

1 *Review*

# 2 Pursuing the potential of heirloom cultivars to 3 improve adaptation, nutritional and culinary features 4 in a changing climate

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12 **Abstract:** The burdens of malnutrition, protein and micronutrient deficiency, and obesity cause  
13 enormous costs to society. Crop nutritional quality has been compromised by the emphasis on  
14 edible yield and through the loss of biodiversity due to the introduction of high-yielding uniform  
15 cultivars. Heirloom crop cultivars are traditional cultivars grown for a long time (> 50 years), and  
16 whose heritage has been preserved by regional, ethnic or family groups. Heirlooms are recognized  
17 for their unique appearance, names, uses and historical significance. They are gaining in popularity  
18 because of their unique flavors and cultural significance to local cuisine, and their role in sustainable  
19 food production for small-scale farmers. As a contrast to modern cultivars, heirlooms may offer a  
20 welcome alternative in certain markets. Recently, market channels have emerged for heirloom  
21 cultivars in the form of farmer-breeder-chef collaborations and seed savers organizations. There is  
22 therefore urgent need to know more about the traits available in heirloom cultivars, particularly for  
23 productivity, stress tolerance, proximate composition, sensory quality and flavor. This information  
24 is scattered and the intention of this review is to document some of the unique characteristics of  
25 heirloom cultivars that may be channeled into breeding programs for developing locally adapted  
26 high value cultivars.

27 **Key words:** culinary and nutritional traits, farmer-breeder-chef-consumer nexus, folk cultivars,  
28 genetic diversity, global warming, heritage seedbank, local food systems, seed savers, stress  
29 tolerance

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31 **1. History and survival of heirloom or folk cultivars**

32 Heirloom cultivars are generally characterized as traditional or older cultivars that are open  
33 pollinated, passed down from gardener to gardener or handed down in families, and often not used  
34 in large-scale agricultural enterprises. The definition of heirloom varies, and the term does not carry  
35 a precise scientific designation. One of the most typical concepts of an heirloom is its  
36 open-pollinated, or non-hybrid, nature. Because of this fact, some heirloom cultivars may be quite  
37 variable, and it is therefore apparent why heirlooms may not fit as well into modern agricultural  
38 systems that place great value on uniformity. Votava and Bosland [1] found that the pepper cultivar  
39 'California Wonder' had substantial amounts of genetic variability compared to a standard modern  
40 cultivar. They recommended that this cultivar not be used for genetic analysis because of this  
41 variability. This is often the case for heirlooms; they are known to possess more inherent variation  
42 compared to modern cultivars. Some of this could be due to their open pollinated nature, and some  
43 might be due to the fact that they are often associated with seed saving. The appearance of F<sub>1</sub> hybrids  
44 during the 20<sup>th</sup> century was arguably a tremendous advance in terms of crop productivity and seed  
45 commercialization. Some advocates of heirloom cultivars may, however, view the advance of F<sub>1</sub>  
46 hybrids as an incursion on traditional cultivars, as they rapidly usurped the use of traditional open  
47 pollinated cultivars for crop production purposes. While the open pollinated cultivar became a  
48 source for extracting inbred lines that became parents of F<sub>1</sub> hybrid cultivars, the populations  
49 themselves were not maintained or advanced as they once had been.

50 As F<sub>1</sub> hybrid cultivars became more common, gardeners and farmers began to notice the  
51 disappearance of heirloom or traditional cultivars. Importantly, many plant breeders and seed  
52 companies have invested their time and resources in hybrid cultivars for decades, thereby leaving  
53 heirloom, open pollinated cultivars with a lower commercial status. In some parts of Europe, laws  
54 were passed that made it illegal to sell cultivars that were not on government-approved lists. Some  
55 of these laws also required substantial time and effort in the testing of cultivars before they could be  
56 listed. Part of the rationale was to ensure that cultivars were distinct, uniform, and stable, but many  
57 heirloom cultivars did not fit well into these criteria. Thus, heirloom cultivars were in some cases  
58 relegated to the agricultural fringe.

59 Kingsbury [2] commented that at times of technological and social change, it is common to look  
60 back on simpler times. He suggests that the interest in heirloom cultivars may be due in part to this  
61 phenomenon, which idealizes the past. Another aspect of this yearning for simplicity is the fact that  
62 gardens represent for some a retreat from the stress of modernity. In this way, cultivating heirlooms  
63 may offer an opportunity for the gardener or eater to reconnect with a different age.

64 Additional aspects of the heirloom cultivar experience are the unique flavors and culinary  
65 qualities that generations of people had come to know and appreciate. Such qualities may be absent  
66 in modern cultivars bred for modern cropping systems, creating a desire for the heirloom. An  
67 example of such a quality is the creamy mouthfeel caused by high levels of water-soluble  
68 polysaccharides (also described as phytyglycogen) in older, heirloom sweet corn cultivars. The  
69 creamy mouthfeel caused by the polysaccharides was an important attribute of the *sugary-1* allele,  
70 which reduced starch accumulation in the maize endosperm and increased the amount of sugars. As  
71 newer F<sub>1</sub> hybrid cultivars were developed with the *shrunkn-2* allele, the *sugary-1* allele was replaced.  
72 Cultivars homozygous for *shrunkn-2* are noticeably sweeter; perhaps even twice as sweet as those

73 carrying *sugary-1*. However, they lack the creamy mouthfeel and some of the aromatics associated  
74 with older sweet corn cultivars [3]. Thus, an heirloom may represent flavors and culinary qualities  
75 associated with specific, old cultivars and may thus represent an important heritage.

76 Heirloom cultivars are also associated with seed saving, and in fact the generation to generation  
77 transfer of heirloom seed is often one of the defining features of a heirloom. Navazio [4] commented  
78 that the post-World War II era in the USA saw a major transition in agriculture where more and  
79 more farmers were willing to purchase seed every season from seed companies. Prior to that time,  
80 farmers were heavily involved with producing their own seed, and with selecting and maintaining  
81 good seed stock. As farmers began purchasing seed annually from seed companies, heirloom  
82 cultivars and their systems of maintenance through seed saving gradually diminished. Fortunately,  
83 a resurgence of interest in heirlooms has taken place in the last several decades. Several examples  
84 may illustrate this point. Today, some seed companies feature and celebrate heirloom cultivars in  
85 their catalogues. Gardeners and farmers regularly seek out, save, and preserve heirloom seed in  
86 order to continue the traditions of these unique cultivars, and consumers are willing to pay  
87 substantially more at the market for their products. The development of “new heirlooms” is also  
88 discussed in plant breeding fora, where the breeding program may begin with heirloom populations  
89 that are subject to selection for current conditions but under the careful guidance of a seed saver or  
90 local plant breeder. The Slow Food movement maintains a catalogue of heritage foods, including  
91 heirloom cultivars, run by the Ark of Taste. These foods, which include crop cultivars, are  
92 “culturally or historically linked to a specified region, locality, ethnicity, or traditional production  
93 practice.”

