The Reflective Plant Breeding Paradigm: A Robust System of Germplasm Development to Support Strategic Diversification of Agroecosystems

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ABSTRACT

Over the last half-century, crop breeding and agronomic advances have dramatically enhanced yields in temperate summer-annual cropping systems. Now, diversification of these cropping systems is emerging as a strategy for sustainable intensification, potentially increasing both crop production and resource conservation. In temperate zones, diversification is largely based on the introduction of winter-annual and perennial crops at spatial and temporal locations in annual-crop production systems that efficiently increase production and resource conservation. Germplasm development will be critical to this strategy, but we contend that to be feasible and efficient, germplasm improvement must be closely integrated with commercialization of these crops. To accomplish this integration, we propose a novel approach to germplasm development: the reflective plant breeding paradigm (RPBP). Our approach is enabled by developments in genomics, agroecosystem management, and innovation theory and practice. These developments and new plant-breeding technologies (e.g., low-cost sequencing, phenotyping, and spatial modeling of agroecosystems) now enable germplasm development to proceed on a time scale that enables close coordination of breeding and commercialization (i.e, development of cost-effective production systems and supply–value chains for end-use markets). The RPBP approach is based on close coordination of germplasm development with enterprise development. In addition to supporting strategic diversification of current annual-cropping systems, the RPBP may be useful in rapid adaptation of agriculture to climate change. Finally, the RPBP may offer a novel and distinctive pathway for future development of the public plant-breeding programs of land-grant universities with implications for graduate education for public- and private-sector plant breeders.

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Abbreviations: RPBP, reflective plant breeding paradigm; FGI, Forever Green Initiative; WCSP, Wildlife Conservation Sunflower Plots.

Agriculture is now called to achieve sustainable intensification by producing more food, feed, bioproducts, and bioenergy, while also improving conservation of soil, water, and biodiversity (Garnett et al., 2013; Heaton et al., 2013). One strategy for such intensification is cultivation of winter-annual and perennial crops at spatiotemporal locations in annual-cropping systems that efficiently increase production and resource conservation (Schulte et al., 2006, Heaton et al., 2013). A large base of evidence shows that this strategy can enhance yields of summer-annual crops, enable production of new commodities, enhance soils and wildlife, and improve water resources (Scheinost et al., 2001; Teasdale et al., 2007; Gopalakrishnan et al., 2009; Dale et al., 2010; Davis et al., 2012). Recent scenario analyses suggest that broad and substantial increases in total productivity are possible

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(Dale et al., 2010; Valentine et al., 2012) and might strongly contribute to meeting the most profound challenges facing agriculture in the decades to come (Schulte et al., 2006; Foley et al., 2011). Here, we propose a strategy for strongly accelerating strategic diversification by rapidly improving the genetic quality of winter-annual and perennial crops and coupling germplasm development closely to advances in the commercialization (i.e, production and end use) of these crops. Currently, these crops offer high potential to support sustainable intensification but are in need of germplasm development to be fully viable.

Current winter-annual cover and cash crops can provide a wide variety of ecosystem services (Snapp et al., 2005). For example, winter rye (*Secale cereale* L.) can mitigate the off-site nutrient transport, soil erosion, and loss of soil organic matter that occurs under a corn (*Zea Mays* L.) and soybean (*Glycine max* L. Merr.) rotation without excessive interference with summer-annual production (Creamer et al., 1996; Strock et al., 2004; Kaspar et al., 2012; Baxter et al., 2011; Feyereisen et al., 2013). However, there is need for improvement of cover-crop germplasm with respect to many traits, including weed suppression (Foley, 1999), stress tolerance, N-fixation by legumes (Sims and Slinkard, 1991), and biomass accumulation (Maul et al., 2011). Also needing improvement are traits related to establishment and termination, as farmers commonly find current cover-crop options difficult to establish and terminate without increasing risk to subsequent crops (Leavitt et al., 2011). New winter-annual cash crops also provide promising options for incorporation into summer-annual production systems. For example, pennycress (*Thlaspi arvense* L.) and camelina (*Camelina sativa* L.) are under active development because both produce valuable oilseed in addition to other ecological benefits (Phippen and Phippen, 2012; Gesch, 2014).

