

Crops and Soils Review

Cite this article: Colley MR, Dawson JC, McCluskey C, Myers JR, Tracy WF, Lammerts van Bueren ET (2021). Exploring the emergence of participatory plant breeding in countries of the Global North – a review. *The Journal of Agricultural Science* **159**, 320–338. <https://doi.org/10.1017/S0021859621000782>

Received: 11 June 2021
Revised: 31 August 2021
Accepted: 9 September 2021
First published online: 20 October 2021


Key words:

Genetic diversity; organic seed; seed sovereignty

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Exploring the emergence of participatory plant breeding in countries of the Global North – a review

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Abstract

Participatory plant breeding (PPB), commonly applied in the Global South to address the needs of underserved farmers, refers to the active collaboration between researchers, farmers and other actors throughout the breeding process. In spite of significant public and private investments in crop variety improvement in the Global North, PPB is increasingly utilized as an approach to address cropping system needs. The current study conducted a state-of-the-art review, including a comprehensive inventory of projects and five case studies, to explore the emergence of PPB in the Global North and inform future PPB efforts. Case studies included maize (*Zea mays*), tomato (*Solanum lycopersicum*), Brassica crops (*Brassica oleracea*), wheat (*Triticum aestivum*) and potato (*Solanum tuberosum*). The review identified 47 projects across the United States, Canada and Europe including 22 crop species representing diverse crop biology. Improved adaptation to organic farming systems and addressing principles and values of organic agriculture emerged as consistent themes. While projects presented evidence that PPB has expanded crop diversity and farmer's access to improved varieties, obstacles to PPB also emerged including challenges in sustained funding as well as addressing regulatory barriers to the commercial distribution of PPB varieties. Agronomic improvements were only one lens motivating PPB, with many projects identifying goals of conservation of crop genetic diversity, farmers' seed sovereignty and avoidance of certain breeding techniques. The authors conclude that a multidisciplinary approach is needed to fully understand the social, political and agroecological influences driving the emergence of projects in the Global North and factors impacting success.

Introduction

Plant breeders, farmers and other stakeholders across the United States (US), Canada (CA) and Europe are working together to breed new or improved crop varieties, an approach commonly known as participatory plant breeding (PPB) (Chiffolleau and Desclaux, 2006; Dawson *et al.*, 2011; Shelton and Tracy, 2016). PPB is a collaborative relationship between professional plant breeders or researchers, farmer-breeders and other stakeholders to share and leverage knowledge, decision making and resources in breeding efforts. PPB methodologies are more commonly applied in countries with low-income economies, particularly employed by the Consultative Group on International Agricultural Research (CGIAR), to improve the adaptation of crops grown in marginal and heterogeneous environments and to bolster seed security of farmers underserved by the Green Revolution (Weltzien *et al.*, 2003; Morris and Bellon, 2004). A recent global review of the literature on PPB (Ceccarelli and Grando, 2019) identified 66 countries where PPB has been implemented, including nine countries with high-income economies – the US, CA and several European countries. Despite the strong economies, significant public and private investments in modern breeding programmes and consistent seed availability in the Global North, PPB projects are employed to address farmers' needs throughout the region. This raises the question of what is driving researchers and farmers to collaborate.

Many of these projects focused on breeding for organic agriculture. Organic farmers are more and more legally obligated to use organically produced seed as part of their certification requirements in Europe (EC 2018/848) and in the US (7 CFR § 205.204). They increasingly have access to commercially available organic seed sources. Additionally, producers are allowed to use conventionally grown, untreated seeds when suitable organic sources are not available. The organic seed industry is also growing and organic farmers report using an increased

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quantity of organic seed over the last decade (Hubbard and Zystro, 2016). Yet, access to seed does not always mean that farmers are satisfied with their seed options. As Shelton and Tracy (2016) point out, many organic seed options are cultivars bred in and for conventional systems where the seed is simply produced in organic systems, and there is evidence that performance in conventional systems does not always translate to optimum performance under organic conditions (Murphy *et al.*, 2007; Lammerts van Bueren *et al.*, 2011). In addition, organic breeding programmes are still relatively young and the size of the organic market, as well as lack of pressure from organic seed regulations, often limits the research investments of larger commercial seed companies (Mendum and Glenna, 2010; Hubbard and Zystro, 2016).

Organic farm environments in countries with high-income economies often, though not always, hold environmental similarities to subsistence and low input farms in countries with low-income economies. There is also often greater variation among farms than in conventional systems because farm management practices are more site-specific. Many organic farmers are also in locations outside of major production regions targeted by breeding companies. Thus, organic breeding efforts often strive for either specific adaptation or the use of crop genetic diversity to mitigate risks and address crop challenges (Dawson *et al.*, 2008; Wolfe *et al.*, 2008). Organic markets also value greater diversity in crop species and cultivar type including minor crops (Shelton and Tracy, 2016). At the same time, certain socio-economic factors influencing farmers in countries with the high gross domestic product must be noted, including the high value of organic products and land costs, the dynamics of governance of farming and seed, variable access to research support for agriculture, as well as philosophical values of the organic movement and citizen concerns for environmental impacts (Mendum and Glenna, 2010). Lastly, it must be acknowledged that unequal wealth distribution within countries with high-income economies often leaves some sectors of society marginalized, operating in low-income economic environments and underserved by public and private agricultural research and policies (Horst and Marion, 2018; Lyon *et al.*, 2021).

The growing number of PPB cases in the US, CA and Europe provides the opportunity to assess who is engaging in PPB; what the scope of crop types is, and methods applied; what is motivating the actors engaged in PPB; and what the outcomes and impacts are to date. The current study aimed to conduct a comprehensive inventory and state of the art review of PPB projects in these countries to analyse and inform future PPB efforts. Objectives of the current study were to assess whether there is evidence that PPB is addressing the agronomic needs of farmers, whether it is motivated by societal goals beyond organic agriculture, and if there are trends in the experiences to date that may provide insights to inform the successful institutionalization of PPB in current in and future research programmes.

Materials and methods

The current study presents a state-of-the-art review of PPB projects in the US, CA and Europe. A review of scientific and grey literature served to develop a comprehensive inventory of PPB projects. Five case studies of PPB projects with different crop species provided deeper analysis across crop biological types. The inventory allowed reflection on the magnitude and scope of PPB implementation while the case studies provided deeper

context for exploring the motivations, experiences and outcomes of PPB projects across a diversity of crop biological types.

The literature review included a search of the following databases Agricola (National Agricultural Library), ABI/INFORM and CAB Abstracts. Key search words included 'participatory plant breeding', 'community breeding' and 'multi-actor breeding'. The database searches produced 311 articles and articles related to specific projects outside of the US, Europe and Canada were eliminated. An internet search with Google and Google Scholar followed using the same key words as the scientific databases in order to capture projects described in grey literature and online sources such as reports, proceedings and websites not included in peer-reviewed journals. The online search was limited to the years 2000–2020 with the search as in-title or in-text and in quotations to limit hits to the full term. The search of Google and Google Scholar produced 184 and 992 links, respectively. Sources that did not identify a specific project and those that did not fit the criteria of collaboration between researchers and farmers or other actors in both the decision making and activities of the selection in plant breeding were eliminated. Projects exclusively involving farmers in the variety-evaluation phase, commonly referred to as participatory variety selection (PVS) or solely farmer-managed breeding activities without researchers participating in the breeding activities were also excluded. The resulting full list of citations is provided as a 'complete bibliography' in supplemental materials. As plant breeding takes time to set goals, implement methods and result in outcomes, only projects with more than 3 years duration were included in the inventory of projects (Table 1).

The remaining articles from the full search were selected for review based on the above criteria, including articles covering both applied research projects and those addressing the broader methodology, organizational, institutional, policy or conceptual aspects of PPB within the context of the US, CA or Europe. Information on crop types and locations, actors involved and their roles, the motivations driving PPB, whether projects were conducted in organic agriculture, breeding goals and methods and reported outcomes were tracked. The inventory of projects including location, actors and drivers is presented in Table 1. Additional details on each project including the project goals, methods and reported outcomes, are presented as 'project details' in the supplemental material. After compiling the inventory of projects from the literature review, the preliminary list was shared with 36 researchers who were either primary authors of published PPB projects or recommended by an author as a researcher familiar with the field of PPB. The contacts were asked to review the list, identify missing projects and contribute any relevant literature covering their own projects or other topics pertinent to the current study. Twelve researchers provided clarification and additional details on projects through personal communications.

Many research institutions manage several breeding projects within one crop species in which case each crop was only counted as one case so that the resulting inventory represents both the breadth of crops as well as the breadth of institutions that have implemented PPB and their locations.

