems, plant breeders will need to focus on the traits and systems needed to enhance diversity in agricultural landscapes. When breeding for multicrop systems, specific objectives vary widely, depending on the cropping system context. This context includes the component crops of the cropping system, the purpose(s) for which farmers are growing them, and numerous environmental and management factors influencing the competitive and cooperative interactions among crops.

In the most straightforward case, plant breeders can breed crops that are adapted to diverse rotations (e.g., Fig. 1*G*) with the overarching goal of increasing the number of crops and cultivars that can be grown profitably and that are adapted to diverse agricultural landscapes (e.g., Fig. 1*D*). In many cases, the selection objectives in breeding for diverse rotations do not differ from current breeding programs. The primary breeding goal is productivity, but in the context of a diverse crop rotation—a new target population of environments—where selection must be performed to maximize genetic gain. The key traits remain: yield and yield stability, postharvest quality, and particulars related to disease and insect pests that arise within the crop rotation. In some cases, crops may be bred for new regions in which they have not previously been selected, and, in other cases, new crops may be developed which have not previously received major breeding efforts, for example, development of intermediate wheatgrass as a perennial grain crop, pennycress as a winter oilseed, and hairy vetch as a cover crop. In these cases, crops may require focus on key domestication traits such as seed shattering, harvestability, or others (27–30).

Many multicrop systems incorporate additional crops grown when fields would otherwise be fallow in dominant cropping systems (here referred to as alternate-season crops, e.g., Fig. 1*E*), which collectively result in year-round

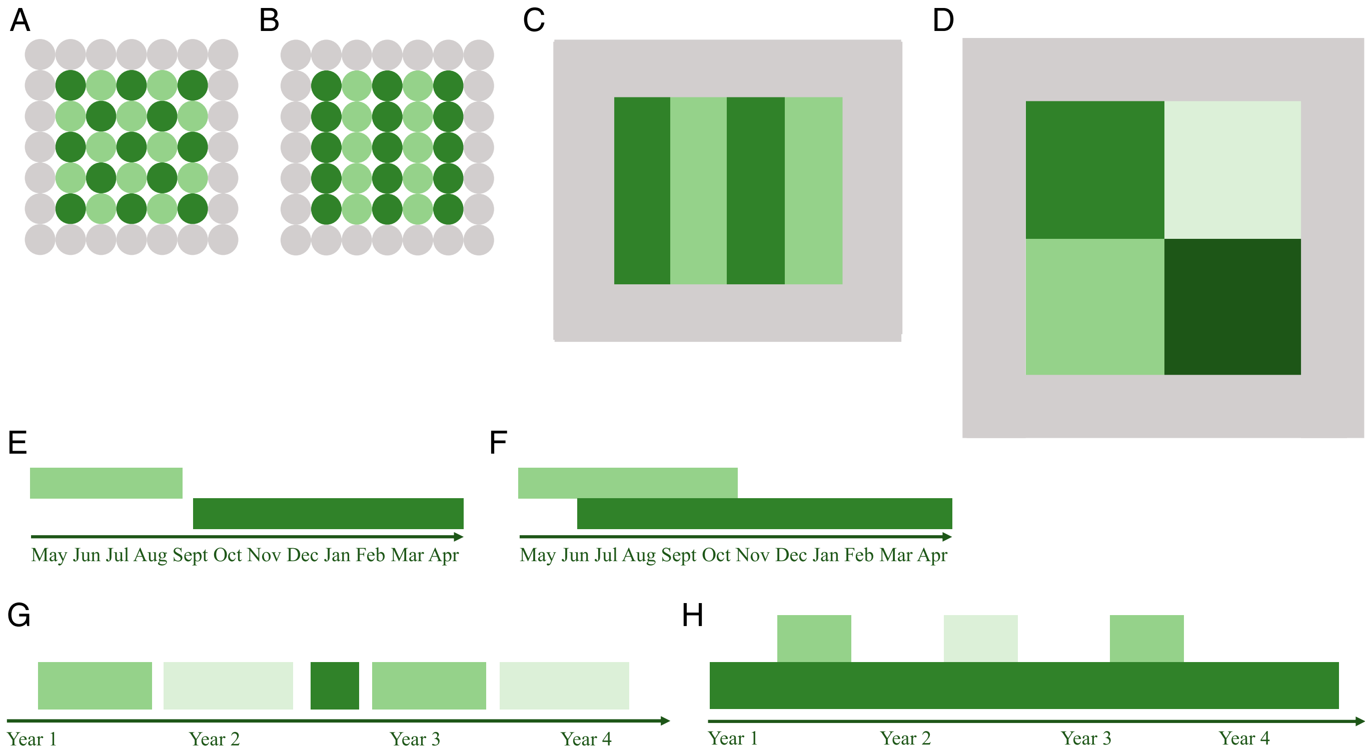

Fig. 1. Multicrop systems with varying degrees of spatial and temporal diversity. Each panel represents a different type of multicrop system, with shades of green representing different crop species. (*A*) Crop mixtures (e.g., grass-legume forage mixtures), (*B*) row intercropping (e.g., oat–pea row intercropping), (*C*) strip intercropping (e.g., corn–alfalfa strip intercropping), (*D*) field-scale crop diversification, (*E*) sequential planting of crop species within the same year (e.g., winter wheat–double crop soybean system), (*F*) relay intercropping (e.g., winter oilseed–soybean system), (*G*) long-term diversified crop rotation, and (*H*) perennial groundcover systems (e.g., an annual row crop rotation interplanted with perennial turfgrass or clover species).