Similarly, perennial grains and herbaceous perennial crops also have high potential for production of commodities and provision of ecosystem services (Sanderson and Adler, 2008; Glover et al., 2010, Karp et al., 2011). As with winter annuals, germplasm of these crops is relatively undeveloped. For example, breeding of perennial grain crops has not yet produced high grain yields, with yields ranging from 10 to 70% of related annuals (Scheinost et al., 2001; Sacks et al., 2003; Sacks et al., 2006). However, progress is being made on grain yield in a number of species (Cox et al., 2010), including rice (*Oryza sativa* L.) (Sacks et al., 2003; Sacks et al., 2006), sunflower (*Helianthus annuus* L.) (Kantar et al., 2014), and intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey] (Cox et al., 2010). Even if grain yield is lower than in annual grain crops, lower input costs (Bell et al., 2008) and improved stress tolerance and adaptation of perennials (Glover et al., 2010) may make them well-suited to niches in certain agroecosystems (Gopalakrishnan et al., 2009). Germplasm improvement in perennial grain and biomass crops is needed in many traits related to productivity, adaptation, and interactions with pests, pathogens, and beneficial organisms (Karp and Shield, 2008; Cox et al., 2010; Van Tassel et al., 2010).

A wide range of barriers stand in the way of extensive cultivation of winter-annuals and perennials, including market structures, policy incentives, and knowledge institutions (Reganold et al., 2011). Here, we focus on a barrier of predominant importance—the limitations of current germplasm of these crops (Brummer et al., 2011). We contend that progress on other barriers is contingent on the availability of agronomically and commercially viable germplasm. To address this barrier, we propose an integrative program for rapid germplasm development closely coordinated with commercialization of the resultant germplasm, which we term the reflective plant breeding paradigm (RPBP). We have developed this approach for temperate-zone cereal production systems in the United States, but we believe our proposals are relevant to other strategies, now targeted at hundreds of millions of hectares worldwide, where sustainable intensification is being pursued through diversification practices such as conservation agriculture (Kassam et al., 2009) or the African evergreen agriculture movement (Garrity et al., 2010).

The RPBP harnesses the power of coordinated innovation that can emerge from multi-stakeholder engagement in collective processes of learning and action (Leeuwis and Aarts, 2011). Coordination of these processes serves to identify and develop desirable phenotypes in these crops and to help design and develop new production systems and supply–value chains that capitalize on these phenotypes. Below, we describe the elements of our program.

THE REFLECTIVE PLANT BREEDING PARADIGM

The RPBP is motivated by developments in communication–innovation science (Leeuwis and Aarts, 2011), science studies (Latour, 1999; Warner, 2007), participatory breeding (Ceccarelli and Grando, 2009; Almekinders, 2011), and development of a sustainable supply–value chain (Peterson, 2009; Lusch, 2011). Conceptual understanding of innovation for sustainable intensification in agriculture—and practical experience with such innovation—are rapidly growing (Bos et al., 2009; Klerkx et al., 2012; Schut et al., 2014) and form the basis for the model that underlies the RPBP (Fig. 1). In essence, this model posits that germplasm development and commercialization can proceed in a closely coordinated fashion because of recent advances in plant breeding (Hartung and Schiemann, 2014), agricultural management (Heaton et al., 2013, and development of supply–value chains for products that make value claims related to sustainability (Peterson, 2009). The