The crops selected for case studies represent diverse crop reproductive biology (mating systems and life cycles) including annual, biennial, self-pollinated, cross-pollinated and vegetatively propagated examples as well as grain, vegetable and arable crops. The authors selected crops that had multiple projects to compare and the diversity of species in order to compare across contrasting crops. Crop case studies included *Brassica oleracea* (cabbage,

Table 1. PPB projects identified in the United States, Canada and Europe

Crop common name and species	Mating system/Life cycle ^a	Country	Institution(s)	Year initiated	Actors ^b	Drivers ^c
Apple and Pear (<i>Malus pumila</i> , <i>Pyrus communis</i>)	OB, P	DE	University Agroscope Changins-Wädenswil; University of Oldenburg, Saat:gut	–	FN, PR	OA, AB
Barley (<i>Hordeum vulgare</i>)	IB, A	IT	Rete Semi Rurali	–	F, FN, NR	OA, RA, UC, AB
	IB, A	IT	Italian Association for Organic Agriculture	2013	F, FN, NR	OA, RA, UC, AB
Beet root (<i>Beta vulgaris</i>)	OB, B	US	University of Wisconsin-Madison	–	F, PR, Cu, EU	CQ
Broccoli (<i>Brassica oleracea</i>)	OB, A	US	Oregon State University	2008	F, PR	OA, RA, BM, SS
Broccoli, Purple Sprouting (<i>B. oleracea</i>)	OB, A	US	Organic Seed Alliance	2009	F, NR	OA, RA
	OB, A	FR	French National Research Institute INRAE	2011	F, PR, FN	OA, RA
Buckwheat (<i>Fagopyrum esculentum</i>)	OB, A	FR	French National Research Institute INRAE	2018	F, PR, Cu, Ps	RA, AB, CQ
Cabbage (<i>B. oleracea</i>)	OB, B	FR	French National Research Institute INRAE	2001	F, FN, PR, SN	BM, RA, SS, AB
	OB, B	US	Organic Seed Alliance	2014	F, NR	BM, RA, SS
Cauliflower (<i>B. oleracea</i>)	OB, B	FR	French National Research Institute INRAE	2001	F, FN, PR, SN	RA, BM, SS, AB
Clover, Yellow Sweet (<i>Melilotus officianalis</i>)	OB, A	US	United States Department of Agriculture/ Agricultural Research Service USDA/ARS	2017	FN, PR, NR	OA, RA, UC
Einkorn (<i>Triticum monococcum</i> sp.)	IB, A	IT	Rete Semi Rurali	–	F, NR, Cu, Ps	OA, RA, SS, CQ
	IB, A	FR	French National Research Institute INRAE	2014	F, FN, PR, Ps	OA, RA, SS
Maize (<i>Zea mays</i>)	OB, A	PT	Polytechnical Institute of Coimbra IPC, University of Lisbon ITQB NOVA	1984	F, PR, Cu	AB, CQ, SS
	OB, A	US	University of Wisconsin-Madison	2012	F, PR, NR	OA, RA, CQ
	OB, A	FR	Organic Food and Farming Institute ITAB	2017	F, FN, PR	RA, AB
Oat (<i>Avena sativa</i>)	IB, A	CA	University of Manitoba	2011	F, PR, NR	OA, RA, UC
Onion (<i>Allium cepa</i>)	OB, B	IT	Italian Research Institute CREA	2012	F, PR	OA, RA
Peas (<i>Pisum sativum</i>)	IB, A	IT	Italian Research Institute CREA	2013	F, PR	OA, RA
	IB, A	US	United States Department of Agriculture/ Agricultural Research Service USDA-ARS	2016	F, FN, PR, NR	OA, RA, UC
Pepper (<i>Capsicum annuum</i>)	OB, A	US/CA	Cornell University/SeedChange	2016	F, PR	OA, RA, SS
Potato (<i>Solanum tuberosum</i>)	V	CA	University of Manitoba	2013	F, PR	OA, RA, UC
	V	NL	Wageningen University, Louis Bolk Institute	2009	F, PR, NR, SC	OA
	V	US	University of Wisconsin-Madison	2014	F, PR	OA
	V	DE	State Research Institute of Bavaria	2012	F, PR	OA
Quinoa (<i>Chenopodium quinoa</i>)	OB, A	US	Washington State University	2014	F, PR	OA, RA, SS, DM, UC
	OB, A	US	Organic Seed Alliance	2014	F, NR	OA, RA, SS, DM, UC
Spinach (<i>Spinacea oleracea</i>)	OB, A	US	Organic Seed Alliance	2003	F, NR	OA, RA, SS
Sweet potato (<i>Ipomoea batatas</i>)	V	US	North Carolina State University	1997	F, PR	RA

(Continued)

Table 1. (Continued.)

Crop common name and species	Mating system/Life cycle ^a	Country	Institution(s)	Year initiated	Actors ^b	Drivers ^c
Tomato (<i>Solanum lycopersicum</i>)	IB, A	IT	Italian Research Institute CREA	2012	F, PR	OA, RA
	IB, A	ES	Miquel Agustí Foundation/Polytechnic University of Catalonia	2011	F, PR	AB, RA, DM, CQ
	IB, A	IT	Rete Semi Rurali	2018	F, NR, SC	OA, RA
	IB, A	IT	Italian Research Institute CRA	2017	F, PR, SC	OA, RA
Wheat (<i>Triticum aestivum</i>)	IB, A	IT	Rete Semi Rurali	2006	F, NR, CU, PS	OA, SS, CQ, AB
	IB, A	US	University of Nebraska Lincoln, Northern Plains Sustainable Agriculture Society Famer Breeder Club	1999	FN, PR	OA, RA, BM, SS, CQ, AB
	IB, A	UK	Organic Research Centre	2005	F, NR	OA, RA, AB
	IB, A	US	Washington State University	2002	F, PR	OA, RA
	IB, A	US	University of Vermont, University of New England, Cornell University	2008	F, FN, PR, CU, PS	OA, RA, DM, CQ
	IB, A	CA	University of Manitoba	2011	F, PR, NR	OA, RA, SS, AB
	IB, A	FR	French National Research Institute INRAE	2006	F, FN, PR, NR, SN, CU, PS	OA, RA, BM, SS, DM, CQ, AB
Wheat (<i>Triticum durum</i>)	IB, A	NL	Wageningen University, Louis Bolk Institute	2009	F, PR, NR	OA, RA
	IB, A	IT	Italian Research Institute CREA	2011	F, PR	OA, RA
	IB, A	FR	French National Research Institute INRAE	2001	F, FN, PR, PS	OA, RA, AB
Vetch (<i>Vicia villosa</i>)	OB, A	US	United States Department of Agriculture/Agricultural Research Service USDA/ARS	2017	F, FN, PR, NR	OA, RA, UC
Zucchini (<i>Cucurbita pepo</i>)	OB, A	US	Organic Seed Alliance	2006	F, NR	OA, RA, SS
	OB, A	IT	Italian Research Institute CREA	2012	F, PR	OA, RA

^aMating system is categorized as either primarily inbreeding (IB) or primarily outbreeding (OB). The life cycle is categorized as either annual (A), biennial (B), perennial (P), or vegetatively propagated (V).

^bActors refers to those directly participating in the plant breeding project decision-making activities. Actors are categorized as individual farmers (F), farmer networks or cooperatives (FN), public researchers such as universities (PR), non-profit researchers (NR), seed companies with private breeders (SC), culinarians (such as chefs and bakers) (Cu), processors (such as millers) (Ps), retailers (Rt), and end-users (EU).

^cDrivers refers to the motivation of the actors in engaging in PPB. Drivers include adaptation to organic agriculture (OA), regional adaptation (RA), avoidance of breeding methods (BM), seed sovereignty (SS), culinary qualities (CQ), and conservation of agrobiodiversity (AB).

cauliflower, kale and sprouting broccoli), *Zea mays* (maize, both grain and sweet types), *Solanum tuberosum* (potato), *Solanum lycopersicum* (tomato) and *Triticum aestivum* (bread wheat).

Results

The resulting inventory of PPB projects includes an inventory of 22 crop species listed in Table 1, along with locations, actors involved and drivers of the projects. Additional details on projects are provided in supplemental materials. The current study identified 47 PPB crop projects with 25, 19 and three projects in Europe, US and CA, respectively. Canada holds a history of PPB approach in international aid in developing countries led by the Unitarian Service Committee of Canada (USC), but it is only in the last decade that a new initiative implementing PPB domestically has emerged, the Bauta Family Initiative on Canadian Seed Security. Additional projects were recently initiated in CA on carrot, broccoli, summer squash and winter

squash, but are not reported here as they were less than 3 years of experience. Within Europe, programmes in Italy and France are implementing PPB across the greatest number of crop types with 10 and five crops respectively. In the US, projects include grain, pulse, cover crops and horticultural crops and are led by seven institutions.

The longevity of projects varied widely with at least six projects initiated in the last 5 years whereas the VASO project in Portugal started in 1984 and the sweet potato project in the US in 1997, with both projects still running at the time of the current study. Thirty-eight projects (84%) identify breeding for organic agriculture as a factor motivating the PPB project. A few projects reported that farmers received a share of royalties when varieties are commercialized.

The inventory does not suggest that the crop mating system influences the propensity for PPB as projects included a range of reproductive types with 21 projects on inbreeding crops, 18 on outbreeding crops and five on vegetatively propagated crops

(Table 1). Crops also represent a diversity of species and crop types including vegetables, staple crops, cover crops, pulses, bread grains, other small grains as well as a project on apple and pear, an example of PPB in perennial tree fruit crops. The most frequent crops included wheat, tomato and potato, with ten, four and four projects respectively, demonstrating that PPB is not limited to minor and novel crop types.

Actors, roles and methods in PPB

The role of farmers and stages of involvement in the breeding process varied across projects. In addition to the information presented in Table 1, information on project methods and outcomes is provided as supplemental materials. In nearly all cases farmers provided input in setting breeding objectives. Therefore they often evaluated varieties in trials at the beginning of the project to identify traits for improvement and again after several cycles of selection to assess progress and determine if the population was ready for market. Researchers most frequently conducted the pre-breeding effort (making initial crosses or developing the initial breeding population or introgressing traits from wild relatives). In some projects including tomato, potato and sweet potato researchers advanced selections by conducting marker-assisted selection (MAS) to select for key traits, such as disease resistance, in early segregating generations. Many projects involved diverse actors beyond farmers and researchers including farmer networks and cooperatives, seed companies, food processors such as millers and culinary professionals such as bakers and chefs. The role of the other actors focused primarily on informing breeding objectives, participating in variety evaluation that provided input into breeding selections and market development for novel and heterogeneous varieties.