soil cover and improved water and nutrient retention. Cover crops are commonly used specifically for these purposes. When alternate-season crops are also cash crops (i.e., harvested for their commercial value), they may provide an opportunity to increase farm incomes by growing an additional crop when fields would otherwise be fallow. The potential for additional income generation can provide incentives for adoption of alternate-season crops. Examples of existing alternate-season cash crops include wheat/soybean double cropping or the addition of winter grain crops (e.g., wheat or rye) or winter oilseed crops (e.g., camelina or carinata) to crop rotations (31, 32). Alternate-season crops and their main-season counterparts often need to be selected for traits related to phenology and timing of field operations in order to increase their compatibility with each other, for example, selection for early vigor and early flowering. Alternate-season crops often need to overwinter, and selecting traits related to winter survival and productivity under cold conditions may also be important in some regions.

While most crops are planted for their ability to produce food, feed, fiber, fuel, or other output with commercial value, others are planted primarily for the ecosystem services they provide (in addition to crop yield). Annual cover crops are perhaps the most obvious example, but there are other examples, including species used in hedgerows, companion plants used for pollinator or pest management, or species used as perennial groundcovers between rows of cash crops. We refer to these crops collectively as ecosystem service crops; they may be selected for traits that enhance their environmental benefits, such as increased biomass production (e.g., to enhance weed suppression and soil organic matter contributions) (33), increased nitrogen fixation (34, 35), or even the release of biological nitrification inhibitors in the soil to reduce nitrogen loss (36). They are also often selected for the timing-related traits important for alternate-season crops (35, 37, 38) and for any other traits that reduce negative impacts on the cash crop.

Both cash crops and ecosystem service crops may be bred specifically for intercropping systems including various spatial and temporal intercropping such as mixtures, strips, and relay systems (e.g., Fig. 1 *A–C*, *F*, and *H*). Compared with other multicrop systems described so far, intercropping involves more direct interactions among crop species. Therefore, in addition to the breeding goals described above, breeding programs focused on intercropping will select plants to enhance positive interactions (e.g., facilitation, niche differentiation) and reduce negative interactions (e.g., competition) among intercropping partners (39).

Breeding Methods for Multicrop Systems

What does it mean in practical terms to breed plants for multicrop systems? The answer to this question depends in large part on the multicrop system of interest. If the primary goal is to increase diversity in time (e.g., through increasing rotational diversity), then the breeding objectives or the target population of environments may shift, while the experimental methods could remain similar to breeding methods in monoculture systems. However, breeding for diversity in space (i.e., intercropping) has a unique set of challenges that requires adaptation of typical breeding methods. The need to breed specifically for intercropping systems has been noted in the literature since at least the 1940s (40), and methods to do so have been well described (3, 39, 41–43), although implementation in breeding programs has been more limited. Moore et al. (39) described core experimental activities when setting up and carrying out a breeding program focused on intercropping, and these principles are salient for other multicrop systems as well. These activities include 1) defining a target population of environments; 2) identifying variation for performance in multicrop systems; 3) detecting interactions among genotypes, environments, and management systems; 4) and identifying traits of interest (Fig. 2). These activities will drive decisions about the locations, cropping systems, and species included in a breeding program; the size and complexity of breeding nurseries and trials; and the phenotyping activities that take place. However, the plant breeder's activities and decision-making are also nested within a much larger context; the ability of a plant breeder not only to develop cultivars adapted to multicrop systems but to promote adoption of these cultivars will depend on "enabling conditions," including appropriate policy, market demand, and a constellation of research supporting the development of multicrop systems.

Defining a target population of environments, or the conditions for which you are selecting, is key to decision-making in any breeding program. The task becomes more complicated in multicrop systems because, in addition to climate and soil properties that influence cultivar performance, breeders must consider a wide range of possible rotational or intercropping partners that may vary regionally, by farm, and by season. A breeder must determine which multicrop system(s) is (are) most relevant and to what degree systems can be grouped for breeding purposes. Such decisions can be made through consultation with farmers and other stakeholders (e.g., through interviews, focus groups, surveys) and review of relevant literature identifying promising systems and crop partners. Because use of multicrop systems has declined over time, in many cases, best management practices for a given multicrop system are not established, and cropping system design must also take place in tandem with breeding efforts. In the context of multicrop systems with increased