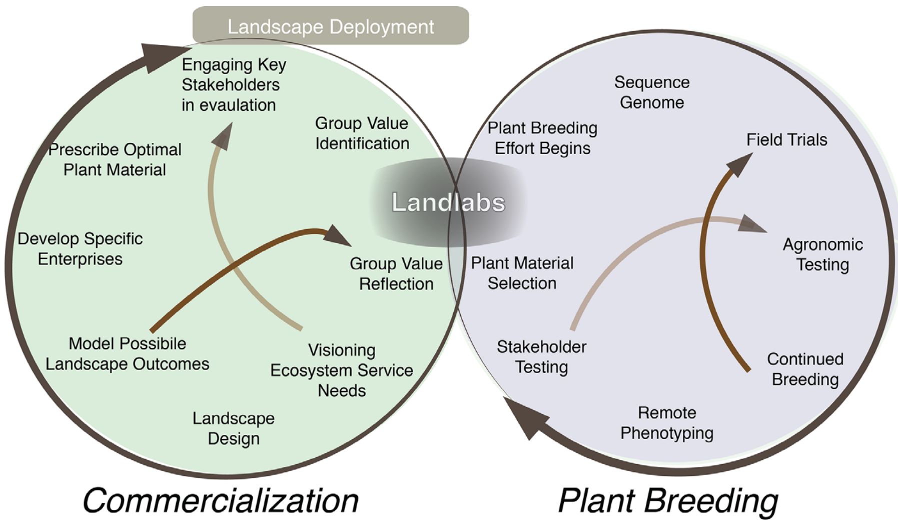

Figure 1. Conceptual model of germplasm development through coupled processes of commercialization and plant breeding. Landlabs (Jordan et al., 2013) are boundary organizations (Clark et al., 2011) in which this process occurs and is similar conceptually to Nassauer and Opdam (2008). Commercialization involves development of new, strategically diversified production systems and new supply–value chains. Information is exchanged on an ongoing basis between the two processes (circles in the diagram).

RPBP process begins by first defining an overarching set of goals through critical reflection, deliberation, and social learning among multiple stakeholders (Jordan et al., 2013; Klerkx et al., 2012; Sumberg et al., 2013). Germplasm development and commercialization then proceed in parallel, coordinated by ongoing feedback between the two processes (Sumberg et al., 2013).

RPBP is based on the following key premises:

1. Germplasm improvement is closely coordinated with commercialization.
2. New institutions, that is, boundary organizations (Clark et al., 2011), can provide this coordination, as exemplified by landlabs (Jordan et al., 2013).
3. By way of such new institutions, the RPBP engages many scientific disciplines and regional and supply–value chain stakeholders in defining desirable phenotypes from agronomic resource conservation and end-use perspectives.
4. New plant breeding technologies (Hartung and Schiemann, 2014) are used to accelerate germplasm improvement so that germplasm development proceeds on the same time scale as commercialization (years, not decades).
5. Facilitated by new technologies, centralized and decentralized (participatory) germplasm development can be integrated into an intensive–extensive system that provides a robust capacity for rapid germplasm development.

Below, we explain each of these premises and the novel processes of germplasm development that follow. We conclude with several vignettes from ongoing implementation efforts at the University of Minnesota.

Integration of germplasm improvement with sustainable commercialization. Our overarching goal is to use winter-annual and perennial crops in new agricultural enterprises that are sustainable in environmental, economic, and social terms (Klerkx et al., 2012; Jordan et al., 2013). To realize these opportunities, germplasm improvement is essential but, of course, not sufficient. It is also necessary to develop new germplasm, production systems, and agricultural landscapes that integrate these production systems (Haughton et al., 2009) and to establish new supply–value chains that meet key needs of end users, including meeting customer demands for sustainability attributes (Peterson, 2009). Moreover, these developments must be coordinated, because the overall costs of germplasm development and commercialization are considerable. Therefore, by coordinating the innovation and development needed to improve and commercialize new winter-annual and cover crops, the risk of stranding resources in either germplasm development or commercialization is decreased.

New institutions can provide this integration. Boundary organizations integrate and coordinate resources across sectors to enable complex agricultural innovation processes, such as coordinated germplasm improvement and commercialization (Klerkx et al., 2009; Kristjanson et al., 2009; Clark et al., 2011; Klerkx et al., 2012). For example, landlabs (Jordan et al., 2013) are place-based, coordinated efforts that provide a setting in which a wide range of resources (e.g., knowledge and economic, human, and social capital) can be integrated (Jordan et al., 2011; Jordan et al., 2013). Landlabs are institutions without bricks-and-mortar infrastructure. Rather, they organize and support place-based communication, design, and implementation efforts in which local and regional stakeholders innovate through collaboration and coordination (Bos et al., 2009). In essence, landlabs function as active incubators for coordinating technological, economic, environmental, and policy innovations in commercialization, thus providing a social and institutional context for the integration of germplasm development with commercialization (Fig. 1).