94 Heirloom cultivars are a part of the farming system in many regions of the world. For example,  
95 southern Appalachia is an area of high crop biodiversity in the USA where many heirloom cultivars  
96 remain. Veteto [5] documented 134 heirloom cultivars that were still being grown in the region in a  
97 recent survey. He found that even though one or two individuals in a community were usually  
98 involved in maintaining significant numbers of heirloom cultivars, many communities had lost their  
99 heirloom vegetable cultivars. He found that both the decline of the farming population and the lack  
100 of cultural continuance in family seed-saving traditions were likely responsible for this loss.

101 Among the problems associated with heirloom cultivars is their susceptibility to pathogens. In  
102 many cases, modern breeding has helped to improve host plant resistance; thus, it is not surprising  
103 that heirloom cultivars may lack resistance to important pests. Heirloom tomato production can be  
104 limited by soilborne diseases such as bacterial wilt and fusarium, caused by the pathogens *Ralstonia*  
105 *solanacearum* and *Fusarium oxysporum* f.sp. *lycopersici*, respectively. One of the creative approaches to  
106 this problem was discussed by Rivard and Louws [6], who grafted heirloom scions onto resistant  
107 rootstock. In naturally infested soil, bacterial wilt incidence for nongrafted 'German Johnson' was  
108 79% and 75%, but had no symptoms of bacterial when grafted onto the resistant genotypes CRA 66  
109 or Hawaii 7996. Fusarium wilt incidence was 46% and 50%, respectively, in nongrafted and  
110 self-grafted 'German Johnson' controls, but no symptoms of fusarium wilt were seen when plants  
111 were grafted onto resistant genotypes. Thus, grafting may be an appropriate approach for heirloom  
112 production in infected soils.

113 A debate is occurring as to whether modern cultivars are less nutritious than their heirloom  
114 counterparts. Barker et al. [7] examined differences in mineral nutrient concentrations between  
115 modern F<sub>1</sub> hybrids and heirloom cultivars of cabbage, and also looked at fertilization practices with  
116 either organic fertilizer and compost or conventional fertilizers. Crop production increased with  
117 conventional or organic fertilizers compared to compost. Mineral nutrient composition did not vary  
118 between modern or heirloom cultivars or among different fertility practices; however, the authors  
119 did find cultivar differences for nutrient concentration. The fact that mineral nutrient content did not  
120 vary between modern and heirloom cultivars is important in that it runs counter to popular press  
121 articles that suggest the nutritional quality of our food supply is decreasing. Flores et al. [8]  
122 examined carotenoid levels of traditional tomato cultivars. They found substantial amounts of  
123 variation for many carotenoids in colored fruit from these traditional cultivars, suggesting new  
124 opportunities for breeding. There is little doubt that heirloom cultivars contain reservoirs of useful  
125 traits, including those that might be able to contribute to improved human nutrition.

126 van der Knaap and Tanksley [9] examined the genetic basis of the unique phenotype of the  
127 heirloom tomato cultivar 'Yellow Stuffer' which looks more like a bell pepper than a traditional  
128 tomato. Their analysis was based on a segregating population derived from a cross between 'Yellow  
129 Stuffer' and a wild species of tomato. They found three QTL that influenced fruit shape and seven  
130 QTL that influenced fruit mass; many of which had already been identified in other tomato mapping  
131 research. They were able to pinpoint an allele at fs8.1 that caused convex locule walls that were  
132 responsible for the extended, bumpy shape characteristics of the pepper fruit in 'Yellow Stuffer.'  
133 They surmised that the evolution of bell pepper-shaped tomato fruit may have proceeded through  
134 mutations of some of the same genes that led to bell pepper-type fruit in garden pepper.

135 Heirloom potatoes offer unique flavors and qualities that are sought by consumers. Production  
136 of these heirloom types is, however, not well understood in the context of modern farming systems.  
137 Fandika et al. [10] investigated how irrigation and nitrogen management might be best employed in  
138 heirloom potatoes. They found that modern cultivars were more responsive to irrigation and  
139 nitrogen than heirloom potatoes. Interestingly, they found that higher applications of nitrogen  
140 decreased the yield of heirloom potato cultivars whereas yields of modern cultivars were increased.  
141 Heirloom cultivars were more drought tolerant, but required larger water inputs because of later  
142 maturities. Overall conclusions of this study suggested that production of heirloom types could be  
143 more expensive than modern cultivars.

144 Interest in seed saving continues to grow in many parts of the developed world, perhaps as a  
145 response to the increasing consolidation of the global seed industry and a desire for more local  
146 control of plant genetic resources. Interest in heirloom cultivars goes hand in hand with this  
147 expanded interest in seed saving. For the most part, these efforts are celebrated by communities who  
148 wish to build closer relationships with their seed sources. However, not everyone is celebrating. In  
149 the last five years, efforts have been made to close seed lending libraries, which allow gardeners to  
150 check out packets of seed and return the seeds they save from the crop grown. The cultivars made  
151 available by lending libraries are typically open pollinated and often heirloom. Efforts to close  
152 lending libraries were based on an interpretation of the US federal Seed Act, which would have  
153 required seed lending libraries to test seeds for germination and purity. In 2016, a state department

154 of agriculture in Pennsylvania determined that such seed libraries are noncommercial seed  
155 exchanges and therefore not subject to the Seed Act. And a number of efforts have been initiated to  
156 resume breeding and seed saving of open pollinated cultivars. The Open Source Seed Initiative  
157 ([www.osseeds.org](http://www.osseeds.org)) is a clearinghouse for primarily open pollinated cultivars that have been  
158 released into a “protected” commons. The protected nature of this commons means that anyone can  
159 breed with or save seeds of these open source cultivars, but cannot restrict others’ use of them. Some  
160 of the cultivars contained in this registry include open pollinated types, such as the new carrot  
161 cultivar ‘Dulcinea’ that were bred recently to fill gaps in commercial seed company catalogs. Such  
162 open pollinated types might be considered a modern spin on an heirloom cultivar.