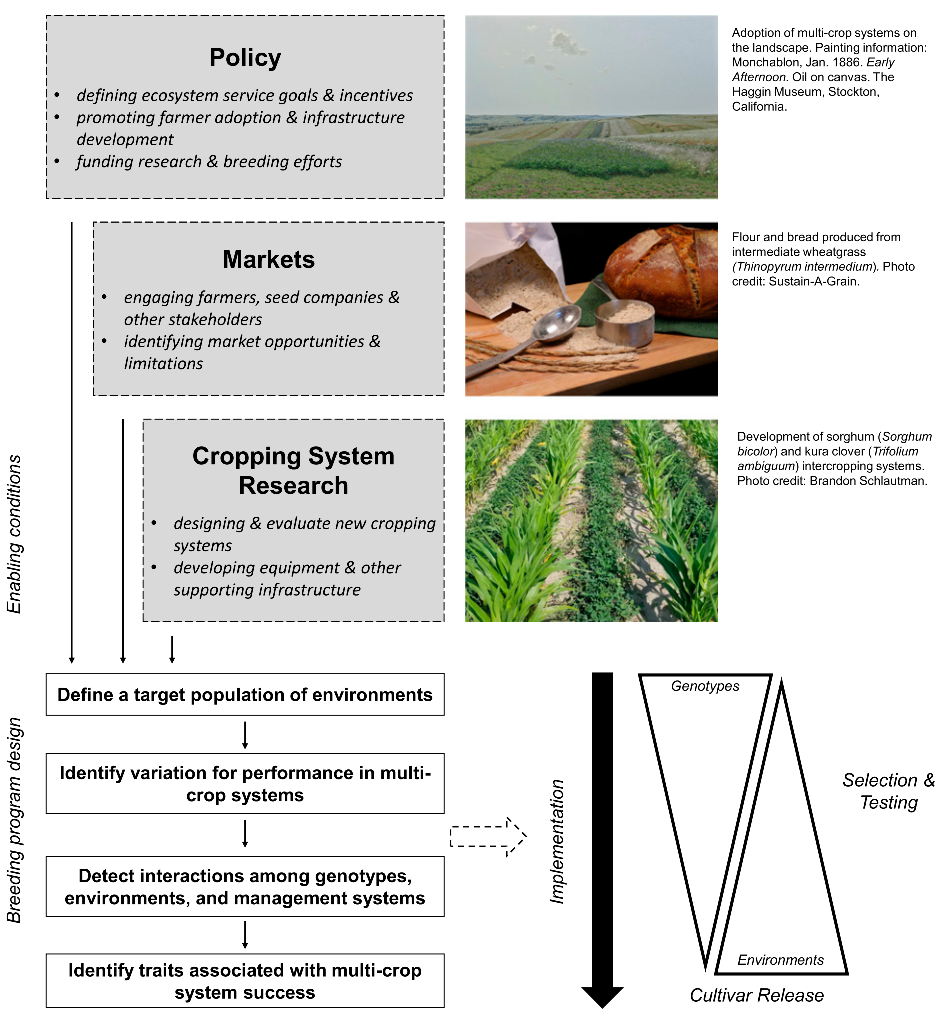

Fig. 2. The success of plant breeding for multicrop systems will require a set of enabling conditions, including appropriate policy, market demand, and other research supporting the development of multicrop systems. When setting up a breeding program for multicrop systems, core experimental activities should take place, including 1) defining a target population of environments, 2) identifying variation for performance in multicrop systems, 3) detecting interactions among mixture partners as well as environments and management systems, and 4) identifying traits of interest. These activities will inform the overall design and implementation of the breeding program. Implementation consists of successive cycles of selection, testing, and cultivar release. Breeding programs typically test many genotypes in fewer environments at the outset and expand the number of environments as best-performing genotypes are identified. The expected timeline for cultivar development and release varies by species, from 6 y to 8 y for an annual species to 25 y or more for perennial trees.

spatial diversity (e.g., intercropping systems), breeding programs will need to consider possible crop species combinations; the timing of planting, harvest, and other field operations; and possible spatial arrangements in the design of appropriate breeding nurseries and trials. In the context of increasing temporal diversity (e.g., rotations with increasing complexity), it may be sufficient to plan appropriate rotations prior to nursery and trial planting, or to plant multiple environments that follow different crops when interaction effects are expected. Collaboration with agronomists, pathologists, agroecologists, engineers, and other relevant researchers will be important in the design process.

Variation for relevant performance targets is a prerequisite for any breeding program, regardless of the cropping system context. In the context of multicrop systems, early studies should screen diverse germplasm for performance in the system of interest (42, 44). In the absence of meaningful genetic variation for required traits, adjustment of management practices or species combinations may be required to address the multicrop system challenge. It will also be critical for plant breeders to evaluate germplasm performance according to metrics of "success" for various relevant stakeholders. For example, farmers may focus on yield or harvestability, food processors may focus on quality parameters, policy makers may focus on environmental outcomes, etc.