Engagement of many scientific disciplines and stakeholders in germplasm development and commercialization. Landlabs integrate multiple types of knowledge (Almekinders, 2011) to identify key factors and unknowns in germplasm development and commercialization, which can then be addressed through technological, social, or institutional means (Leeuwis and Aarts, 2011). To address these factors and unknowns, multiple scientific disciplines are needed. In addition to plant breeders and genomic scientists, relevant disciplines include agronomists, soil scientists, hydrologists, wildlife ecologists, agricultural and chemical engineers, and other scientists involved in transportation, processing, and use of materials from winter-annual and perennial crops. Decision-support models (e.g., Bals and Dale 2012) support integration of the work of these diverse disciplines. Such models are now emerging as powerful tools for the design and evaluation of new production systems and supply chains based on winter-annual and perennial crops (Jordan et al., 2011). Decision-support models are not panaceas (Kristjanson et al., 2009; Sterk et al., 2009; Le Gal et al., 2011); however, when used in a collaborative process, such models support integrative and deliberative decision making by scientists and stakeholders (Jakku and Thorburn, 2010). Taken together, these efforts identify goals for germplasm improvement in winter-annual and perennial crops, which may range from improvement of a single key attribute to development of entirely new ideotypes. Crop breeders can then implement efforts to achieve these goals,

New plant-breeding technologies are used to accelerate germplasm improvement. New technologies (Table 1), coordinated within integration institutions, can accelerate germplasm development (Lui et al., 2012; Mammadov et al., 2012; O'Driscoll et al., 2013). As a result, germplasm development can now proceed at a pace that allows for breeding, commercialization, and other relevant processes, such as policy development, to be coordinated. Formerly, all other processes had to be deferred while a slow and uncertain breeding process proceeded. Presently, new sequencing technologies and emerging methods such as genome editing (Hartung and Schiemann, 2014) are revolutionizing plant breeding. Such methodologies require little prior genetic information for the species under investigation beyond its ploidy level and mode of reproduction. Previous generations of molecular markers, including restriction fragment length polymorphisms and simple sequence repeats, required massive investments to develop and use the markers and thus were available for only high acreage or very high value crops; however, as the cost of markers and DNA sequences are dramatically reduced by new technologies, these technologies are driving innovations as they are more fully used in breeding across a wider array of crops (Edwards and Batley, 2010; Jackson et al., 2011). Now, DNA sequencing and other genomics technologies can be readily applied to virtually any plant species. Genotyping by sequencing (Elshire et al., 2011) is a whole genome marker strategy that holds great promise, even in species with a high amount of repetitive DNA and otherwise poor marker and sequence resources. We have used this technology with wheat (*Triticum aestivum* L.) and intermediate wheatgrass to produce thousands of markers per genotype at a sequence acquisition cost of $20 or less per genotype. As a result of decreased cost and the proven effectiveness of such technology, genomic selection, based on estimating breeding values using a large number of genetic markers, is being used as a means to reduce cycle time and to speed breeding progress (Ornella et al., 2012; Poland et al., 2012; Combs and Bernardo, 2013; Storlie and Charmet, 2013). This approach is especially attractive for perennial species because of their longer breeding cycle time, that is, the number of years required before superior progeny are identified and recycled as parents. With genomic selection, the cycle time could be reduced to <0.5 yr, allowing for more than two cycles of crossing per year. Shortening the breeding cycle will increase genetic gain per year, assuming that other factors affecting genetic gain such as trait heritability, phenotypic standard deviation, and the selection differential, remain unchanged. Taken together, the advent of inexpensive DNA sequencing and the emergence of selection methodologies that can use genotypic data have ushered in a new era in plant breeding in which unprecedented rates of genetic progress are expected, even in species with

Table 1. Changes in technology have facilitated the ability to target new crops for breeding.

Enabling technology	20th century	21st century	Reference
Sequencing capacity	Sanger†; ~672 kb day^{-1}	Next-generation sequencing; ~60 GB day^{-1}	Liu et al. (2012)
Genotyping	Restriction fragment length polymorphisms, simple sequence repeat, etc.; 1000s of markers per population.	Single nucleotide polymorphisms, genotyping by sequencing; 10,000–100,000s of markers per population	Mammadov et al. (2012)
Phenotyping	Manual, visual; 100s to 1000s of data points per day, large variances	Remote sensing, automated greenhouses; millions of data points per day, small variances	Araus and Cairns (2014)
Data storage, analysis	kilobytes	Terabytes	O'Driscoll et al. (2013)

† Sanger identifies a DNA sequencing technology developed by Frederic Sanger based on chain-termination method.

little or no previous breeding history. Additionally, new remote and high-throughput phenotyping technologies can facilitate the identification of feasible phenotypes that are compatible with the goals of enterprise development (Araus and Cairns, 2014) and are integrated into new systems of integrated centralized and decentralized germplasm development (see below).