163 Navazio [4] stated that the seed “is a reflection of the farming system as it is grown, cultivated,  
164 selected, and fully incorporated into that system.” In this way, heirloom cultivars represent a  
165 farming system that considers and prizes traits of long-term interest to the farmer and consumer, the  
166 incorporation of seed saving, family and community traditions, and the transference of plant genetic  
167 resources from generation to generation. Heirloom cultivars long cultivated locally by people  
168 around the world may be a critically important tool in creating a more sustainable food supply given  
169 the tremendous challenges of climate change, food production, and food security [11].

170

## 171 **2. Heirlooms and sustainable agriculture**

172 Local landraces –defined as traditional cultivars developed over time after adapting to both natural  
173 and cultural environments– or heirloom cultivars may perform better than modern bred-cultivars,  
174 particularly in marginal and climatic vulnerable sites. Heirlooms are known for their great trait  
175 diversity, e.g. for, *inter alia*, colour, shape, size, growth, height, phenology, yield and flavor. This  
176 wide diversity –which is the main feature capturing the attention from consumers seeking unique,  
177 nutritious, local food sources–also plays a key role in the risk management strategy of farmers if  
178 modern bred-cultivars are unsuitable for the local context [12]. Both crop heterogeneity and  
179 diversity should be therefore included in a national asset strategy by rural development policy  
180 makers because such a valuable genetic endowment will be useful for further breeding, particularly  
181 when facing the shocks associated with climate change. In this regard, Newton et al. [13] noted that  
182 landraces are sources of host plant resistance and abiotic stress tolerance genes, as well as of  
183 phytonutrients with desired micronutrient concentration that alleviate human aging-related and  
184 chronic diseases, and nutrient-use efficiency traits –which are very important for sustaining  
185 agriculture. Indeed, landraces show variation in their response to diverse stress-prone environments  
186 and this heritage may be used as genetic resources for breeding future crops [14]. For example,  
187 sweetpotato heirlooms exhibit moderate to high host plant resistance to soil insects that are  
188 interesting sources for developing new cultivars [15]; Hopi farmers in Arizona in the United States  
189 still plant ‘Hopi blue maize’ because it is adapted to drought and the short growing season and  
190 because of cultural significance [16]; native black and yellow maize landraces from Los Tuxtlas,  
191 Mexico are efficient phosphorus (P) colonizers and thus adopted to low soil P conditions [17];  
192 farmers from north east India still cultivate and maintain traditional rice cultivars because of their

193 adaptation to harsh growing conditions [18–20]; heritage durum wheat cultivars are more tolerant to  
194 drought than modern cultivars [21]; Spaniards and Italian farmers in some regions still cultivate  
195 tomato landraces that are highly adapted to drought and salinity [22–23].

196

### 197 **3. Genetic enhancement using heirlooms and further seed supply of bred-cultivars for organic** 198 **farming**

199 Crossbreeding –based on controlled crossing, population improvement and family selection– is  
200 pursued to develop cultivars showing elasticity for adapting to climate shifts, energy limitations and  
201 low-inputs in organic farming. The main traits of an organic cultivar targeting niches outside  
202 industrial agriculture are host plant resistance to pathogens (e.g. bacteria, fungi, oomycetes,  
203 phytoplasma, viroid or viruses) and pests (birds, insects and nematodes), ability to outcompete  
204 weeds, resource-use efficiency, abiotic stress and pollution tolerance, adaptability to soil quality and  
205 low plant density, improved nutritious content, and high yield under eco-farming. Moreover,  
206 cultivars may be bred under organic husbandry, thus providing suitable germplasm for such  
207 farming system and with the desired quality traits for consumers. For example, dry bean consumers  
208 may like to buy heirlooms with unique colour patterns, which may be also sold at premium prices  
209 [24]. Swergarden et al. [25] further indicated that both yield stability analysis and economic  
210 incentives suggest that heirloom dry bean cultivars –although having 44% lower average grain yield  
211 than commercial checks– may allow diversifying production, differentiating in the market, and  
212 keeping economic returns for their small-scale organic growers.

213 Seed production begins with the developer of the new cultivar, who often retains the original  
214 breeder stock that may be further used as the “golden standard” for such a cultivar and as source for  
215 the foundation stock [26]. The next step is producing registered seed for distribution to licensees,  
216 who produce certified seed, which is the last stage of large-scale seed production. Organic farming  
217 standards asks further for using organically produced seed, unless lacking them for target crop.  
218 Certified organic seed should be only grown in certified organic soil using same inputs as per in  
219 organic farming, and package in a certified facility. Crop husbandry includes protecting soil fertility,  
220 using manure, rotating crops, conserving biodiversity and natural resources, sound plant health  
221 management, recycling, while any practices leading to accumulating heavy metals and other  
222 pollutants are forbidden.

223

### 224 **4. Promoting conservation of heirloom germplasm**

225 **4.1. Seed savers and heritage seedbanks:** Some studies have estimated that up to 75% of plant  
226 genetic diversity has been lost due to rapid expansion of industrial agriculture and large-scale  
227 adoption of monoculture farming [27]. Many such studies are based on a reduction in the number of  
228 cultivars of particular crops, and as such may be inaccurate estimates of the amount of actual plant  
229 genetic diversity present when both genebanks and cultivars are considered. However, it appears



230 likely that the homogenization of agricultural environments around the world and the drive  
 231 towards widely adapted uniform cultivars of a few major crop species have translated into reduced  
 232 genetic diversity currently deployed in farmer's fields. In addition to a narrowing of diversity of  
 233 crop germplasm, there are worrying reports of reductions in the global diversity of plant species.  
 234 The Millennium Ecosystem Assessment Reports state that 60,000 to 100,000 species of plant are  
 235 currently threatened with extinction [28]. It is apparent that some of these species play critical roles  
 236 in agricultural and natural ecosystems, and serve as reservoirs of important genes that could play a  
 237 role in crop breeding. Hence, this reduction in plant biodiversity is a significant global concern.