Plant breeders routinely deal with genotype-by-environment (GxE) interactions in breeding programs. An additional major challenge of breeding and cultivar release for multicrop systems is the large number of possible species, cultivar, and management practice combinations across farms and regions. Given resource limitations in plant breeding programs and the potential for added complexity in breeding methods, especially for intercropping systems, breeders should also evaluate whether plant genotypes perform differently in monoculture and in various multicrop systems of interest. By evaluating the performance of diverse germplasm in a range of cropping systems, plant breeders can detect genotype-by-management (GxM) and GxExM interactions (3) and design breeding programs that meet a wide range of stakeholder needs while using resources efficiently. In the absence of significant rank changes between monoculture and multicrop systems, cultivars bred in one system can be used in multicrop systems without investing in a dedicated multicrop breeding program (45). Likewise, in the absence of rank changes between different multicrop systems or crop partners, breeders can develop crops adapted to a wider range of multicrop systems in a single breeding program. The concepts of general and specific mixing ability (GMA and SMA, respectively) are particularly useful in this context. They are used to describe specificity of genotype compatibility in intercropping systems, and can be examined by testing genotypes with a wide range of intercropping partners (42). Genotypes with high GMA have good performance with a wide range of partners, and high SMA indicates compatibility with a limited set of partners. High GMA may be beneficial to the extent that it can allow breeders to select for a larger number of cropping systems and potential crop partners while limiting the number of combinations that need to be tested (and thus the resources needed to develop multicrop-adapted cultivars). Genomic selection and use of alpha-lattice or other incomplete block designs have the potential to make selection for multicrop systems more feasible even when SMA is high and GMA is low, since these approaches reduce the total number of combinations to be evaluated (44, 46, 47).

Identifying traits that improve performance in the target multicrop system can also increase breeding efficiency. If these traits are known and can be observed in monoculture, then breeders can select for multicrop systems without planting a dedicated multicrop nursery (i.e., a "trait-informed approach") (48). Although plant breeders typically seek to make selections in the target environment (in this case, a multicrop system), a trait-informed approach may be more effective when heritability is low in multicrop systems (e.g., due to greater environmental heterogeneity). In the absence of a highly correlated and observable trait, selection directly in multicrop systems will be necessary for optimal genetic gain to be realized. As high-throughput phenotyping technology improves, there are also increasing opportunities to improve efficiency in breeding programs even when additional nurseries and trials are required. There may be additional opportunities for collaboration with engineers to develop high-throughput phenotyping platforms better able to accommodate complex multicrop systems.

Some or all of the activities described above should be undertaken at the outset of a multicrop breeding program. Together, the results will drive the focus and approaches of the program (e.g., breeding goals, system management, crop partners tested, and traits observed). However, these questions will also be periodically reexamined throughout the breeding process, and breeding approaches will inevitably change over time.

Developing Multicrop System Infrastructure and Practices

For a transition to multicrop systems to occur, both within plant breeding programs and in terms of farmer adoption, a range of supporting infrastructure in both the public and private sector is urgently needed to create, as Montenegro de Wit and Iles (49) define it, "thick legitimacy." This type of legitimacy goes beyond market and policy changes to support new methods of agriculture and extends to practical experience, education, scientific validation, and verification by civil society actors. Importantly, if multicrop systems are to be more widely adopted, scientists will have to enlist partnerships that extend their influence into policy, legal, practical, civic and ethical realms. This type of "thick legitimacy" requires broad investment in infrastructure that includes 1) agronomy and engineering for multicrop systems, 2) reinvigorated public plant breeding programs, 3) private sector investment in multicrop systems and models for cultivar release, and 4) economic drivers for multicrop systems achieved through development of markets and policy incentives.

Agronomic and engineering innovations are needed to support development of multicrop systems in tandem with plant breeding efforts. New crops and cropping systems require the transfer of both new technologies and webs of information (agronomic and cultural) needed for success, new methods for crop protection, availability of processing and handling equipment and facilities, and new market channels (50). Soybean provides a case study of successful introduction of a crop to a new region through substantial public investment and wide-scale cooperation among supply chain actors. Soybean had little to no commercial presence in the United States after World War I, but it surpassed wheat, cotton, and hay to become the nation's second most valuable crop in the 1960s. The widespread adoption of soybean required a multifaceted approach to new crop introduction that included the development of new technologies (cultivars), the creation of new markets for oilseed by-products (agricultural utilization research) and new methods of guaranteeing prices to growers and guaranteeing markets to processors for those by-products ("The Peoria Plan"), and widespread support from the US Department of Agriculture (USDA) and state experiment stations (51). In some cases, adoption of multicrop systems involves integrating crops in one region that are already used elsewhere (as with soybean), while other cases involve domestication of new crop species, with the former being potentially more straightforward than the latter.