In the North, specialization in plant breeding and seed production has clearly resulted in a loss of a direct relationship with seed and reinvigorating farmers' engagement in seed improvement often necessitates restoring knowledge gaps through education and training. Some projects are contributing new varieties to the seed trade, such as the case of potato in the Netherlands, sweet potato in the US, sweet maize in the US and wheat in the Northeast US, but for many projects expanding farmers' access to seed is not focused on the development of commercial markets. The current study also provides examples of learning opportunities not only for farmers, but for researchers who reconsider methods in genetic advancements utilizing new approaches such as breeding for populations, evolutionary adaptation and developing novel statistical tools to adapt to decentralized models.

Drivers of PPB

Researchers' reports of the drivers, or motivations, for initiating PPB consistently fell into distinct categories including addressing traits of priority to organic production, regional adaptation, avoidance of some breeding methods [cytoplasmic male sterility (CMS) in particular], seed sovereignty, culinary qualities desired by organic markets, diversification of crops by improving underserved crops and preservation or enhancement of agrobiodiversity (see Table 1 and supplementary materials). Several projects reported initiating PPB to fill gaps in the availability of cultivars with key traits prioritized by farmers to address organic production challenges (84% of all 45 projects) not fully met by the formal seed sector, such as late blight (*Phytophthora infestans*) resistance in market classes of importance to organic growers in potato and

tomato and seedling vigour under cold soil conditions in sweet maize. The need for adaptation to regional environmental conditions (88%) was frequently mentioned in grain crops reflecting the high genotype by environment interaction in grains. Regional adaptation also motivated breeding in crops newly introduced to a region such as quinoa in the US. Another example is sprouting broccoli, overwintering type broccoli with narrow environmental conditions for overwintering success, recently introduced to north-western France as well as the US Pacific Northwest as a diversification strategy for regional markets. Several projects targeted improvements in cover crops and minor food crops with a low market value that are thus underserved by the formal seed sector. These crops include crimson clover, vetch, buckwheat and fava bean. Avoidance of cultivars with CMS motivated participatory breeding in Brassica crops, where CMS is utilized in the breeding of F₁ cultivars. Researchers also reported farmers' desire for seed sovereignty, often related to breeding open-pollinated cultivars with market quality to avoid dependence on F₁ cultivars, most frequently in out-crossing vegetable crops where F₁ cultivars dominate the market such as Brassicas, maize, chard and zucchini. The goal of seed sovereignty motivated several grain breeding projects when farmers struggled with access to suitable planting stock and on-farm seed saving is feasible. Authors repeatedly discussed the important role of on-farm breeding and seed saving in efforts to preserve and enhance crop genetic resources. At least three projects targeted revival of heritage crops and preservation of agrobiodiversity including a reintroduction of Brassicas in France from the French government seed bank, a reinvigoration of heritage tomatoes in Spain and the development of heritage maize in Portugal for traditional bread type called broa.

The current case studies also clarified that not all farmers want to grow their own seed, for example, in sweet maize in the US and potato in the Netherlands. In these cases, consideration of the role of other aligned actors in the seed system involved in seed production, distribution and marketing were essential to support access to new appropriate varieties. Thus, the broader context of the seed system and roles of farmers engaged in PPB must be considered carefully in the development of projects from the start without assumptions of on-farm seed stewardship in order to ensure breeding outcomes are truly serving defined needs.

Case studies of PPB in five crop species

An in-depth exploration of PPB experiences with five crop species revealed similarities and differences in the drivers, experiences and methodologies employed in PPB. Case studies of maize, tomato, potato, Brassica and wheat are presented below.

Case study of maize (corn)

The morphology and reproductive biology of maize make the breeding of maize relatively easy compared to other crops, but also create some limitations. The monoecious plants are large and produce large naked kernels that adhere to the ear (pistillate inflorescence). The staminate and pistillate inflorescences are physically separated on the plant making controlled pollination easy. The main downside is that pollen is dispersed by wind and while relatively heavy, can travel a considerable distance, making isolation somewhat difficult. Maize also suffers from relatively severe inbreeding depression.

The first hybrid maize cultivars were developed and commercialized in the US in the 1920s. These varieties were largely

tailored to the Upper Midwest region of the US. The early benefits of hybrid maize to farmers were uniformity and standability. Uniformity also provided more predictability in plant behaviour and yield. Uniformity has come with a price of reduced genetic diversity and access to germplasm.

Prior to the broad adoption of hybrid maize in the 1930s and 1940s, farmers planted open-pollinated maize. According to Martin and Leonard (1967), there were over 1000 different maize cultivars grown throughout the US in the early 1900s. PPB provides an alternative that centres farmers as active participants in variety development and seed production, rather than passive seed purchasers at the mercy of hybrid-dominant seed company offerings. The two maize cases reviewed cited meeting the needs of maize growers underserved by the dominant hybrid model.

The current study identified only two established maize PPB projects in the Global North, one in the US and one in Portugal (Table 2). A third project has recently been initiated in France, but no results are reported yet (Rey pers. com, 2021). Farmers established breeding priorities in both projects indicating a common recognition of the importance of centring their input for successful projects. The US project was initiated and grown with an equal partnership between the farmer and researchers. In contrast, researchers initiated the Portuguese project and then sought out an equal partnership with and buy-in from the farmers.

The Portuguese Sousa Valley Project (VASO), was launched in 1984 by Dr Silas Pêgo (Mendes-Moreira, 2006). Underpinning the project is Pêgo's Integrant Philosophy, which he developed in contrast to the Productivist Philosophy that had driven maize monoculture on the US landscape (Pêgo and Pilar Antunes, 1997; Mendes-Moreira, 2006). The Integrant Philosophy model centres on both the agricultural system and the farmer as the most important decision-makers in the breeding process (Mendes-Moreira, 2006). Motivations for the Portuguese researchers and farmers were to establish the integrant approach in on-farm polyculture systems and to preserve genetic diversity in open-pollinated varieties that was eroded with the introduction of high yielding hybrid maize introduced to Portugal by US companies after the Second World War (Mendes-Moreira and Pêgo, 2012). The Sousa Valley region was selected in part because it is a traditional maize production area where maize still played a significant role in the polyculture system. In addition, the region's farmers were still growing traditional maize varieties used to make broa, a culturally significant Portuguese maize bread.

The project includes two parallel breeding programmes developed by researchers and farmer-cooperators. The researcher's programme combines three recurrent selection methodologies: phenotypic mass, S_1 and S_2 lines (Mendes-Moreira, 2006). The farmer's programme uses an improved common mass selection methodology with two-parent control instead of the more traditional one parent control (Mendes-Moreira, 2006; Mendes-Moreira *et al.*, 2017). The project has produced six improved populations that serve smallholder farmers growing for high-quality markets in sustainable systems (Mendes-Moreira, 2006). Researchers believe that populations coming out of the VASO project can also serve as germplasm sources for the hybrid seed industry (Mendes-Moreira, 2006). In this way, the integrant and productivist models could complement one another and offer underserved farmers throughout the world economic opportunities in seed production. Additionally, this would also increase genetic resources instead of replacing them with varieties bred for high-input industrial systems.

Table 2. Farmer-breeders (FB) and researcher-breeders (RB) roles in PPB in maize

Project	Organic Sweet Maize (UW Madison/Organic Seed Alliance), US		The Vaso Project, PT	
	FB	RB	FB	RB
Start	2012		1984	
No. of farms	1		>20	
Breeding roles	FB	RB	FB	RB
Identify breeding goals	X		X	X
Select source germplasm		X	X	X
Pre-breeding		X	X	X
Early selection (F_{1-4})	X	X	X	X
Advanced selection (F_{5-8})	X	X	X	X
Variety evaluation/testing	X	X	X	X
Outcomes (Y/N):				
Variety release	Y	Y	N	N
On-farm use	Y		Y	Y
Royalties	Y	Y		

Conventional maize production in the US operates in what Pêgo defines as the productivist model focused on maximizing yields (Pêgo and Pilar Antunes, 1997). As a response to being underserved by this model, organic farmers and public and independent plant breeders developed the 'who gets kissed?' project to develop an open-pollinated sweet maize variety bred under organic systems (Shelton and Tracy, 2015).

The project was initiated by an organic vegetable grower in Minnesota and a scientist with a non-profit research institute, and later joined by a public sector university plant breeder. The farmer was known in the region for his sweet maize, but was frustrated because his favourite varieties were often dropped by seed companies as they merged or closed. The farmer defined the desired traits and the breeding began with two populations from the university programme. Researchers designed a recurrent selection breeding programme in which, during each summer season, 100 full-sib families from each population were grown in Minnesota. Remnant seed from each family was saved in cold storage in Wisconsin. Researchers and the farmer were involved in quality evaluations, which made this activity much more of a social process than most plant breeding activities. Based on the data, 15–20 families were selected in each population. Remnant seed saved from the selected full-sib families was sent to winter nurseries in Chile where they were intermated within populations and full-sib families were generated for the next round of selection so that a full cycle of selection could be accomplished in 1 year (Shelton and Tracy, 2015). They completed five cycles of selection and in 2014 chose to advance one population as the new open-pollinated sweet maize variety under the name 'who gets kissed?'