238 One traditional practice that may improve the current state of crop genetic diversity is seed  
 239 saving. Practiced since the beginnings of agriculture itself, the simple act of saving and replanting  
 240 seed from a crop was an integral part of food production in many parts of the world until the 20<sup>th</sup>  
 241 century. The development of an efficient and wide-reaching global seed industry, the convenience  
 242 and quality enhancement of purchasing seed each year, and the appearance of technologies such as  
 243 F<sub>1</sub> hybrids and intellectual property rights have played a role in reducing the practice of seed saving.  
 244 From the point of view of crop genetic diversity, revitalizing the practice of seed saving may be,  
 245 however, viewed as vital for the world's sustainable food production and nutritional security.

246 There are several seed-saving projects, in addition to 1700 *ex-situ* genebanks worldwide  
 247 including CGIAR genebanks and Svalbard Global Seed Vault [29], that are involved in collecting and  
 248 maintaining heirloom cultivars across the globe to preserve agricultural biodiversity. ASEED  
 249 Europe, Camino Verde, Hawai'i Public Seed Initiative, Irish Seed Savers Association, Louisiana  
 250 Native Plant Initiative, Man and the Biosphere Programme, Millenium Seed Bank Project, Native  
 251 Seed/SEARCH, Navdanya, National Laboratory for Genetic Resources Preservation, New York City  
 252 Native Plant Conservation Initiative, Australian Plantbank, Seed Savers Exchange, Seesave.org,  
 253 Slow Food International, USC Canada, Vavilov Research Institute, and The World Vegetable Center  
 254 houses many traditional and rare cultivars of fruit, vegetable, flower, and grain crops [30]. Native  
 255 American seed savers are dedicated to on-farm preservation of their agrobiodiversity (heirlooms)  
 256 but unwilling to share their seed heritage for preservation in *ex-situ* genebanks (for fear of loss of  
 257 ownership and access) as they believe that community-based *in-situ* conservation will maintain  
 258 local control and seed viability than *ex-situ* genebanks [29]. One excellent example of a collection of  
 259 heirloom cultivars is held at the Heritage Seed Library (HSL) of Garden Organic, UK. They curate  
 260 and maintain a collection of 800 heirlooms of carrot (*Daucus carota* L.), cucumber (*Cucumis sativus* L.)  
 261 and Brassica oleracea L. var. *acephala* (DC.) Metzq, faba bean (*Vicia faba* L.), pea (*Pisum sativum* L.),  
 262 and lettuce (*Lactuca sativa* L.) [31]. Table 1 presents a list of a few websites providing further  
 263 information on genebanks or seed savers for heirloom cultivars.

264

265 **Table 1.** Some genebanks or seed savers organizations providing heirloom cultivars or related information.

Name	Website
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AVRDC – The World Vegetable Center	<a href="https://avrdc.org/seed/">https://avrdc.org/seed/</a>
Nature and Nurture Seeds	<a href="https://natureandnurtureseeds.com">https://natureandnurtureseeds.com</a>
Organic Seed Producer Directory	<a href="https://seedalliance.org/directory/">https://seedalliance.org/directory/</a>
Seed Savers Exchanges	<a href="https://www.seedsavers.org/mission">https://www.seedsavers.org/mission</a>
Sustainable Seed Company	<a href="https://sustainableseedco.com/#">https://sustainableseedco.com/#</a>
The Kerr Center for Sustainable Agriculture	<a href="http://kerrcenter.com/publication/heirloom-vegetables-genetic-diversity-and-the-pursuit-of-food-security/">http://kerrcenter.com/publication/heirloom-vegetables-genetic-diversity-and-the-pursuit-of-food-security/</a>

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266

267 An in-depth literature search noted several heirloom cultivars of grains such as bean, maize and rice  
 268 (Supplementary Table 1,) or vegetables., e.g. carrot, potato, squash and tomato (Supplementary  
 269 Table 2). Heirloom apples among fruit crops have amazing diversity that is maintained by seed  
 270 savers and gardeners' in North America [<https://www.epicgardening.com/heirloom-apples/>].

271 **4.2. South and Southeast Asia:** 'Vrihi', the largest non-governmental *in situ* seed depository of  
 272 traditional rice cultivars in eastern India, houses 610 rice landraces that withstand a much wider  
 273 range of fluctuations in temperature and soil nutrient levels as well as water stress than modern rice  
 274 cultivars. This collection includes numerous unique landraces, for example, the 'Jugal', the  
 275 doubled-grain rice and 'Sateen', the triple grain rice, long awn and erect flag leaf, or cultivars with  
 276 distinct aroma, color, and tastes. 'Vrihi Seed Exchange Network' has more than 6,000 indigenous  
 277 farmers who have received seeds from 'Vrihi' and continue to cultivate and exchange seeds of these  
 278 folk cultivars (synonymous to heirlooms) among them and to neighboring farmers [19]. At Basudha  
 279 farm located in Rayagada district of Odisha, India, over 1400 folk rice cultivars and 30 other crops  
 280 are grown every year, as a model of ecological agriculture, without any external inputs  
 281 [[www.cintdis.org/basudha](http://www.cintdis.org/basudha)]. The Philippine's Department of Agriculture in collaboration with the  
 282 International Rice Research Institute (IRRI, Philippines), has undertaken a project on raising  
 283 productivity and enhancing the legacy of heirloom/traditional rice through empowering  
 284 communities in unfavorable rice-based ecosystem in Philippines. This project has collected about 74  
 285 variants of 41 heirloom cultivars with distinct characteristics with the sole aim to enhance  
 286 productivity and livelihood and conserve *in situ* on-farm genetic resources [32]

287 **4.3. USA:** Native American seed saving efforts are underway to preserve culturally significant seeds  
 288 and knowledge to promote food sovereignty at the local or tribal level in the USA [29]. These consist  
 289 of farmers and gardeners who share a common interest in keeping traditional and local crop  
 290 diversity alive. They usually grow traditional crops and local cultivars of fruits and vegetables for  
 291 cultural reasons, food preference, risk avoidance, local adaptation, and for niche market  
 292 opportunities. Various groups, including the Indigenous Seed Keepers Network and Seedshed, have