We propose that a similar concerted effort is needed if multicrop systems are to be adopted on a significant scale. Adoption of multicrop systems will require not only introduction of new species but also major philosophical and management shifts relative to current cropping systems. Dominant cropping systems have focused on achieving "zero competition" from weeds, insects, other pests, or other crop species, and this assumption drives a wide range of management decisions. Multicrop systems have the potential to maintain or increase productivity relative to current systems (18), but such systems tend to be knowledge and management intensive (52), and building the knowledge and skills for successful management will require close communication between stakeholders and research disciplines: farmers, extensionists, seed companies, breeders, agronomists, engineers, and others (53). Applied research and extension are needed to improve research-based recommendations and farmer skill in managing multicrop systems. Likewise, most modern farm equipment is designed for monoculture systems. However, given adequate investment, equipment could be developed to support intercropping and other multicrop systems, and agricultural engineering—which is not constrained by the same seasonality of breeding and crop production—can happen at a rapid pace if the appropriate economic drivers are present. Indeed, this work is already occurring; for example, many new management implements have been developed to support organic and/or multicrop production, for example, roller–crimpers (54), cover crop interseeders (55), interrow mowers, shields on combine headers to allow relay intercropping, and hooded sprayers. The ongoing development and use of machine learning, camera visualization, and artificial intelligence for activities such as crop- and herbicide-targeted herbicide or fungicide applications and the creation of small electric and autonomous crop production machine prototypes suggest that other new emerging opportunities for multicrop management are on the horizon. These management and engineering innovations interact with breeding both by expanding the target population of environments and by addressing cropping system challenges through management rather than genetics.

Public sector plant breeders are well positioned to lead efforts to breed for multicrop systems, since they frequently focus on "orphan" crops, that is, crops that receive little scientific focus or funding relative to their importance for food security (56), as well as orphan regions, cropping systems, or traits (57). However, declining federal funding for public sector agricultural research and development (R&D) generally (58–60) and for plant breeding specifically (61–64) has resulted in declining numbers of public plant breeders and underfunding of programs that have remained. Beyond the scarcity of resources, plant breeding positions in both the public and private sector are typically built around a single crop rather than a cropping system. These constraints around funding and professional incentives limit plant breeders' ability to focus on development of multicrop systems as a primary objective of their program.

For plant breeding to shift toward multicrop systems, breeders must address logistical challenges related to cultivar release. Public sector plant breeders working at universities or USDA are not equipped to produce seed at a commercial scale or to market and distribute their own cultivars, so breeders typically work with their institutional technology transfer offices to license finished cultivars to seed companies (65). Whether cultivars are developed in the public or private sector, adoption on the landscape will only occur if private companies are interested in producing seed (or clones) of cultivars adapted to multicrop systems. Industry interest, of course, depends on sufficient farmer demand for seed, and breeders need to engage with seed companies to align their selection program with market needs. The diverse range of cropping systems also has the potential to limit commercialization of multicrop cultivars if cultivar adaptation is highly specific to a rotational or intercropping partner (i.e., a cultivar has high SMA). High SMA is also potentially problematic because breeding programs and seed companies are both highly specialized by crop species and may not have access to germplasm for all partner crops in a given multicrop system. If multicrop systems have a high degree of partner specificity, it may make sense to release multiple cultivars as a multicrop package, but, given the highly specialized nature of public and private breeding, this would necessitate cooperation between breeding programs and companies in sharing and codeveloping intellectual property. Such an approach may be too complex to be tractable, and it is preferable that breeders develop versatile cultivars that can perform well across a wide range of multicrop systems to reduce complexity of breeding methods and cultivar release mechanisms and to maximize the potential seed market for a given cultivar.

Despite strong evidence of environmental benefits of multicrop systems, specific policies and funding to support multicrop systems remain limited. This is, in part, because funding allocations are driven by political will, and multicrop systems lack strong advocacy organizations, unlike the focused advocacy for specific crops by lobbyists for commodity organizations. Multicropping encompasses a wide range of production practices used with many crops, providing benefits to a wide range of potential constituents, but no one organization benefits enough to have multicrop systems as its primary goal. Organizations that develop and advocate for multicrop systems at the state and/or national level can promote R&D in these systems. A mechanism to organize effective lobbying for multicrop systems could evolve from growing public awareness that environmental challenges could be met through development of sustainable agricultural production systems. Thus, opportunities to build diverse coalitions to advocate for these practices are expanding, and there have been successful policy interventions to support research and farmer adoption of multicrop systems at both the federal and state levels. For example, participation in the USDA's Environmental Quality Incentives Program is associated with increased cover crop adoption (66). One of the most dramatic policy interventions for cover crop adoption has been a cover crop cost-sharing initiative in Maryland through the Environmental Protection Agency (EPA)'s Chesapeake Bay Program (67). Direct payments to farmers for planting cover crops have resulted in major increases in cover crop adoption; as of the 2017 Census of Agriculture, Maryland had the highest cover crop adoption rate in the United States at 28.8% of cropland acres, beating its nearest competitor by nearly 10% and far surpassing the national average of 3.9% (68).

The State of Minnesota supports adoption of Kernza, a perennial grain crop, through incentive payments paired with risk mitigation payments up to 50% of the cost of crop production in areas where its ability to scavenge nitrogen is deemed to be of particular interest (e.g., in drinking water protection areas) (69, 70). This public investment is significantly cheaper than the installation of a water treatment facility and encourages farmers to produce a crop that has additional benefits that include reduced erosion and input costs. Similar systems could be implemented to encourage multicrop systems in areas where increased cover and/or the benefits of diverse rotations are predicted to be of greatest benefit.