Given the interests of many in the US organic vegetable farming community 'who gets kissed?' was released with no intellectual property restrictions. Several regional breeding projects have grown out of 'who gets kissed?'. Breeders and farmers in California, New Mexico, Oregon in the US, and in Australia are adapting it to their environmental conditions and local preferences (Colley *et al.*, 2021).

Case study of tomato

Tomato (*S. lycopersicum*) has many different market classes as well as types within market classes making breeding more complex. The major market class split is between processing and fresh market tomatoes. The former tends to be grown on a large, highly industrialized scale to produce tomatoes for canning, soups, sauces and juices. Fresh market tomatoes are diverse with cultivars varying for many traits including plant growth habits, fruit size, shape and colours. The predominant type in terms of the area produced are large-fruited red slicer types. These are often grown in southern temperate and subtropical regions for the winter fresh tomato market. Cherry tomatoes are the second most important market class. These have small red, yellow, orange or green fruit with round, oval or pear shapes. Most major seed companies have tomato breeding programmes, but these are focused primarily on the larger conventional agricultural markets (California and Florida in the US; Spain and Italy in Europe), or on types that are not necessarily in demand by fresh market organic growers (processing, wholesale glasshouse).

Outside of these generalizations, many tomatoes that vary from common market types are grown and sold regionally. Generally classed as 'heirlooms' in the US or 'conservation varieties' in Europe, more accurate terms we will use for the remainder of the paper are 'heritage' or 'landrace' tomatoes. As documented in the European case studies described below, some of the types of tomatoes that have been the subject of PPB have specific characteristics that are valued on a regional basis by growers and consumers. The number of heritage or landrace tomatoes is truly astounding. Nearly all of these were developed without a formal breeding approach and the tradition continues today.

Tomatoes are self-pollinated and lend themselves to varietal development as pure lines or may be utilized as inbreds in crosses to create F_1 hybrids. Most contemporary commercial tomato cultivars are F_1 hybrids and hybrid seed is produced by hand; the high ratio of seed obtained per cross makes F_1 hybrids economically feasible.

Organic fresh market growers consistently rank tomatoes as first or second in terms of vegetable crops needing genetic improvement to meet their production and marketing needs in all regions of the US (Lyon *et al.*, 2015; Brouwer and Colley, 2016; Hultengren *et al.*, 2016; Dawson *et al.*, 2017; Healy *et al.*, 2017). Some organic growers may find that commercial F_1 hybrids are not adapted to their production or marketing needs or may wish to save their own seed from year to year, which cannot be done with F_1 hybrids. Some growers and researchers conducting tomato PPB have justified their projects because of the need to breed varieties for regional adaptation as well as having the capacity to save seed.

Farmer participatory tomato improvement projects have focused on both fresh market and processing types with the main emphasis being field grown medium- to large-fruited types. Most are red fruited although yellow-fruited types have also been the subject of PPB. In the US, the most important types for organic fresh market growers have been indeterminate large-fruited red slicers, while in Europe, there has been an emphasis on the revival of traditional landraces, which vary in size and usage.

The current study identified seven projects in PPB of tomatoes (Horneburg, 2010; Campanelli *et al.*, 2015, 2019; Lange *et al.*, 2018; Casals *et al.*, 2019; Healy and Dawson, 2019; Rodriguez *et al.*, 2020; Petitti *et al.*, 2021), four of which met our criteria

for case studies (Table 3). Six of the seven projects were in Europe (Italy, Spain and Germany) and one in the US. The projects that were excluded were either too new to have achieved 3 years of activity, or they were primarily PVS rather than PPB projects. The pattern of activity compared to other crops is striking in that application of PPB to tomatoes is relatively recent and is concentrated in Europe. None of these projects can be said to have matured; while farmers are locally using selections from these projects, there do not appear to have been any formal variety releases. Traits under selection included yield and other horticultural traits in the field, but there was an especially strong emphasis on fruit quality traits including °Brix, dry matter, and flavour.

Some of the European activity has focused on the revitalization of local landraces, and in some cases using these to breed improved forms of these landraces. For example, the Spanish project by Casals *et al.* (2019) began as an effort to revitalize the 'Mando' local landrace, whose production had dwindled to a single grower. During grow-out and increase, variation from spontaneous outcrossing was observed, and breeders and farmers continued selections over years to stabilize some different yellow flesh lines that farmers thought had potential for commercialization. However, these were rejected on the basis of poor flavour by consumers in the final year of testing. On the other hand, production of 'Mando' did increase and the project was successful in preserving the landrace.

Campanelli *et al.* (2015) described a PPB project carried out in Italy to examine the significance of local adaptation in breeding for organic systems. Researchers first created four populations by selfing F_1 s of four diverse crosses (a Cuor di Bue (Oxheart) fruit type, a long fruit type, a cherry fruit and a green salad fruit type). Seventy-two F_2 s of each of the four populations along with check cultivars were planted in an unreplicated row-column design on four farms and a research station distributed across Italy. Both farmers and researchers evaluated populations and 201 selections over all locations were obtained. For the $F_{2,3}$ in on-farm trials, three selections by farmers, three by researchers, three by both and three by researchers only on-station for each of the four populations were planted. On the research station, six selections per population previously made by researchers were planted back at that site. From these, 115 plants were selected on-farm by farmers and researchers. Extensive replicated trials of selections in year three identified three out of 15 $F_{2,4}$ families that out-yielded commercial check cultivars, and these were being further developed for release. This study compared researchers' selections as opposed to those selections of farmers alone, and farmers' and researchers' joint selections, and found that the best performing were farmers' selections grown in the location in which they were selected. There was a clear pattern of specific adaptation to locality and production system.

Another project in Italy examined the effect of human (farmer) selection *v.* natural selection on specific adaptation (Petitti *et al.*, 2021). Starting with the same base population, farmers at different locations selected desirable plants and fruit from these was saved, while simultaneously, a population of 400 plants was advanced by single seed descent to the next generation. This process was carried out for two cycles followed by a third evaluation generation where all populations were grown at all locations for evaluation and further selection. Results from the comparative trial had not been published at the time of writing, but Petitti *et al.* (2021) found that the success of the project varied by region. There was strong interest by farmers and circulation of seed from selections in the southern region but in another region,

Table 3. Farmer-breeders (FB), researcher-breeders (RB) and commercial-breeders (CB) roles in PPB in tomato

Project	Miquel Agusti Found., ES		Council Res. Agric., IT			Rete Semi Rurali, IT			CRA/ISI Sementi, IT		
	FB	RB	FB	RB	CB	FB	RB	CB	FB	RB	CB
Start	2017		2012			2018			2017 (date of early selections)		
No. of farms	3 farms for PVS ^a		5			5			3		
Identify breeding goals		X		X			X				X
Select source germplasm	X			X	X			X			X
Pre-breeding	X	X		X			X				X
Early selection (F ₁₋₄)	X	X	X	X		X	X		X	X	
Advanced selection (F ₅₋₈)	X	X	X	X		X	X		X	X	
Variety evaluation/testing	X	X	X	X		X	X		X	X	
MAS											X
Outcomes (Y/N):											
On-farm use	Y		Y			Y			Y		

^aParticipatory variety selection.

researchers found that farmers did not use the types of tomatoes used to generate the breeding population, and that farm had to be replaced by another in the region after the second year.

The project reported by Campanelli *et al.* (2019) illustrates an interesting approach to combining PPB with genomic analysis. The researchers conducted PPB using a tomato MAGIC (multi-parent advanced generation intercross) population originally developed by the commercial company, ISI Sementi. The eight founder lines included seven contemporary tomato lines (representing a combination of paste and slicer types) and one wild species (*S. cheesmaniae*) selected for its productivity and biotic and abiotic stress resistance. Public researchers' breeding efforts began with a grow-out of 400 plants from the final eight-way cross, from which 30 plants were selected. Farmer selections began in the next generation where seeds of 370 MAGIC population plants plus 30 selections from the researchers' efforts were grown along with 25 standard cultivars on three farms in Italy representing north, central and south geographic regions. Researchers and farmers jointly selected plants based on a set of visual traits, then the fruit was brought back to the lab for testing Brix, total solids and taste. Differences in mean values for plants selected in different regions were observed; those selected in the north had the greatest vigour and productivity, whereas those selected in the south had the highest brix and total solids. The objectives of this research spanned both researcher and farmer interests including developing a genetic resource for breeders and germplasm representing different market classes and traits of interest to farmers. Future research with these materials included growing all selections along with the eight parents and 500 highly inbred plants of the original MAGIC population, genotyping these and discovering SNPs associated with important field traits while examining the shift in allele frequencies as a function of selection in different regions.

In general, researchers considered tomato as a convenient crop for PPB, noting that the crop is well characterized genetically, that the reproductive biology and breeding methods for self-pollinated crops are translatable to on-farm research, traits of interest are

easy to discern, there is a plethora of germplasm in the form of local landraces, there is strong interest in tomato improvement in the organic community and farmers willing to participate in PPB, and consumers have an interest in novel tomato types. A disadvantage is the large plant size which limits the number of plants that can be grown in farmers' fields. Researchers indicated that small to medium farm operations were often motivated to develop their own varieties and could accommodate around 100–300 plants with minimal compensation. However, larger operations tended to have a more rigid structure and tighter margins and were less inclined to engage in PPB. One characteristic of the tomato PPB projects is that they tended to be more regionally focused, perhaps because the needs of organic farmers across Europe are many and varied, thus local projects are more important than one that encompasses Europe. In some cases, it was apparent that researchers were not targeting the needs of farmers with their choice of initial material. In every case, the parents for crosses to develop populations were selected by researchers without overt input from farmers. Researchers may have had some idea of farmers' needs for markets, but farmers were not brought in from the beginning to design the project. Bringing in farmers at an earlier stage would probably allow better targeting of the project. All of these projects are relatively young considering the decade long duration of most breeding projects and have not had time to develop and formally release varieties. However, farmers are informally saving seed and producing the lines that work best on their farm, so while difficult to measure, the projects are generating impact.