293 formed to foster the preservation and repatriation of heirloom strains of Native American crops,  
294 particularly of maize, bean, squash, tobacco, and sunflower. The Seed Savers Exchange (SSE), a  
295 non-profit heirloom seed genebank based in Decorah, Iowa, saves and sells heirloom fruit,  
296 vegetable, and flower seeds in the US. SSE has in its collection 24,000 rare fruit and vegetable  
297 cultivars [33]. This heirloom collection has immense variability, for example, its over 500 heirloom  
298 potato cultivars differ in tuber shape (round-, oblong-, and fingerling-shaped), skin (white, red,  
299 purple, and variegated) and flesh color (white, yellow, purple), including varying skin and flesh  
300 color combinations, i.e. white skin-white flesh, white-skin-yellow flesh, red skin-white flesh, red  
301 skin-yellow flesh, red skin-red or pink flesh [34]. Seed saving efforts directed at heirloom cultivars  
302 are also found in the southern/central Appalachia region, an area of relatively high crop biodiversity  
303 in the USA. In this region, a collection of 134 heirloom cultivars grown and saved by  
304 home-gardeners was documented, with beans being the most predominant and highly diverse  
305 followed by tomatoes, squash, corn, and potatoes. The decline of the farming population combined  
306 with a lack of cultural continuance in family seed-saving traditions, however, threatens the ability of  
307 communities to maintain this crop biodiversity [5]. Culture and ethnicity also play an important role  
308 in preservation of heirloom cultivars [35–38].

309 **4.4. Europe:** There are numerous examples of seed saver networks, for example, ‘Réseau Semences  
310 Paysannes’, ‘Red de Semillas’, and ‘Rete Semi Rureli’ [39], involved in the organization of regional  
311 and local seed fairs, training workshops, participatory plant breeding activities and transmission of  
312 farmer’s knowledge about the selection and conservation of local cultivars [40]. The ‘Réseau  
313 Semences Paysannes’ in France bring together all who are open to the development of peasant seeds  
314 (local cultivar originating from selection, identified as a collective heritage or heirlooms, and  
315 reproduced by all men and women who produce foods), and work toward the development of  
316 groups for selecting, conserving and distributing peasant seeds. The ‘Red de Semillas’ is a technical,  
317 social and political Spanish organization formed by the people that maintain agricultural  
318 biodiversity on peasant farms and on consumers’ plates, while the ‘Rete Semi Rureli’ has enacted  
319 regional laws to safeguard local agricultural biodiversity in Italy. The researchers associated with  
320 these networks are involved in development of new cultivars shaped by history and coevolved with  
321 farmers. The cultivars are considered ‘peasant varieties’, which is a term meant to encompass the  
322 seed and its constituent reproductive ability, linked to the plant’s terroir [39].

323

## 324 **5. Promoting local food systems**

325 Industrial agriculture, Green Revolution technologies, climate change, civil conflict, and change in  
326 market characteristics, including distance have contributed to the erosion of farm-agrobiodiversity.  
327 The production and sale of heirloom cultivars are interdependent in local market, suggesting that  
328 local food systems help preserve heritage diversity [41]. Modern food production systems based on  
329 ‘Green Revolution’ technologies are neither sustainable nor nutritionally superior. Recent years have  
330 brought increased public awareness that the risk to onset of noncommunicable diseases (cancer,

331 diabetes, heart diseases, and obesity) can be reduced by making changes in lifestyle and food habits  
332 [42–43]. Local food systems may be a critical component of lifestyle and food habits that can  
333 contribute to improved public health.

334 Local food refers to where the food is produced, sold and consumed within a limited  
335 geographical area [44]. What drives consumers to buy locally produced food? Health is the main  
336 driver of local food purchase [45–46]. People perceive that local foods have direct benefits to their  
337 personal health as such products are fresh, nutritious, tasty and safer than non-local food. The  
338 consumption of locally produced food is more environmentally sustainable than procuring food  
339 from global markets. Attitudes towards supporting local agribusiness and preserving local heritage  
340 and tradition, keeping a connectedness with rural life, reducing the carbon footprint (shorter  
341 transportation distance, minimizing the needs of packaging, processing and refrigeration, among  
342 others), and protecting the environment for sustainable ecosystems, also drive the public to consume  
343 locally produced foods [47–49]. Higher prices, accessibility (time constraints to visiting farmers  
344 market multiple retail outlets to purchase local food) and availability are, however, the major  
345 barriers for consumption of local food [50–51]. Farmers' markets (FMs) refer to "markets where  
346 agricultural products are directly sold by producers to consumers through a common marketing  
347 channel" [52]. 'Buy-local initiative' and 'Buy local' movements in North America and western  
348 Europe have reinforced greater patronage at FMs and belief in people that local food is fresher than  
349 food from farther away and that buying local food benefits both local farmers and the local economy  
350 as well as improving environmental sustainability [49, 53].

351 The indigenous farmers in Mesoamerica domesticated bean, maize and squash, famously called  
352 the "Three Sisters", which were cultivated together in the same field providing symbiotic benefit to  
353 each other. The squash shades the ground from heat and acts as mulch to suppress weeds and to  
354 conserve moisture; the maize provide support to beans climb on its stem; while beans fix  
355 atmospheric N, which both the corn and the squash benefit from. The farmers continued to select  
356 genetic variants with preferred characteristics that they cultivated (for food, seed, gifts, and trade)  
357 and passed on the seeds as family heirlooms. The immigrants who carried seeds from Europe grew  
358 out the seeds, there upon selected progenies that were best adapted to the local climate and passed  
359 the seeds as family heirlooms. The examples include 'Anasazi' 'Four Corners Gold', 'Taos Red',  
360 'Mayflower', 'Hutterite Soup', 'Kentucky Wonder', 'Bolita', 'Kickapoo beans' 'Great Northern',  
361 'Jacob's Cattle' and 'Mortgage Lifter' among beans [54], 'Glass Gem', 'Golden Bantam', 'Painted  
362 Mountain', 'Hopi', 'Oaxacan Green', 'Mandan Bride' and 'Cherokee White Flour' among corn [55],  
363 and 'Costata Romanesco', 'Cocozelle', 'Ronde de Nice', 'Sugar Pie' and 'New England Pie' among  
364 squash [56] heirlooms.