The Watershed Restoration and Protection Strategy of the Kansas Department of Health (71) represents another unique program that is funded through the EPA Section 319 and the Kansas State Water Plan to encourage adoption of crops and other conservation practices to improve water quality in specific watersheds. This program has provided incentive payments to producers to adopt cover crops and transition from annual to perennial crops. The program has also created infrastructure, such as purchasing high-clearance seeders/interseeders and placing them at local coops, to assist farmers in planting cover crops within growing maize before harvest. While the policy initiatives described above focus on smaller regions and/or a limited set of crops and cropping systems, they demonstrate the potential to build coalitions around multicrop systems and to pass policy measures with demonstrable impacts on research, development, and adoption of multicrop systems.

Take-Home Message

The current dominant cropping systems tend to pursue production goals(e.g., crop productivity and management of pests, diseases, and weeds) through increased input use in simplified crop rotations, with drastic negative unintended consequences for ecosystems and rural communities. As agricultural inputs become more costly, the climate crisis becomes more immediate, and as environmental costs of dominant agricultural systems become clearer, we see an opportunity for plant breeders to support an alternative path for agriculture. Multicrop systems have the potential to simultaneously support both productivity and sustainability goals. In this paper, we describe our vision of diverse, sustainable, and resilient multicrop systems and the role plant breeding can play in enhancing crop adaptation to and productivity in systems with greater diversity in time and space. However, plant breeders are only one set of actors within a wider ecosystem including farmers, agronomists, engineers, seed companies, equipment manufacturers, environmental groups, and policy makers, all with interests and roles to play in reorienting our current agricultural systems to build multicrop systems of the future. For wide adoption of multicrop systems to occur, we need policies and investments that support a transition to multicrop systems from breeder to consumer; we need collaborative, participatory, and multidisciplinary research that integrates plant breeding with cropping systems development; and we need leadership and coalitions across both the public and private sectors to develop and promote adoption of new cultivars.

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1. M. A. Altieri, The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.* **74**, 19–31 (1999).
2. B. Horwith, A role for intercropping in modern agriculture. *Bioscience* **35**, 286–291 (1985).
3. R. W. Brooker *et al.*, Improving intercropping: A synthesis of research in agronomy, plant physiology and ecology. *New Phytol.* **206**, 107–117 (2015).
4. L. Anil, J. Park, R. H. Phipps, F. A. Miller, Temperate intercropping of cereals for forage: A review of the potential for growth and utilization with particular reference to the UK. *Grass Forage Sci.* **53**, 301–317 (1998).
5. T. E. Crews, M. B. Peoples, Legume versus fertilizer sources of nitrogen: Ecological tradeoffs and human needs. *Agric. Ecosyst. Environ.* **102**, 279–297 (2004).
6. M. S. Crossley, K. D. Burke, S. D. Schoville, V. C. Radeloff, Recent collapse of crop belts and declining diversity of US agriculture since 1840. *Glob. Change Biol.* **27**, 151–164 (2021).
7. D. K. Letourneau *et al.*, Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* **21**, 9–21 (2011).
8. V. B. Cardwell, Fifty years of Minnesota corn production: Sources of yield increase. *Agron. J.* **74**, 984–990 (1982).
9. M. A. Bell, R. A. Fischer, D. Byerlee, K. Sayre, Genetic and agronomic contributions to yield gains: A case study for wheat. *Field Crops Res.* **44**, 55–65 (1995).
10. J. E. Specht, D. J. Hume, S. V. Kumudini, Soybean yield potential–A genetic and physiological perspective. *Crop Sci.* **39**, 1560–1570 (1999).
11. M. Tollenaar, E. A. Lee, Yield potential, yield stability and stress tolerance in maize. *Field Crops Res.* **75**, 161–169 (2002).
12. E. A. Thaler, I. J. Larsen, Q. Yu, The extent of soil loss across the US Corn Belt. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e1922375118 (2021).
13. J. Sanderman, T. Hengl, G. J. Fiske, Soil carbon debt of 12,000 years of human land use. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 9575–9580 (2017).
14. J. Mateo-Sagasta, S. Marjani, H. Turral, "Water pollution from agriculture: A global review. Executive summary" (Food and Agriculture Organization of the United Nations, 2017).
15. N. Band, R. Kadmon, M. Mandel, N. DeMalach, Assessing the roles of nitrogen, biomass, and niche dimensionality as drivers of species loss in grassland communities. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2112010119 (2022).
16. P. H. Raven, D. L. Wagner, Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2002548117 (2021).