Finally, an interesting dynamic was observed that may not play out with other crops, but probably affects the PPB landscape for tomatoes. Tomatoes are a very popular crop in the US with breeders at public institutions and with independent plant breeders. About a half-dozen universities in the US support tomato breeders who release fresh market and processed varieties. With independent plant breeders, Deppe (2021) found that 11 of 35 breeders who release materials under an open seed source initiative (OSS) agreement work on tomatoes. The Dwarf Tomato

Project, an effort that began among growers on a tomato forum on Gardenweb, has released more than 100 varieties (Deppe, 2021). Seed Savers Exchange, a grassroots organization dedicated to preserving landrace varieties, lists 9911 entries of tomatoes on their Exchange website (SSE, 2021). It may be their popularity among independent breeders, and the ability of these breeders to satisfy growers and gardeners' needs that reduces the need for public/private PPB activities, especially in the United States. In Europe, the situation is somewhat different, with larger numbers of locally adapted landraces in need of adaptation to organic production. Also, the costs of the registration requirement for improved 'conservation varieties' for commercial sale in Europe can be a barrier to independent breeders (Petitti M., personal communication). Access to landraces may be more difficult because of the lack of a European-wide organization to preserve traditional varieties. PPB can play a vital role in preserving and improving traditional varieties and preventing their *in-situ* loss.

Case study of Brassica

Vegetable crops of Brassica (*B. oleracea*) are widely grown for premium organic markets across the US, CA and Europe including cabbage, cauliflower, broccoli and kale. Diverse landrace and heirloom varieties, originally domesticated in Europe, are still accessible for breeding (Chable *et al.*, 2008). Until the 1980s open-pollinated varieties were grown commercially, but since then the seed trade-focused almost exclusively on the development of F₁ hybrids (F₁s). The shift towards F₁s was largely due to the allogamous nature of *B. oleracea*, the development of CMS and the use of double haploids to facilitate the production of inbred lines. F₁ breeding is primarily focused on achieving crop uniformity and narrowing the maturity window for mechanical harvests, further incentivizing breeders towards F₁ development for large scale, mechanized agriculture (Chable *et al.*, 2008; Myers *et al.*, 2012; McKenzie, 2013). Yet, many organic producers seek quality traits with less emphasis on uniformity in the timing of maturity (McKenzie, 2013). CMS use in breeding is also not in alignment with organic principles as in *B. oleracea* it is commonly derived through protoplast fusion, though there are also now organic breeding companies producing F₁s through naturally derived self-incompatibility. The use of double haploids is also questioned by the organic sector (Chable *et al.*, 2008; Myers *et al.*, 2012; Sahamishirazi *et al.*, 2018). All cases cited the avoidance of F₁ breeding techniques, lack of quality open-pollinated varieties, need for local adaptation and farmers' desire for greater control over their seed as reasons motivating participatory breeding (Chable *et al.*, 2008; Myers *et al.*, 2012; McKenzie, 2013; McKenzie L., personal communication).

The current study identified five Brassica projects on PPB in the Global North, all located in the Pacific Northwest region of the US and the Brittany and Normandy regions of France where the locations share an environment optimum for seed production of a diversity of *B. oleracea* crop types (Table 4). Farmers established breeding priorities in all projects indicating a shared recognition of the importance of farmers' input from the start to ensure the outcome suits the target market and production environment. Researchers sourced germplasm and developed initial crosses in four of the five projects. In the case of kale in the US, the farmer initiated the project and only involved researchers in the advanced stage after frustrations of not achieving adequate uniformity for a variety release. The stage of researcher involvement varied in the early to advanced breeding phases with the researcher coordinating early phase population development in

the case of broccoli and cabbage in the US, but the farmer leading early progress through mass selection in the US kale and purple sprouting broccoli projects and French cabbage and cauliflower projects. In all cases early to advanced breeding was conducted on-farm to leverage selection under the target environment. Researcher involvement in advanced breeding phases employed coordination of half or full-sib progeny selection methods with farmers' participating in the in-field evaluation and decisions in selection.

Brassica crops are well suited to on-farm breeding as Myers *et al.* (2012) noted, since advancements can easily be made through mass selection if enough genetic diversity is created and maintained as selection occurs prior to flowering. Selection in on-farm production fields can also serve as an advantage as the large population size allows leveraging selection pressure while maintaining adequate heterogeneity to avoid inbreeding depression (McKenzie L., personal communication). An added benefit is that farmers can harvest the crop for market, while evaluating quality and then subsequently harvest seed from select plants for breeding purposes (McKenzie, 2013). On-farm reproduction of biennial crop types, including cabbage and some cauliflowers, can however be a barrier to PPB as they require conditions suitable for vernalization, either in the field or by lifting and storing plants through the winter which is likely why projects are limited to conducive production regions. The promiscuous nature of *B. oleracea* can also present a challenge to manage isolation on farms with diversified Brassica crops in production or nearby (McKenzie, 2013). High levels of outcrossing, self-incompatibility and propensity for in-breeding depression present challenges in breeding Brassicas for recessive traits and achieving high levels of uniformity in open-pollinated populations (Myers J. R., personal communication; McKenzie L., personal communication). For this reason, researcher involvement in advanced breeding stages can aid in the implementation of progeny selection (Myers *et al.*, 2012). The challenge of managing breeding populations given these biological factors may be one of the reasons; there are not many examples of Brassica PPB projects.

It is unlikely that open-pollinated Brassica varieties will achieve enough uniformity to replace the demand for F₁ varieties in large scale production, so it is likely that there will remain two different markets for hybrids and open-pollinated Brassicas unless there is increased pressure from organic regulations to restrict the use of CMS varieties or other market incentives. In spite of this fact, three of the four projects have already resulted in the release and commercialization of new open-pollinated varieties for specialized markets demonstrating the demand for alternatives to hybrid varieties.

Projects exhibited innovative breeding strategies that leverage farmers' and researchers' knowledge and resources while engaging multiple farmers as a participatory breeding network. The US broccoli breeding project followed a divergent–convergent scheme of population improvement, first described by Atlin *et al.* (2001), in which a genetically diverse breeding population is distributed to farmers for on-farm selection and then recombined annually (Myers *et al.*, 2012). This allowed decentralized selection under diverse farm environments leveraging farmers' input in selection criteria in the pre-breeding phase. After 7 years of population development, the researchers and two of the farmers each continued breeding through half-sib progeny selection for at least 6 years resulting in several new and distinct varieties. The cabbage and cauliflower projects in France similarly

Table 4. Farmer-breeders (FB) and researcher-breeders (RB) roles in PPB in *Brassica oleracea* crops

Project	Broccoli (OSU), US		Cabbage and Cauliflower (INRAE), FR		Cabbage (OSA), US		Kale (OSA), US		Purple Sprouting Broccoli (OSA), US	
	Start	2001	2001	2001	2014	2014	2007	2007	2009	2009
No. of farms	6		>10		1		1		4	
Breeding roles	FB	RB	FB	RB	FB	RB	FB	RB	FB	RB
Identify breeding goals	X		X		X		X		X	X
Select source germplasm		X		X	X		X			X
Pre-breeding		X		X	X			X	X	X
Early selection (F ₁₋₄)	X		X		X		X	X	X	
Advanced selection (F ₅₋₈)	X	X			X	X	X	X	X	X
Variety evaluation/testing	X	X			X	X		X	X	X
Outcomes (Y/N):										
Variety release	Y		Y		Y		N		N	
On-farm use	Y	Y	Y		Y		Y		Y	
Seed network distribution		Y	Y		N		N		N	
Royalties	N		N		N		N		N	

leveraged a farmer network, including seven farms, with breeding integrated into on-farm variety trials of heritage varieties from the French national seed bank. The researcher coordinated the farmers' variety evaluations. Each farm then conducted mass selection and saved seed from one variety ensuring a different variety was selected by each farm to preserve as much diversity as possible. Based on farmer's input the research institute then also crossed similar, but complimentary lines to generate new F₁ breeding populations for further on-farm selection and development of improved varieties. In the US cabbage project, the researcher facilitated the annual advancement of cabbage, a biennial, by lifting selected plants from the farmer's field and then reproducing in a greenhouse to advance the seed maturation early enough to again plant the following summer achieving annual selection. In the US kale project, the researcher self-pollinated plants by hand (bud pollination) to achieve full-sib progeny for repeated on-farm selection of families, a task too tedious to manage on a working farm. Each of these projects demonstrates the creative use of complementary skills and capacities to achieve greater advancement in *B. oleracea* development through farmer–researcher collaboration than could be achieved individually.

Case study of potato

Potato (*S. tuberosum* L.) is the fourth most important food crop worldwide, and also an important crop in organic farming systems. Consumers have different preferences as to tuber skin or flesh colour for consumption (including mealy to firm cooking types). But there are also special varieties for the processing industry such as french fries (long tuber shapes) or chips (round tuber forms).