365

## 366 6. Heirlooms nutritional, sensory and culinary characteristics

### 367 6.1. Grain Crops

368 The literature suggests significant genetic variation for physico-chemical, sensory and culinary  
369 characteristics among heirloom cultivars. The unique seed coat colors and patterns as well as seed  
370 size and shape differentiate heirlooms from modern bean cultivars. Heirloom beans had relatively  
371 higher protein, total fiber and soluble fiber, and greater *in vitro* antioxidant capacity than controls,  
372 while took less time to hydrate (4.33 to 5.07 hours compared to 8.1 hours for the control) but with  
373 similar cooking time (~ 1 hour). A few heirlooms even after cooking had high flavonoids and  
374 differed in softness. 'Hutterite Soup' and 'Jacob's Cattle' showed lower firmness than 'Kornis  
375 Purple' and 'Tiger's Eye' whose texture was similar to the control [57–58]. 'Ganxet' heirloom bean, a  
376 landrace from northeast of the Iberian Peninsula, Spain, has greater protein, less total dietary fiber,  
377 more digestible dietary fiber, a higher proportion of seed coat, more glucose and less starch than  
378 controls, which is greatly appreciated for its culinary qualities (i.e., seed coat tenderness and its  
379 buttery texture) [59]. Twenty-four heirloom beans from western Washington have been identified  
380 with distinct appearance and great culinary value [60]. The Italian heirloom 'Monachine' is famously  
381 known as Pellegrini in honor of Seattle's culinary icon Angelo Pellegrini who enjoyed this bean for  
382 decades, and it is now featured by a high-end regional restaurant because of its great culinary  
383 quality [61].

384 There is growing demand for maize with blue kernels because of its significant health benefits  
385 and unique culinary applications. Blue kernel maize typically produces anthocyanins in aleurone  
386 layer of the endosperm, while in purple maize, the anthocyanin is predominantly produced in the  
387 pericarp of kernel [62]. The variation in total anthocyanin content among maize heirlooms ranged  
388 from 17.6 to 65.1 mg 100 g seed<sup>-1</sup>, with an average of 49.6 mg 100 g<sup>-1</sup>. Cyanidin and pelargonidin were  
389 the major components, while peonidin and succinyl 3-glucoside, the minor components. Heirlooms  
390 with blue kernels had higher anthocyanin than those with purple or red kernels. 'Navajo Blue' and  
391 'Ohio Blue' displayed highest anthocyanin values, while 'Santa Clara Blue and Flor del Rio had  
392 highest oil and protein contents [63]. The variants of a pericarp-pigmented heirloom 'Apache Red  
393 Purple' showed greater variation on anthocyanin concentrations (210-6183 µg g<sup>-1</sup> pericarp), with  
394 some having greater proportions of either pelargonidin- or cyanidin/peonidin-derived anthocyanins  
395 [64].

396 Several Indian rice folk cultivars are either very nutritious or maintain their distinctive aroma  
397 and colors. 'Kalanamak' (black husked and short-grained rice) among non-basmati aromatic rice  
398 types, the heritage rice from eastern India in cultivation in the last 4000 years, is famous for its  
399 distinct aroma, color and taste [65]. Unpolished brown rice such as 'Bhadoi', 'Kabiraj Sal', 'Shatia' or  
400 'Agniban' are high in iron and antioxidants, while 'Shatia' and 'Kartiksal' are rich in fiber but low on  
401 carbohydrates [66]. Many of the traditional cultivars are of immense medicinal significance. For  
402 example, 'Pichha vari', 'Karthigai samba', 'Dudhsar', and 'Bhejri' enhance milk production in  
403 lactating mothers, 'Kelasa' and 'Bhutmoori' cure anemia, 'Paramai-sal' improves child growth,  
404 'Nyavara' treats neurotic disorders, 'Karhainy' alleviates paralysis; and 'Gudna' to treat gastric  
405 ailment [20, 67]; 'Karanga' to treat dysenteric complains, 'Bora' to treat jaundice, and 'Pakheru',  
406 'Saraiphool', 'Karia Gora', 'Dani Gora' and 'Punai Gora' traditionally used a tonic; and people

407 consuming 'Bhama', 'Danigora', 'Karhani', 'Ramdi', 'Muru', 'Hindmauri' and 'Punaigora' rice's can  
408 work in their field for whole day without feeling hungry [67].

409 The white-seeded durum wheat landrace 'Aybo' is highly preferred for use in holy communion  
410 and for making difo-dabo, while 'Set-Akuri', 'Arndeto', 'Loko', 'Kurkure' and 'Mengesha' are  
411 known for their superior baking quality and used for making difo-dabo and injera. Difo-dabo is a  
412 traditional homemade bread prepared from flour by fermenting thick dough, while injera is a thin,  
413 flat and spongy pancake-like product from fermented dough baked using traditional mitad [68].  
414 Farmers in northeast Ethiopia maintain several landraces for specific-end uses, for example,  
415 'Nechita' for preparing genfo (thick porridge), shorba (semi fluid drink from cracked grain) and  
416 kinche (a dish prepared from cracked barley grains), 'Tikur gebes' for beverage, 'Temej' for kolo  
417 (roasted grain), and 'Enat gebes', 'Sene gebes' and 'Meher gebes' for injera [69].

## 418 6.2. Vegetable crops

419 The Puglia region in Italy is a rich source of tomato landraces maintained by farmers by repeated  
420 selection generation after generation for desired organoleptic quality. Keeping shelf life after harvest  
421 is among the most sought-after quality traits in tomato. 'Regina', a landrace adapted to coastal saline  
422 soils of the central Puglia, is known for its unique qualitative profile characterized by high  
423 concentrations of tocopherols, lycopene and ascorbic acid and long shelf life [70]. 'Corbarino' and  
424 'Lucariello' tomatoes are highly prized by consumers in Italy for superior quality of their fruits and  
425 shelf-life. 'Corbarino' produces intense red color and high levels of soluble and total solids, while  
426 'Lucariello' possesses a heart-shaped fruit with a pronounced pointed apex of less intense red and a  
427 thick cuticle [23]. 'Criollo' tomatoes from Andean valley in Argentina are highly valued for flavor  
428 and taste [71]. Heirloom tomatoes from North America show abundant diversity in fruit weight  
429 (5–150 g), shape (elongated, flattened, rounded, heart-shaped, pyriform), color (white ivory, yellow,  
430 orange, red, black), firmness and brightness as well as chemical quality characteristics (TSS, total  
431 soluble solids), (TA, titratable acidity), TSS:TA ratio, flavor intensity and ascorbic acid [72]. A few  
432 populations of heirloom tomatoes from eastern Spain showed high mean values for ascorbic acid  
433 (308 mg kg<sup>-1</sup> fruit weight, fw), lycopene (130 mg kg<sup>-1</sup> fw),  $\beta$ -carotene (30 mg kg<sup>-1</sup> fw), total phenolic  
434 (89 mg caffeic acid 100 g<sup>-1</sup> fw), and may therefore be best suited as source of functional compounds  
435 [73].