17. D. L. Karlen, J. L. Kovar, C. A. Cambardella, T. S. Colvin, Thirty-year tillage effects on crop yield and soil fertility indicators. *Soil Tillage Res.* **130**, 24–41 (2013).
18. C. MacLaren *et al.*, Long-term evidence for ecological intensification as a pathway to sustainable agriculture. *Nat. Sustain.*, https://doi.org/10.1038/s41893-022-00911-x. Deposited 27 June 2022.
19. M. S. DeLonge, A. Miles, L. Carlisle, Investing in the transition to sustainable agriculture. *Environ. Sci. Policy* **55**, 266–273 (2016).
20. D. J. Andrews, A. H. Kassam, "The importance of multiple cropping in increasing world food supplies" in *Multiple Cropping*, R. I. Papendick, P. A. Sanchez, G. B. Triplett, Eds. (ASA Special Publications, John Wiley, 1976), **vol. 27**, pp. 1–10.
21. K. Spangler, E. K. Burchfield, B. Schumacher, Past and current dynamics of U.S. Agricultural land use and policy. *Front. Sustain. Food Syst.* **4**, 98 (2020).
22. S. Di Falco, C. Perrings, Crop biodiversity, risk management and the implications of agricultural assistance. *Ecol. Econ.* **55**, 459–466 (2005).
23. E. J. O'Donoghue, M. J. Roberts, N. Key, Did the Federal Crop Insurance Reform Act alter farm enterprise diversification? *J. Agric. Econ.* **60**, 80–104 (2009).
24. F. Annan, W. Schlenker, Federal crop insurance and the disincentive to adapt to extreme heat. *Am. Econ. Rev.* **105**, 262–266 (2015).
25. T. Deryugina, M. Konar, Impacts of crop insurance on water withdrawals for irrigation. *Adv. Water Resour.* **110**, 437–444 (2017).
26. S. Ceccarelli, Efficiency of plant breeding. *Crop Sci.* **55**, 87–97 (2015).
27. K. R. Altendorf, L. R. DeHaan, S. R. Larson, J. A. Anderson, QTL for seed shattering and threshability in intermediate wheatgrass align closely with well-studied orthologs from wheat, barley, and rice. *Plant Genome* **14**, e20145 (2021).
28. J. A. Cubins *et al.*, Management of pennycress as a winter annual cash cover crop. A review. *Agron. Sustain. Dev.* **39**, 46 (2019).
29. R. Chopra *et al.*, Identification and stacking of crucial traits required for the domestication of pennycress. *Nat. Food* **1**, 84–91 (2020).
30. L. Kissing Kucek *et al.*, Pod dehiscence in hairy vetch (*Vicia villosa* Roth). *Front. Plant Sci.* **11**, 82 (2020).
31. C.-J. Zhang, C. Auer, Overwintering assessment of camelina (*Camelina sativa*) cultivars and congeneric species in the northeastern US. *Ind. Crops Prod.* **139**, 111532 (2019).
32. C. M. Gasol *et al.*, Life cycle assessment of a *Brassica carinata* bioenergy cropping system in southern Europe. *Biomass Bioenergy* **31**, 543–555 (2007).
33. N. P. Wiering, N. J. Ehlke, C. C. Sheaffer, Lidar and RGB image analysis to predict hairy vetch biomass in breeding nurseries. *Plant Phenome J.* **2**, 190003 (2019).
34. K. E. Muller, J. Guinness, M. Hecking, L. E. Drinkwater, Estimating agronomically relevant symbiotic nitrogen fixation in green manure breeding programs. *Crop Sci.* **61**, 3314–3330 (2021).
35. V. Moore *et al.*, Phenotypic and nodule microbial diversity among Crimson Clover (*Trifolium incarnatum* L.) accessions. *Agronomy (Basel)* **10**, 1434 (2020).
36. D. Villegas *et al.*, Biological nitrification inhibition (BNI): Phenotyping of a core germplasm collection of the tropical forage grass *Megathyrsus maximus* under greenhouse conditions. *Front. Plant Sci.* **11**, 820 (2020).
37. L. K. Kucek *et al.*, Environmental influences on the relationship between fall and spring vigor in hairy vetch. *Crop Sci.* **59**, 2443–2454 (2019).
38. N. P. Wiering *et al.*, Winter hardiness and freezing tolerance in a hairy vetch collection. *Crop Sci.* **58**, 1594–1604 (2018).
39. V. M. Moore *et al.*, Plant breeding for intercropping in temperate field crop systems: A review. *Front. Plant Sci.* **13**, 843065 (2022).
40. W. Keller, Designs and technic for the adaptation of controlled competition to forage plant breeding. *Agron. J.* **38**, 580–588 (1946).
41. J. Hamblin, J. G. Rowell, R. Redden, Selection for mixed cropping. *Euphytica* **25**, 97–106 (1976).
42. A. J. Wright, Selection for improved yield in inter-specific mixtures or intercrops. *Theor. Appl. Genet.* **69**, 399–407 (1985).
43. J. Hill, The three C's–competition, coexistence and coevolution–and their impact on the breeding of forage crop mixtures. *Theor. Appl. Genet.* **79**, 168–176 (1990).
44. B. Haug *et al.*, Advances in breeding for mixed cropping–Incomplete factorials and the producer/associate concept. *Front. Plant Sci.* **11**, 620400 (2021).
45. P. Annicchiarico *et al.*, "Do we need specific breeding for legume-based mixtures?" in *Advances in Agronomy*, D. L. Sparks, Ed. (Academic, 2019), chap. 3, pp. 141–215.