Technically, making crosses in potatoes is not too complicated, but many factors influence the success (Tiemens-Hulscher *et al.*, 2013). Most varieties can be used as seed or pollen parents, but some varieties do not produce viable pollen. Some varieties only occasionally produce flowers and cannot be used for

crossing. Sometimes flowers or berries are aborted, or pollen is not shed under conditions that are too moist or too dry. Most modern varieties are to a large degree self-pollinating, but in the field between 0 and 20% cross-pollination occurs by wind or bumble bees. Often the anthers are removed from the seed parent with a pair of tweezers to avoid self-pollination. Hand crossing can be done in the field early in the morning before bumble bees have visited the flowers. Parental tubers can also be planted in greenhouses in the ground or in buckets, enabling removal of the newly formed tubers to allow more inflorescences to be produced.

Potato is one of few vegetatively propagated root crops that are involved in participatory breeding programmes in the Global North: in the Netherlands (Lammerts van Bueren *et al.*, 2008; Tiemens-Hulscher *et al.*, 2012; Keijzer *et al.*, 2021), Germany (Sieber *et al.*, 2018) and CA (Entz, 2019), US (Genger, 2018) (Table 5). The reasons for starting such programmes are the lack of available organically produced seed potatoes (CA and US). In Europe, such as in the Netherlands and Germany, potato breeding companies are interested in the organic market and provide sufficient quantities of organic seed potatoes, but their breeding programmes do not prioritize late blight resistance which is of high priority for most organic growers.

The potato programmes were usually initiated when researcher–breeders were approached by organic growers with an urgent call for action. As the late blight resistance genes that were derived from *S. demissum* are no longer effective, new resistance genes need to be introgressed from wild relatives and the expertise of specialized pre-breeders from one of the universities or institutes is required. Most cultivated potato (*S. tuberosum* L.) is tetraploid, so introgressing new resistance traits from wild relatives needs an extra step as many of them are diploid. Many wild relatives do not produce tubers and need to be converted from short day types to long day types to match the northern long day growing conditions. After the introgression and pre-breeding phase of some

Table 5. Farmer-breeders (FB), researcher-breeders (RB) and commercial-breeders (CB) roles in participatory breeding projects on potato

Project	WUR, LBI, BioImpuls, NL			Lfl Bayern, Bavaria, DE		Univ of Wisconsin Madison, US		Univ of Manitoba, CA	
	2009			2012		2014		2013	
No. of farms	12			3		9		20	
Breeding roles	FB	RB	CB	FB	RB	FB	RB	FB	RB
Identify breeding goals	X	X	X	X	X	X	X	X	X
Select source germplasm	X	X	X	X	X	X	X	X	X
Pre-breeding		X			X		X		X
Early selection (F ₁₋₄)	X	X	X	X		X		X	
Advanced selection (F ₅₋₈)		X	X		X		X		X
Variety evaluation/testing			X		X		X		X
MAS		X	X		X				
Outcomes (Y/N):									
On-farm use	Y				N		N		Y
Commercialization	Y		Y ^a		N ^b		N		N
Seed network distribution			N		N		N		N

^aFirst varieties are under registration trialling (2019).

^bPromising clones are handed over to commercial breeders for further selection (2018).

10 to sometimes 20 years, including several generations of back-crossing the wild relative with modern varieties with good agronomic properties, the scientist breeders can then produce commercial crosses and distribute seeds from relevant crosses to the farmers to select during several early field generations. Some breeders provide true seeds and others grow out first-year seedling tubers for the growers. Usually, farmer-breeders select over 3–5 years and then return the selected, promising clones to the researchers or breeding companies who organize testing across various locations in replicated trials. The number of seeds or seedling tubers that farmers select on a yearly basis differs; in many programmes farmer-breeders yearly receive a minimum of 200 seeds up to 3000 of two or more populations. They discard approximately 95–98% in the first 3–4 years.

As the F₁ progeny of potato crosses are vegetatively propagated, the populations do not segregate. This makes it relatively easy for growers to be involved in the early stages of the programme, visually selecting clones that perform well, with good and regular tuber shape, smooth skin, good storability, sufficient disease resistance and other desirable traits.

As genotype-by-environment interaction is very large for potatoes, testing and selection over many years is needed to select a clone that is stable in performance across years and multiple locations. The programmes described above are not yet quite in the stage that clones can be marketed (usually up to 10 years of selection after the initial cross). However, some farmer-breeders sell quality clones through their own farm sales and do not pursue registration and commercialization (Table 5). Most projects aim at the commercialization of the selected clones. It is custom in the Netherlands to register a potato variety on the names of both the involved farmer-breeder and commercial breeder, so that ownership is shared which is expressed in sharing the royalties on a 50–50% base (Almekinders *et al.*, 2014).

Specific to late blight being very sensitive to mutations under a high disease pressure, it is important to prevent the breakdown of

late blight resistance by stacking various resistance genes (Pacilly *et al.*, 2019). The advantage for farmer-breeders collaborating with universities is access to molecular markers for each source of late blight resistance which can be used to check whether the farmer's selected clones contain two or more resistance genes (Lammerts van Bueren *et al.*, 2010).

For many modern farmers, the skill of breeding has declined due to specialization. As a response, the Dutch project introduced a yearly training course for farmers or young breeders on potato breeding, and the course manual is published to make the practical potato breeding knowledge publicly available (Tiemens-Hulscher *et al.*, 2013).

Case study of wheat

Bread wheat (*T. aestivum*) has a large number of published projects ranging from conference proceedings to peer-reviewed journal articles. Projects exist in Europe (Dawson *et al.*, 2010, 2011; Enjalbert *et al.*, 2011; Goldringer *et al.*, 2012, 2019; Malandrini and Dvortsin, 2013; Rivière *et al.*, 2013a, 2013b, 2014, 2015; Rivière, 2014; Da Via, 2015; Vindras-Fouillet *et al.*, 2016; Petitti *et al.*, 2018; van Frank, 2018; Berthet *et al.*, 2020; van Frank *et al.*, 2020), CA (Bauta Family Initiative on Canadian Seed Security, 2013; Entz *et al.*, 2015, 2016, 2018; Kirk *et al.*, 2015), and the US (Murphy *et al.*, 2005, 2013; Lazor, 2008; Darby *et al.*, 2013; Kissing Kucek *et al.*, 2015; Kissing Kucek and Sorrells, 2016; Kissing Kucek, 2017) (Table 6). The large number of examples for bread wheat may be due to the existence of public plant breeding programmes at many universities and research institutions. It may also be due to the strong genotype by environment interactions that are observed in small grains, meaning that varieties developed for other regions or other management systems may not perform well for farmers in another region or using a different management system. The relative ease of logistics in managing participatory breeding projects with small grains is also likely a factor in the development of new projects.

Table 6. Farmer-breeders (FB), researcher-breeders (RB) and commercial-breeders (CB) roles in PPB in wheat

Project	Manitoba, CA		Washington State, US		Northeast and Midwest US		France, EU		Italy, EU	
	FB	RB	FB	RB	FB	RB	FB	RB	FB	RB
Start	2011		2002		2012		2006		2011	
No. of farms	8 (start)–75 (current)		1		4 (start)–8 (current)		1 (start)–80 (current)		1 (start)–4 (current)	
Identify breeding goals	X	X	X	X	X	X	X	X	X	
Select source germplasm	X	X	X	X		X	X	X	X	X
Pre-breeding		X		X		X	X	X	X	X
Early selection (F_{1-4})	X		X		X		X		X	
Advanced selection (F_{5-8})	X		X		X		X		X	
Variety evaluation/testing	X	X		X		X	X	X	X	X
Outcomes (Y/N):										
On-farm use	Y		Y				Y		Y	
Commercialization	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Seed network distribution							Y		Y	

The motivation for starting participatory breeding projects often comes from farmers who have been unable to find suitable varieties for their production. In most examples here (Table 6), farmers have been targeting a value-added market for artisanal bread and have not found varieties that are competitive in organic production with the high quality they need for artisanal bread-making quality. Frequently crosses are made between higher-yielding modern varieties that have been tested in organic systems and landraces or historic varieties known for artisanal bread-making quality, particularly those known to produce high-quality bread at lower protein levels (i.e. around 10 v. 12.5% for most conventional bread wheat). High protein percentage in winter bread wheat is often achieved either by growing in areas with less rainfall and lower yield potential such as the Mediterranean or the Great Plains and intermountain region of the US. Participatory breeding programmes in areas with higher rainfall such as Northern France and the north-eastern and midwestern US have goals of increasing baking quality in winter wheat, which is preferred by growers because of its agronomic advantages but not by bakers due to its typically lower protein (Dawson *et al.*, 2011; Kissing Kucek *et al.*, 2015; Vindras-Fouillet *et al.*, 2016; Kissing Kucek and Sorrells, 2016). In these climates, selection for resistance to *Fusarium* head blight (FHB, *Fusarium graminearum*) and resistance to pre-harvest sprouting is also critical, and these two traits are difficult to score on-farm. Participatory breeding projects in areas where bread wheat is typically grown often have goals of increasing yield under stressful conditions and lower inputs or organic systems while maintaining good artisanal bread-making quality.

The genotype by environment interactions seen in small grains often leads breeders and farmers to a decentralized model of selection to serve organic farmers in multiple ecological regions. There is also a lack of breeding in conventional systems for weed competitive ability or seed-borne disease resistance, which are major issues for organic farmers. Organic farmers frequently prefer lines that are taller with more tillering and biomass as long as lodging is minimal to compete with weeds during the season and to reduce the weed seed bank over the long term, as winter

small grains are an excellent rotation crop to break up weed dynamics on organic farms that also grow row crops or vegetables. The desire for high biomass is also a trait that is more specific to organic farmers, who value the straw for soil building carbon or for livestock bedding or mulch. This is in contrast to goals of a high harvest index and a focus on grain yield in conventional systems.