436 A multicolored landrace of carrot, 'yellow-purple Polignano', included in the 'slow food' list of  
437 traditional products (<https://www.fondazione Slow Food.com/en/what-we-do/slow-food-presidia/>),  
438 has been in cultivation for decades by small farmers in Italy's Puglia region. This landrace is greatly  
439 appreciated for its multicolored roots (outer core ranges from yellow or deep orange to dark purple,  
440 while the inner core from pale yellow to light green), special taste, tenderness, crispness, flavor, and  
441 fragrance. On average it contains 22% lower total glucose, fructose and sucrose content but with  
442 similar sweetness as a commercial control. Fructose is the major contributor to its distinctive flavor  
443 as well as to its glycemic index. The purple variants of this cultivar showed high levels of  
444 antioxidant activity, total phenols, carotenoids and  $\beta$ -carotene [70, 74]. Another colored race from  
445 the Apulia region of southern Italy, 'Taggiano' (or Saint Ippazio), possesses an outer and inner core

446 with purple and yellow-orange color, respectively. This heirloom is known for the popular cult of  
447 the Saint Ippazio; i.e., protection from Saint Ippazio against hernias or male impotency. It has high  
448 levels of bioactive compounds and antioxidant capacity compared to orange-rooted controls [75].

449

### 450 **7. Assessing diversity among heirloom germplasm**

451 Assessment of genetic diversity and population structure of heirloom cultivars will be of great help  
452 to identify diverse heirloom germplasm with beneficial traits for further use in breeding or farming.  
453 For example, AFLP analysis of 171 heirlooms from the Heritage Seed Library (HSL) of Garden  
454 Organic revealed 1.5 to 2-fold differences in heterozygosity within carrot, cucumber and *Brassica*  
455 accessions, as well as 3.6 to 9-fold differences within faba bean, pea, and lettuce accessions [31].  
456 Heirloom beans from southern Italy exhibited significant diversity in seed shape (cuboid, kidney,  
457 oval, round, truncate), seed coat pattern (absent, bicolor, pattern around hilum, speckled, spotted  
458 bicolor, stripped), seed color (black, brown, grey, vine, violet, white), seed weight (21-74 g 100 seed),  
459 and phaseolin (C, T, S) [76]. 'Badda', a round large-seeded bean with a partially coloured seed coat,  
460 has been in cultivation for more than two centuries by Sicilian farmers. Over the centuries of its  
461 cultivation, this landrace has diverged into two easily distinguished morphotypes; i.e., 'Badda  
462 bianco' (white badda) and 'Badda nero' (black badda). The 'Badda' morphotypes grouped into three  
463 distinct clusters, namely 'Badda bianco' accessions in one cluster and those of 'Badda nero' in two  
464 separate well-distinguished clusters [77].

465 Microsatellite-based genetic diversity analysis of over 100 rice heirlooms from Northeast India  
466 detected three genetically distinct groups: most *joha* rice accessions from Assam and *tai* rices from  
467 Mizoram and Sikkim were in cluster 1, while *chakhao* rices from Manipur grouped in cluster 2, and  
468 aromatic accessions from Nagaland in cluster 3. Pairwise FST between three clusters varied from  
469 0.223 to 0.453 [78].

470 'Candy Roaster' heirloom squash fruits differs in size (10–250+ lbs), shape (round, cylindrical,  
471 teardrop, blocky, etc.), and color (pink, tan, green, blue, gray or orange), yet most have fine-textured  
472 orange flesh [79], while variants of 'Cappello da prete', another squash heirloom of 19<sup>th</sup> century still  
473 grown in the Po Valley of northern Italy, differ significantly in fruit weight, pulp thickness, rind  
474 thickness, peduncle diameter and seed weight [80].

475 Italian tomato landraces, 'Coarbrino' and 'Lucariello', are known for adaptation to water deficit,  
476 prolonged fruit shelf-life and good fruit quality. Whole-genome sequencing revealed 43,054 and  
477 44,579 gene loci annotated in 'Coarbrino' and 'Lucariello.' Both genomes exhibited novel regions  
478 with similarity to *Solanum pimpinellifolium* and *S. pennellii*, and SNPs or candidate genes associated  
479 with fruit quality, shelf-life, and stress tolerance in 'Coarbrino' and 'Lucariello' [23]. Heirloom  
480 tomatoes, e.g. 'Criollo' from an Andean valley in Argentina, are known for their excellent  
481 organoleptic quality, especially flavor and aroma. Aroma and sourness in 'Criollo' fruit correlate  
482 with citrate and several volatile organic compounds, such as  $\alpha$ -terpeneol, *p*-menth-1-en-9-al, linalool  
483 and 3,6-dimethyl-2,3,3a,4,5,7a-hexahydrobenzofuran (DMHEX), which is a novel volatile discovered  
484 in this heirloom [71]. The fruit shape among Italian tomato landraces ranged from flattened or



485 ribbed through pear or oxheart to round or elongate types. While the round or elongate types were  
486 rich in glycoalkaloids, the flattened types are in phenolic compounds [81]. North American heirloom  
487 tomatoes varied in fruit color (white, yellow, orange, red or black), shape (elongated, flattened,  
488 heart-shaped, pyriform, rounded), weight (4.2 to 265 g), firmness, total soluble solids (TSS) content,  
489 titrable acidity (TA), TSS:TA ratio, flavor intensity and ascorbic acid concentration [72, Fig. 1].  
490 Clearly, heirloom cultivars across crops, as noted above, maintain unique diversity, and can serve as  
491 a valuable resource for gardeners, farmers and plant breeders.



492  
493 **Figure 1.** Diversity in fruit, root, and tuber size and color of heirloom cultivars of capsicum, carrot, potato, and  
494 tomato.