46. J. Bančič *et al.*, Modeling illustrates that genomic selection provides new opportunities for intercrop breeding. *Front. Plant Sci.* **12**, 605172 (2021).
47. M. D. Wolfe, J.-L. Jannink, M. B. Kantar, N. Santantonio, Multi-species genomics-enabled selection for improving agroecosystems across space and time. *Front. Plant Sci.* **12**, 665349 (2021).
48. S. Barot *et al.*, Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agron. Sustain. Dev.* **37**, 13 (2017).
49. M. Montenegro de Wit, A. Iles, Toward thick legitimacy: Creating a web of legitimacy for agroecology. *Elementa* **4**, 000115 (2016).
50. D. L. Van Tassel *et al.*, New food crop domestication in the age of gene editing: Genetic, agronomic and cultural change remain co-evolutionarily entangled. *Front. Plant Sci.* **11**, 789 (2020).
51. W. Lockeretz, Agricultural diversification by crop introduction: The US experience with the soybean. *Food Policy* **13**, 154–166 (1988).
52. L. Carlisle *et al.*, Transitioning to sustainable agriculture requires growing and sustaining an ecologically skilled workforce. *Front. Sustain. Food Syst.* **3**, 96 (2019).
53. B. C. Runck *et al.*, The reflective plant breeding paradigm: A robust system of germplasm development to support strategic diversification of agroecosystems. *Crop Sci.* **54**, 1939–1948 (2014).
54. D. L. Ashford, D. W. Reeves, Use of a mechanical roller-crimper as an alternative kill method for cover crops. *Am. J. Altern. Agric.* **18**, 37–45 (2003).
55. G. Roth, B. Curran, J. Wallace, M. Ryan, S. Mirsky, Cover crop interseeder: Improving the success in corn. https://extension.psu.edu/cover-crop-interseeder-improving-the-success-in-corn. Accessed 30 May 2022.
56. R. L. Naylor *et al.*, Biotechnology in the developing world: A case for increased investments in orphan crops. *Food Policy* **29**, 15–44 (2004).
57. J. C. Dawson, V. M. Moore, W. F. Tracy, Establishing best practices for germplasm exchange, intellectual property rights, and revenue return to sustain public cultivar development. *Crop Sci.* **58**, 469–471 (2018).
58. P. G. Pardey, C. Chan-Kang, J. M. Beddow, S. P. Dehmer, Long-run and global R&D funding trajectories: The U.S. farm bill in a changing context. *Am. J. Agric. Econ.* **97**, 1312–1323 (2015).
59. B. Meyer, R. L. Ridgway, "Pursuing a unifying message: Elevating food, agricultural and natural resources research as a national priority" (Charles Valentine Riley Memorial Foundation, 2014).
60. K. D. Rubenstein, P. W. Heisey, C. Klotz-Ingram, G. B. Frisvold, Competitive grants and the funding of agricultural research in the United States. *Rev. Agric. Econ.* **25**, 352–368 (2003).
61. A. C. Shelton, W. F. Tracy, Cultivar development in the U.S. Public Sector. *Crop Sci.* **57**, 1823–1835 (2017).
62. D. K. J. Frey, "National Plant Breeding Study. I: Human and financial resources devoted to plant breeding research and development in the United States in 1994" (Spec. Rep. 98, Iowa State University, 1996).
63. G. Traxler, A. K. A. Acquaye, K. Frey, A. M. Thro, *Public Sector Plant Breeding Resources in the US: Study Results for the Year 2001* (US Department of Agriculture, 2005).
64. M. T. Coe, K. M. Evans, K. Gasic, D. Main, Plant breeding capacity in U.S. public institutions. *Crop Sci.* **60**, 2373–2385 (2020).
65. W. F. Tracy, J. C. Dawson, V. M. Moore, J. Fisch, Eds., *Intellectual Property Rights and Public Plant Breeding: Recommendations, and Proceedings of a Conference on Best Practices for Intellectual Property Protection of Publicly Developed Plant Germplasm* (University of Wisconsin–Madison, 2016).
66. B. Park, *et al.*, Payments from agricultural conservation programs and cover crop adoption. *Appl. Econ. Perspect. Policy*, 1–24 (2022).
67. P. Fleming, Agricultural cost sharing and water quality in the Chesapeake bay: Estimating indirect effects of environmental payments. *Am. J. Agric. Econ.* **99**, 1208–1227 (2017).
68. US Department of Agriculture, 2017 Census of Agriculture. https://www.nass.usda.gov/Publications/AgCensus/2017/index.php#full_report. Accessed 29 December 2020.
69. J. M. Jungers, L. H. DeHaan, D. J. Mulla, C. C. Sheaffer, D. L. Wyse, Reduced nitrate leaching in a perennial grain crop compared to maize in the Upper Midwest, USA. *Agric. Ecosyst. Environ.* **272**, 63–73 (2019).
70. Forever Green Initiative, 2021 UMN Forever Green Kernza®: Forever Green EECO Implementation Program. https://kernza.org/wp-content/uploads/UMN-FGI_EECO-Implementation-Program-Flier.pdf. Accessed 20 April 2021.
71. J. R. Williams, C. M. Smith, J. D. Roe, J. C. Leatherman, R. M. Wilson, Engaging watershed stakeholders for cost-effective environmental management planning with watershed manager. *J. Nat. Resour. Life Sci. Educ.* **41**, 44–53 (2012).