In most cases, farmers approached the research team to initiate the project, often after trialling many modern and historic varieties which did not meet their needs. While there is a wide diversity of approaches to the details, there is a common breeding scheme that involves farmers proposing parental varieties to the research team, which makes the crosses in a greenhouse and then multiplies the first two generations on a research station or in a greenhouse without selection to get enough seed for farmers to plant in a small plot on their farm. In some cases such as France, the F_1 may be returned directly to the farmer who grows it in a protected plot (Dawson *et al.*, 2011). In some other cases, the lines may be more advanced before they are put on farmers' fields, due to difficulties in finding small scale equipment for on-farm trials.

For most projects, on-farm trials start with the F_3 generation and are managed in small plots with shared equipment, either from the research team or from a farmers' organization. As bread wheat is a self-pollinating species with the harvested grain also being the seed for the next cycle of selection, on-farm management of multiple populations is primarily constrained by access to small plot scale equipment.

For the projects in this case study, the selection is done on-farm within populations by using negative selection to eliminate plants that are undesirable and positive selection to choose spikes from plants that have the desired characteristics. Farmers also choose between populations that come from different crosses. The selected spikes are frequently given to the research team for threshing and measurement (grain filling, protein content etc.) and then returned to the farmer for planting. Farmers frequently also visit research station trials of lines developed in the participatory breeding programme to observe and select among more lines

than they can manage on-farm. Research station trials might include dozens of lines while on-farm trials typically have 5–10.

Projects vary in terms of how much selection is done on the research station to complement the on-farm selection. All projects have an on-farm selection and on-farm evaluations of more advanced lines involving more farmers. Some also add research station selection for certain traits. The project in France is based entirely on on-farm selection, with researchers measuring traits such as protein and thousand-kernel-weight on selected spikes to return information to farmers on the results of their selection (Dawson *et al.*, 2011; Rivière, 2014). The project in the Northeast region of the US uses a combination of on-farm selection for production traits and on-station selection for traits like FHB and pre-harvest sprouting resistance, which are difficult to rate on-farm and is much more reliably scored in an inoculated nursery for FHB and in greenhouse misting conditions for pre-harvest sprouting, which are labour intensive and not realistic for an on-farm trial (Kissing Kucek, 2017). Similarly, pre-harvest sprouting is scored by researchers using a specialized nursery and greenhouse misting to create the ideal conditions for sprouting (Kissing Kucek, 2017). The research team also usually does grain protein and quality measurements are also done by the research team with information returned to farmers (Rivière, 2014; Kissing Kucek, 2017). Researchers may also do their own selection, often with input from farmers attending field days and winter meetings and maintain researcher and farmer selections in parallel.

Longer running projects have more varieties that are in production and in the stages just prior to release. For any participatory selection process, a long-term commitment is required to see results, both because of how long it takes to get from a cross to a new variety and because selection involves a learning curve for many farmers without prior experience, just as it does for new breeders. It can be difficult for farmers who are new to on-farm breeding to select efficiently. This can lead to unwanted increases in height of plants for example, or a reduction in tillering, or an unintentional reduction of diversity in the population. Managing on-farm trials can also be tricky and some experience is needed to manage the trial in a way that allows selection primarily on genetic merit rather than micro-environmental differences. As everyone learns, selection becomes more efficient and progress is clearer. Selection results after only a few years may not show many advantages to on-farm selection. However, after several years, projects in Manitoba, Washington, France, Italy and the north-eastern US all showed that farmer developed varieties had equivalent yields to modern varieties with some of the important additional traits that farmers developed and frequently greater stability over time and space than pure-line varieties. Varieties are in the release process in CA and the north-eastern US and are in production in France and Italy with each farmer doing their own seed multiplication due to more restrictive regulations on the types of varieties that can be commercialized.

The main difference in programmes in different geographic locations is in their ability to release lines from participatory projects as commercial varieties. Europe has the most restrictive seed regulations, and the varieties of the PPB programme cannot go through the normal commercialization process. The farmers seed network that developed these varieties however is not interested in commercialization or royalties from other farmers using their varieties. They see these varieties as a shared resource among members of the network, which each member can multiply and

produce them on their own farms. About ten varieties have been named and circulated among the farmer group (Rivière P., personal communication). The Canadian system of registration is similar to the European one but is slightly more flexible and the fact that breeders participating in the projects have access to the registration trials and can put forward varieties developed with farmers means that these varieties may be commercialized and can also be grown by the farmers that developed them. In the north-eastern US, many farmers are not interested in producing their own seed due to the risk of seed-borne diseases, and the formal variety release process allows for the release of heterogeneous varieties as long as they can be adequately described. The varieties developed could either be released with a plant variety protection (PVP) certificate with farmers named as co-developers, or through an alternate mechanism such as the Open Source Seed Initiative (<https://osseeds.org>). There are regional independent seed companies interested in commercializing such varieties for the organic market.

In terms of methodology, many of these programmes are in close contact with one another to share best practices, and there are many similarities among the programmes. In Europe, farmers are more self-sufficient in terms of plot scale equipment and the ability to manage trials with farmers organizations. This is in part due to the fact that they have to produce their own seed of unregistered varieties so they have had to gain the knowledge and equipment to do so. In the US, typically individual farmers work directly with the research team, and other organizations help with coordination, communication and education, particularly in developing a market for the resulting varieties.

High-value markets for the varieties that result from PPB are critical, and one of the reasons that farmers become involved in these projects. The farms working on these varieties typically are interested in value-added production by creating a short chain from the farm to the consumer. This involves building on-farm mills and bakeries or working closely with local mills and artisanal bakers. In Europe, farms tend to be smaller in size, and more diversified with other crops (grains and vegetables/fruit/dairy/livestock for example) and rely more on very local marketing. In the US and CA, projects and markets are organized on a regional scale, with larger farms (although still smaller and more diversified when compared to conventional farms growing wheat). The common thread among all these projects is the desire to create well-adapted varieties for specific environmental conditions and management systems with excellent baking quality for local consumers.

Discussion

The current study reinforces the premise that the formal seed sector leaves gaps in farmers' seed needs, but also reveals more complex motivations for PPB. Overall, the drivers of PPB can be divided into two primary groups. One is leveraging PPB to optimize genetic advancements through decentralization and the incorporation of a farmer or other stakeholder preferences in selection. The second is a more philosophical or socio-political lens with PPB initiatives centred around farmers' rights to save seed and achieve autonomy or seed sovereignty, as well as preservation of biodiversity and upholding organic principles of health, ecology, fairness and care set forth by the International Federation of Organic Agriculture Movements (IFOAM International) (Chable *et al.*, 2014). In practice, PPB projects are dynamic in motivations and adaptive in methods employed over time.

Coordination is commonly approached through an action learning model in which participants share roles in decision making and their goals and skills change over time. This reality, coupled with balancing farmers' benefits over scientific hypothesis testing, may be reasons that many PPB projects are not published in peer-reviewed journals, but instead shared through informal publications, conferences or personal communications.

PPB and organic agriculture

The current study confirmed that there are clear synergies between PPB and organic agriculture as proposed by prior authors (Dawson *et al.*, 2011; Chable *et al.*, 2014; Shelton and Tracy, 2016; Ortolani *et al.*, 2017). While the majority of projects reviewed were conducted in organic agriculture, the scope of implementation of PPB was not limited to organic systems exclusively as exemplified by the long-standing sweet potato programme in the United States. Many projects stated the goal of improving adaptation to organic farming environments, but projects were also motivated by organic principles and values. The current study identified that projects commonly prioritized breeding goals of improving traits crucial to organic producers that are not a priority in conventional breeding programmes, for example, the case of resistance to late blight (*P. infestans*) in potatoes (Keijzer *et al.*, 2021) and seedling vigour in cool soil conditions in sweet maize (Shelton and Tracy, 2016).

The number of projects and geographical and institutional representation indicates growth in PPB in developed countries, but still represents a finite body of experience and only select cases demonstrate commercialization of new cultivars. This is not surprising as most PPB projects started within the last decade, so additional releases are anticipated in the future. It is promising that several projects include mechanisms for managing the testing and registry requirements for commercialization and even shared royalties with farmer-breeders as in the case of potato in the Netherlands, sweet maize in the US and future plans for wheat, oats and potato in CA and the US. As Desclaux *et al.* (2008) states organic and low-input systems are characterized by a wide diversity of locations, farming and market systems and farmers' needs and thus require highly diverse seed options. It is unlikely that all needs will be met in the foreseeable future even with increases in organic cultivar options, and PPB will remain a viable complement to the formal seed sector to fulfil gaps in access to suitable seed.