The ability to quickly and inexpensively develop and evaluate genetic resources in winter-annual and perennial crops enables rapid response to the germplasm development goals that emerge from multi-stakeholder innovation processes, as outlined above. Indeed, these new technologies may change the very notion of the domestication of crops; it has been shown in several cases that it is now possible to domesticate plants in a very short time period (Shapter et al., 2013). For example, SGB, a biotechnology and bioenergy research and development firm, has claimed great improvements in the productivity and adaptation of the perennial oilseed crop Barbados nut (*Jatropa curcas* L.) in a 5-yr period (Keller, 2014), although these claims have not been fully verified. This apparent development stands in stark contrast to the perspective provided by Achten et al. (2010) who, writing in 2010, emphasized barriers and challenges to J. *curcas* breeding. Certainly not all of these barriers will be overcome by new breeding technologies, but these cases, and several from our ongoing work (below), suggest that substantial increases in the tempo of plant germplasm improvement are at hand, and these developments may enable major expansions in breeders' abilities to develop improved germplasm for strategic diversification in agroecosystems (Table 1).

Integration of centralized and decentralized germplasm development. Increasingly, the necessity of *extensification* of plant breeding has been recognized (Brummer et al., 2011). Extensification means that farmers and other nonbreeders must play an integral role in the development of new material that is part of a broader process of germplasm improvement that integrates centralized and decentralized approaches. Centralized germplasm improvement—that is, work to characterize desirable phenotypes for new end uses, and to improve germplasm via new breeding technologies—will certainly remain essential. We call for integration of these centralized efforts with decentralized or participatory breeding. Participatory breeding efforts can produce traits and phenotypes that are well-adapted to local conditions (Ceccarelli et al., 1997) and otherwise test and refine new germplasm for practical use. For example, farmers can provide real-time phenotype information via mobile devices, greatly enriching information on germplasm performance. Decentralized and participatory approaches (Ceccarelli and Grando, 2009) have been shown to improve many aspects of the efficiency of germplasm improvement when breeding objectives are complex and site specific (Desclaux et al., 2008; Ashby, 2009), for example, as in the integration of *J. curcas* biofuel crops in diversified agroforestry systems as opposed to monoculture plantations (Achten et al., 2010). In our view, integration of centralized and decentralized efforts will be necessary to address the scale, scope, and complexity of germplasm improvement for sustainable commercialization of winter-annual and perennial crops. Additionally, with the rise of new financial strategies such as online crowdfunding, which can amass budgets up to $200K for socially beneficial projects (Ordanini et al., 2011), we envision regional stakeholders and the interested public funding some significant portion of germplasm development.

The Forever Green Initiative: Pilot Implementation of the Reflective Plant Breeding Paradigm

The Forever Green Initiative (FGI) is a vision and work plan for the sustainable intensification of U.S. Upper Midwest agroecosystems via the RPBP. The initiative involves more than 15 disciplines (Table 2) to examine a wide range of crops, including winter annuals, short-rotation woody species, perennial grains, and perennial plants that produce biomass and bioproducts. This range provides a diversified plant-breeding portfolio of highly promising options for improving the Upper Midwest agricultural productivity, efficiency, and adaptability to variable climates, as well as a starting point for discussions of potential plant ideotypes that can rapidly be placed on the landscape. Below, we provide several vignettes that illustrate the activities of the FGI.

Developing a Multifunctional Biomass Production Landscape. The landlab approach to integrating germplasm improvement with new production systems and value chains is being explored in a pilot project in Minnesota. The FGI has convened a multi-stakeholder group to design and plan biomass production areas and infrastructure (storage areas, etc.) for a planned biomass processing facility. This effort focuses on a small watershed near St. Peter, MN, as a potential biomass production area. We call this area a *fuelshed*. The stakeholder group is comprised of three sectors: production agriculture, resource conservation (soil, water, and biodiversity), and local government. They are working to answer the question, "What do we grow, where, and for what purpose?" to produce annual crops and biomass that could provide economic gains as well as improve soil, water, and wildlife conservation. The group is using a variety of visualization and modeling tools (Jordan et al., 2011) to support its work. The biomass processing facility will use a new biomass processing technology—ammonia fiber expansion (Dale et al., 2010). This effort is part of a larger consortium for the development of multifunctional bioenergy production systems in the Upper Midwest, which includes a strong emphasis on germplasm development (Jordan et al., 2013).