The impact on farmers' access to seed should not only be measured by cultivar releases. Many of the farmers involved are already bringing crops to market and engaging culinary professionals and other end users in the variety evaluation, thus developing future market demand. In many cases, farmers are also sharing seed within farmer networks and coordinating with other farmers for multiplication and commercialization as in the case of the French seed cooperative, Réseau Semences Paysannes, the VASO project farmer network in Portugal, and the sweet potato breeding in North Carolina, US. While the number of institutions involved is limited, researchers, like farmers, exchange seed and in several cases a PPB cultivar developed in one location is shared and tested, and even selected in additional regions of the country and even internationally. For example, the case of a broccoli PPB project from the US shared some breeding populations with the organic seed and breeding company De Bolster in the Netherlands who selected for several generations and recently registered a new organic variety (Myers and

Lammerts van Bueren, personal communication). As most PPB projects are focused on open-pollinated varieties the ability to continue breeding with PPB cultivars is also possible as in the case of the recently released sweet maize cultivar, 'Sweet Kisses', selected out of the US commercialized PPB cultivar 'who gets kissed?' (Shelton and Tracy, 2016; Open Source Seed Initiative, 2021). Researchers' engagement in organic, participatory breeding can also raise awareness of the importance of key traits that in a related, conventional breeding programme might otherwise rank lower in priority. An example is a case of the late blight resistance breeding in the Dutch PPB potato programmes stimulating commercial companies to place greater priority on resistance in their own selection programme resulting in 29 resistant ('robust') varieties released by 2020 (Bionext, 2021). These varieties are now also used by conventional potato growers (Agrico, personal communications). Given these far-reaching, but often unaccounted for ripple effects of PPB it is short-sighted to assess the agricultural impacts solely by the number of cultivars released from PPB projects alone.

PPB and agrobiodiversity

The emergence of PPB is attributed in part as a response to counter trends towards consolidation in the seed industry, narrowing crop genetic diversity and an emphasis of multinational corporations on breeding for major crops and large-scale agricultural regions (Pimbert, 2011). Emphasizing intra- and inter-specific genetic diversity is recognized as an important part of systems-based farm management in organic and low-input systems (Finckh, 2008; Pimbert, 2011; Dwivedi *et al.*, 2017; Chable *et al.*, 2020). Several projects in the current study focused on breeding for increased genetic diversity to counter inbreeding depression, and improve the crop's ability to adapt to environmental challenges (Murphy *et al.*, 2005; Philips and Wolfe, 2005; Döring *et al.*, 2011). Other cases strive to improve yield stability under heterogeneous environments by developing genetically diverse populations (Dawson *et al.*, 2010). Evolutionary participatory breeding (EPB), a methodology described by Philips and Wolfe (2005) and employed in several PPB projects refers to breeding for local adaptation by creating highly genetically diverse populations and allowing several cycles of natural selection prior to trait selection, and also continued selection after release by repeated seed saving. The evolutionary potential of EPPB and PPB methods is argued as a means to cope with climate change (Ceccarelli *et al.*, 2010; Murphy *et al.*, 2013; Entz *et al.*, 2015), but additional research to document evidence of responses to climate change would strengthen this breeding approach.

Efficiency and PPB

Based on prior experience of PPB in the Global South, there is evidence of improved efficiency in achieving breeding objectives through collaboration also in the North (Almekinders *et al.*, 2014; Ceccarelli, 2015), and this premise was reinforced in several projects in the current study. Participation of multiple farms provides more sites and thus the capacity for screening early generation material, testing late generation materials and enabling decentralized selection for regional adaptation, potentially improving the adaptation across a region rather than on a single farm site while conserving greater genetic diversity of the metapopulation (Enjalbert *et al.*, 1999, 2011; Goldringer *et al.*, 2001;

Porcher *et al.*, 2004; Dawson *et al.*, 2011). A common approach to many PPB projects is to target specific adaptation, rather than minimizing genotype-by-location interaction as is practised in most centralized breeding programmes. These programmes seek to buffer genotype-by-year interactions by creating genetically diverse, heterogeneous populations that may evolve specific adaptation through on-farm selection (Murphy *et al.*, 2005; Petitti *et al.*, 2021). All of the PPB wheat projects in the current case study highlighted the need to breed for specific adaptation not addressed by breeding programmes that aim for broad adaptation.

Similar to the experience of PPB in the Global South, there is evidence of improved efficiency in achieving breeding objectives through collaboration in the North (Almekinders *et al.*, 2014; Ceccarelli, 2015) and this premise was reinforced in several projects in the current study. Participation of multiple farms provides more sites and thus the capacity for screening in early generations testing in later generations. Participation enables selection for regional adaptation under decentralized locations, potentially improving the adaptation across a region rather than on a single farm site while conserving greater genetic diversity of the meta-population (Enjalbert *et al.*, 1999, 2011; Goldringer *et al.*, 2001; Porcher *et al.*, 2004; Dawson *et al.*, 2011). Many researchers and farmers alike value the ‘farmers’ eye’ in selection as farmers hold an intimate familiarity with their crop qualities and market demands as well as an ability to evaluate specific adaptation (Dawson *et al.*, 2011; Almekinders *et al.*, 2014). One of the Italian tomato project reviewed in the current case study found that farmers’ selections resulted in improved local adaptation compared with the researcher selections (Campanelli *et al.*, 2015).

PPB challenges and opportunities

In spite of the potential benefits of PPB, barriers clearly exist. The explicit objective of breeding for increased intra-cultivar genetic diversity creates a tension between the desire to retain genetic diversity and achieve adequate phenotypic uniformity to meet the Distinctness, Uniformity and Stability (DUS) requirements of the official variety testing and registry systems within Europe and CA. PPB is thus influencing the broader regulatory system to accommodate and expand agrobiodiversity. Several of the researchers involved in projects in the current study have pushed for reform of the seed regulations and as a result the European Commission now accommodates a temporary experiment (2014–2021, COM2014/150/EU) to explore new ways of registering and marketing heterogeneous materials for four cereal crops (wheat, barley, oats and maize). The new EU regulation for organic farming (EC 2018/848) that will come into force in 2022, officially allows marketing of ‘heterogeneous material’.

Market acceptance, however, is an important consideration in the adoption of new varieties or populations resulting from PPB projects. As an example, consumers and retailers are used to the names of potato varieties, it is not easy to enter the market with new, unknown resistant varieties that have an advantage for growers in the first place (Nuijten *et al.*, 2018). Therefore, in the Netherlands a covenant was established in 2017 by the Dutch organic umbrella organization signed by all supermarkets to only sell late blight resistant (‘robust’) varieties for the organic potato segment by 2020, which was indeed achieved by 2020 (Raaijmakers, 2019; Bionext, 2021). Other programmes in France, Italy and Portugal similarly report collaboration with bakers and other culinarians supports the market development for PPB varieties (Chable *et al.*, 2014; Powell, 2016). These

experiences show that collaboration between farmers and breeders is important but when the market players further up in the value chain are not involved and committed it can limit or even block successful marketing of varieties.

There is a lack of research exploring financing models for PPB and consideration of the long-term sustainability of PPB projects. Many of the PPB projects reviewed were funded by large, collaborative research and education grants and operate through a project framework including the EU-funded projects Solibam, Diversifood and LiveSeed and the USDA-funded projects such as Northern Organic Vegetable Improvement Collaborative and other USDA Organic Research and Extension Initiative projects in multiple crops, and the privately funded Bauta Family Initiative on Canadian Seed Security (2020). While the public investments in PPB are encouraging given the potential for the public benefit of expanded seed access and expansion of agrobiodiversity, it also raises the question if these projects could be supported by market-driven returns on investments.

Finally, there is a need to support education in PPB at various levels (GAFF, 2020). Many modern farmers have lost the skills of breeding, and search for some background when getting involved in a breeding project, as was reported from the Dutch potato project. At universities, there is also a need for education in PPB to train the plant breeders not only on technical issues but also on the social implications of making PPB with stakeholders a success (Lammerts van Bueren *et al.*, 2021).

PPB and seed systems

Analysis of PPB necessitates a multi-disciplinary approach to fully understand the social, political and agroecological influences driving the emergence of projects in the Global North and factors impacting implementation. The current study underscores that project goals and outcomes cannot be assessed through an agronomic lens alone. It is also clear that while the term PPB is broadly defined as a collaboration in breeding, each project is unique with a spectrum of scales of operations, methods employed and relationship dynamics between actors. Common themes that emerged include motivation to address gaps in seed needs that are not served by the formal breeding sector coupled with repairing a sense of loss of seed sovereignty and seed knowledge by farmers. The desire of farmers for seed autonomy and avoidance of hybrid varieties was a common motivating aspect of PPB in the current study across the maize, tomato and Brassica case studies underscoring the desire for restoring farmers’ control of the seed in farming systems in the Global North (Kloppenborg, 2010). It is clear from the current study that farmers in the North and South share the commonality that the dominant commercial seed sector’s emphasis on breeding for major production regions and broad adaptation is not serving all farmers’ needs to the extent that underserved farmers are motivated to take seed improvement into their own hands. What makes the PPB projects in the North different from those in the South might be the further developed specialization in the value chain in the North. Examples have shown that it is often important to engage not only farmers and breeders, but to also involve other actors including seed producers, processors and retailers further up in the value chain for successful adoption of new PPB varieties (Nuijten *et al.*, 2018). It is also clear that PPB projects are embedded in a broader seed system and that ‘system’ varies from project to project. The success of projects additionally necessitates consideration of the broader regulatory, social and

economic context in the planning and decision-making process in order to maximize intended outcomes and impacts.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0021859621000782>

Acknowledgements. The authors acknowledge with gratitude the valuable input from Dr Conny Almekinders on interpretation of results and the development of the discussion. The authors are also grateful for the time of numerous PPB researchers who helped clarify project details through personal communications, providing valuable insights on their own work. Lastly, the authors wish to acknowledge the valuable contribution to society and agroecology served by the farmers who engage in PPB and on-farm stewardship of seed.

Financial support. This study was supported in part by the USDA/NIFA-funded project award number 2018-51300-28430, the Northern Vegetable Improvement Collaborative (NOVIC).

Conflict of interest. The authors declare there are no conflicts of interest.

Ethical standards. Not applicable.

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