Table 2. Crops under active germplasm development via the Forever Green Initiative.

Crop	Description of program	University of Minnesota departments involved	Stakeholders engaged
Intermediate wheatgrass	A perennial grass crop traditionally used as a forage, being bred for grain and biofuel (cellulosic ethanol) production, providing economic opportunities that in turn support the environmental benefits that perennials provide.	Agronomy and Plant Genetics Applied Economics Soil, Water, and Climate Ecology, Evolution, and Behavior Food Science and Nutrition Plant Pathology Public Policy	Growers General Mills
Field pennycress	A new winter-annual cover crop for corn/soybean farmers. It is planted after harvest of corn or soybean and resumes growth in early spring after winter dormancy	Agronomy and Plant Genetics Applied Economics Soil, Water, and Climate Ecology, Evolution, and Behavior Plant Biology Plant Pathology Bioproducts and Biosystems Engineering Animal Science	Growers
Winter malting barley	A potentially high value cover crop that could be double cropped with soybeans.	Agronomy and Plant Genetics Animal Science Plant Pathology	Growers
Winter cereal rye	A winter-annual cover crop that provides many environmental services without impacting soy yields.	Agronomy and Plant Genetics	Growers
Perennial flaxseed	An excellent source of omega-3 fatty acids, whose value as a dietary supplement is widely recognized.	Agronomy and Plant Genetics	Growers
Perennial sunflower	An emerging perennial crop that can produce food oils as well as providing a trap crop to protect current sunflower production	Agronomy and Plant Genetics Ecology, Evolution, and Behavior Horticulture Law School Entomology American Indian Studies	Growers National Sunflower Association USDA
Willows	A rapidly growing woody perennial crop used for cellulosic ethanol production or incinerated that can support the environmental benefits.	Agronomy and Plant Genetics Horticulture Plant Biology Forestry	Growers
Alders	Woody trees and shrubs with the capacity to be grown on sites that cannot support traditional row-crop agriculture.	Agronomy and Plant Genetics Horticulture Plant Biology Forestry	Growers
Native perennial species	Native species across the Upper Mississippi River Basin have been examined for antimicrobial, antifungal, and antioxidant activity. Promising species have been examined and selected for larger-scale production.	Agronomy and Plant Genetics Horticulture Plant Biology Law School American Indian Studies	Estee Lauder Aveda White Earth Tribe of Ojibwa

Perennial Sunflower. The perennial sunflower breeding program at the University of Minnesota was established in the early part of the 21st century with the goal of creating a perennial oilseed crop that can contribute to multifunctional continuous living cover. Here advancement of yield is being weighed against other essential agronomic characteristics such as synchronous flowering time and shattering (Kantar et al., 2014). The program was initiated with crosses between wild-collected Jerusalem artichoke (*Helianthus tuberosus* L.) and domesticated sunflower lines (Hulke and Wyse, 2008). While initial work was targeted toward developing a perennial oilseed sunflower, discussions with growers suggested a new breeding objective—creating a trap crop to mitigate bird feeding on grain crops. This suggested a new set of phenotypes and new plant ideotypes that had been previously unexplored (Kantar et al., 2014). Bird damage to sunflower and corn in North Dakota is estimated at approximately $5 million annually (Klosterman et al., 2013). Research had shown that bird damage was lower in commercial sunflower fields closely associated (≤2.4km) with Wildlife Conservation Sunflower Plots (WCSP) than at commercial sunflower fields positioned more than 10 km from WCSP (Avery, 2002; Peer et al., 2003; Hagy et al., 2008). However, the high cost of hybrid sunflower seed and the costs associated with yearly cultivation have prevented the WCSP method from being widely implemented. The cost–benefit ratio might be improved if the WCSP were planted with a productive perennial sunflower. These discussions led to funding by a growers' association to investigate perennial sunflower's potential as a tool to alleviate bird damage in annual sunflower production. This initial funding has led to the use of molecular tools (Kantar et al., 2014), and stakeholder interaction has supported new avenues of research and development of practically useful perennial sunflower germplasm. The FGI is now trying to build on this accomplishment by attracting resources to support continued improvement of grain yield in perennial sunflower.

Field Pennycress. Field pennycress is a weedy winter annual that is being evaluated as an oilseed crop (Moser et al., 2009; Phippen and Phippen, 2012). Pennycress oil is easily converted to biodiesel (Hojilla-Evangelista et al., 2013) that can be formulated into jet fuels (Boateng et al., 2010). Pennycress was selected to be part of the FGI because of its potential compatibility as a relay crop harvested in late spring, which would still allow production of a summer-annual crop such as soybean. It has the potential to provide a range of benefits to agroecosystems and to resource conservation, including soil protection, suppression of weed emergence, and provision of pollen and nectar for pollinators. In addition, oilseed production is estimated to yield between \$150 and \$300 of additional profit per acre for growers (Wyse, unpublished data, 2013). After discussions with farmers, the FGI targeted more resources toward this crop, focusing on developing both the agronomic and genetic resources (Dorn et al., 2013) that are critical for assessing pennycress's agricultural potential. Until quite recently, there had been no genetic work done on pennycress; however, in the last 2 yr, a transcriptome has been sequenced and made publicly available (Dorn et al., 2013). The genome is well on its way to being sequenced, and an association panel has been assembled to help assess phenotypes important for the breeding program. New genetic technologies, in this case involving transcriptome data, provide an opportunity to rapidly characterize traits relevant to yield and oil quality, and preliminary trials have stimulated grower interest in participating in the breeding program. Currently, seed is being multiplied for on-farm evaluation.

Implications for the Future

We propose that the RPBP provides a useful vehicle for advancing production and resource conservation in 21st-century agriculture by leveraging recent advances in germplasm technologies, agricultural management, and coordinated innovation. We also propose that the RPBP may provide a useful pathway to further develop public breeding programs at U.S. land-grant universities. To further explore these claims, we pose several questions about implementation and expansion of the RPBP.

1. Can the RPBP vision be fully implemented and integrated on the necessary timescales? While aspects of the RPBP have been implemented, the full vision, as described, has not yet been fully tested. As illustrated in Table 2, the primary point of engagement has been farmers and end users. The next steps will involve scaling up innovation processes, coordinated by institutions such as landlabs, to address the full range of effort needed for germplasm development and sustainable commercialization. Sustaining such efforts over the time scales required (e.g., 10 yr) will require capacity for ongoing coordination and integration, engagement with policy development and capital providers, and managing inevitable conflicts of interest among stakeholders and other disruptions to innovation and research and development processes.
2. Can public plant breeding programs sponsor the RPBP? In the United States, many public breeding programs have experienced reduced investment from state and federal sources, while private breeding capacities have expanded for major commodity crops such as corn and soybean (Mba et al., 2012). In many cases, the public programs are now redesigning themselves in response to these developments. The RPBP might serve as one niche for these public breeding programs, much as organic and specialty crops have in other countries (Osman et al., 2008). In our experience, private breeding and biotechnology firms are interested in cooperating with public-sector efforts on projects such as strategic diversification of cropping systems. Such cooperation should certainly be expanded, but we believe that private firms cannot be expected to take the lead in breeding for winter-annual and perennial crops that may not produce acceptable returns on investment. Rather, we view multifunctional agriculture and sustainable intensification as public goods, which should be developed by public investment.
   In the United States, land-grant universities would seem to be the societal institutions best positioned to organize and lead broad-based efforts to produce germplasm that can support sustainable intensification. In the United States, land-grant universities have a historic and unique role as incubators of technical innovation and knowledge dissemination (Christy and Williamson, 1992). We acknowledge that as established institutions, such universities could potentially hinder progress on more disruptive innovations (Sumberg et al., 2013). However, given the existing aggregation of social, intellectual, and financial resources within land-grant universities, they are the most obvious institutional setting in the United States for implementation of the RPBP.
3. Can the RPBP offer helpful guidelines in the ongoing development of graduate education for plant

breeders? The skills needed to participate in work guided by the RPBP complement and substantially extend the priorities for graduate education of plant breeders identified by Repinski et al. (2011). We hypothesize that students trained under the RPBP model will be able to easily transition between crops and public- and private-sector employment opportunities (Jordan et al., 2012).

4. Will the RPBP be useful for developing germplasm that can help agriculture manage the impacts of climate change? Society will need to enhance its capacities for rapid and efficient deployment of resources to adapt to the social, economic, and environmental changes that may result from climate change. The RPBP may contribute to such capacities in the context of agriculture and its interconnections with food, land, water, biodiversity, and energy.

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