495

## 496 **8. Retaining culinary and nutritional traits and improving heirlooms productivity**

497 There is wide variation in productivity among heirloom cultivars when grown in organic farming  
498 systems. One a few heirlooms can compete with modern cultivars in organic systems, while almost  
499 no heirlooms can compete with modern cultivars under intensive production systems [24–25, 82–84].  
500 However, heirlooms cultivars possess great diversity in fruit and seed size, shape and appearance,  
501 may often be superior in culinary and nutritional quality, and possess a rich source of many health  
502 promoting compounds. Thus, improving the productivity while retaining the culinary, nutritional,  
503 and health promoting compounds of heirloom cultivars is a great challenge for future plant breeding  
504 efforts [85]. For example, the heritage rice from eastern India ‘Kalanamak’ is a tall, low-yielding,  
505 black-husked short grained rice superior to ‘Basmati’ in aroma and taste. Its acreage has gone down  
506 (from 50,000 to almost extinction) over years of cultivation due to its low grain yield and  
507 deteriorating aroma and taste. A systematic attempt was made to collect and evaluate variants of



508 'Kalanamak', collected from farmers, identify accession as most aromatic and true to perceived  
509 'Kalanamak' quality. Using pure line selection, UPCAR-KN-1-5-1-1 was released as 'Kalanamak 3'  
510 (KN3) for cultivation in eastern Uttar Pradesh, India. Subsequently, several semi-dwarf breeding  
511 lines, developed through hybridization or induced mutation, outyielded 'KN3' by 40% [65]. A first  
512 semi-dwarf non-black husk cultivar 'Bauna Kalanamak 102' with comparable cooking quality and  
513 aroma as of 'KN3' was also released for cultivation in eastern Uttar Pradesh [86].

514 Spaniards highly appreciate 'Ganxet' bean, which is a landrace adopted in the Iberian Peninsula  
515 due to its culinary values; i.e., seed coat tenderness and buttery texture. Over the years of its  
516 cultivation, the original 'Ganxet' bean became contaminated possibly due to cross hybridization  
517 with other beans. Several variants (inbred lines) derived from the 'Ganxet' populations were  
518 evaluated against commercial controls. These lines showed great variability in protein content, total  
519 dietary fiber, digestible dietary fiber, seed coat, glucose and starch contents than controls. An inbred  
520 line L67 had many favorable characteristics (greater protein, less total digestible fiber, more  
521 digestible dietary fiber, a higher proportion of seed coat, more glucose and less starch than controls)  
522 that resulted in commercialization as true to the original 'Ganxet' [64]. 'Caparrona' is another  
523 heirloom bean that was largely grown by farmers in Monzón, Italy. The increasing modernization of  
524 agriculture at the end of 20<sup>th</sup> century resulted in its replacement by modern cultivars. Today, only a  
525 few local growers continue producing 'Caparrona' beans mainly for family use. A systematic effort  
526 was made to recover this landrace from extinction. Seed samples from growers were grown and two  
527 progenies true to 'Caparrona' types in morphology, chemical composition, and agronomic  
528 performance were identified for commercializing 'Caparrona' beans as a gourmet product by a local  
529 producers' association [87].

530 A major seed company 'Seminis Vegetable Seeds' has released a multiple resistance heirloom  
531 type tomato hybrid, 'Purple Boy' with great taste and unique appearance (purple), which are often  
532 the characteristics of heirlooms germplasm for US heirloom gardeners  
533 [<http://www.hortibiz.com/item/news/seminis-releases-first-purple-tomato-hybrid/>].

534 Intensive breeding of crops with a focus on yield and stress tolerance has indirectly led to  
535 reduction in nutrition and flavor [88–89]. The environment and agricultural practices also impact the  
536 intensity of flavor and aroma [90–92]. Flavor improvement is most difficult to achieve because of the  
537 difficulty of assessing the phenotype as well as a lack of basic knowledge about the chemicals  
538 driving consumer preferences, the pathways of their synthesis, and genes regulating the output of  
539 these pathways [93]. Analyses of consumer preferences together with accurate phenotyping and use  
540 of modern genomics and analytical chemistry tools in breeding, as evidenced in case of melon,  
541 strawberry and tomato, and participatory farmer-breeder-chef-consumer collaborations may  
542 facilitate development of next generation of crops to meet the growing demands of safe and  
543 nutritionally enhanced foods with good flavor, color, aroma and texture [84, 94].

544

545 **9. Farmer-breeder-chef-consumer partnerships to preserving heirlooms unique cultural and**  
546 **culinary significance**

547 Within the last decade, several organizations began collaborative breeding efforts among farmers,  
548 chefs, culinary professionals, and plant breeders. One of those is the Culinary Breeding Network,  
549 which is based at Oregon State University in Corvallis. The goal of this organization is to build  
550 communities of plant breeders, seed growers, farmers, produce buyers, chefs and other stakeholders  
551 to improve quality in vegetables and grains. The Culinary Breeding Network is interested in  
552 facilitating communication, collaboration, and participation in selection so that cultivars with  
553 superior performance, flavor, texture, and culinary attributes may be developed. They are also  
554 trying to promote and expand the awareness of cultivars developed by independent and public  
555 sector plant breeders and particularly those that have been selected for organic systems. Similar  
556 efforts are being made by another collaborative endeavor formed at the University of Wisconsin in  
557 Madison under the direction of Professor Julie Dawson. This effort is known as the Seed to Kitchen  
558 Collaborative. In addition, a seed company known as Row 7 has recently been established to foster  
559 close cooperation between chefs, farmers, and plant breeders to heighten the focus on culinary trait  
560 breeding.

561 These efforts are not directed solely at heirloom cultivars that possess unique culinary  
562 attributes. Instead, they are trying to capitalize on the connection between the cultivar and the user  
563 of that cultivar that is celebrated with many heirlooms, but with cultivars that have been selected for  
564 modern cropping systems. Thus, the goal is to combine the satisfaction of heirloom cultivars with  
565 the modern traits needed for high intensity farming, often in organic systems.

566 Part of the impetus for these efforts is the realization that many plant breeders must necessarily  
567 focus their efforts on commodity markets. In so doing, they often need to place greater emphasis on  
568 traits such as postharvest storability, harvestable yield, and host plant resistance to pathogens. There  
569 was little question that such traits were of great importance for crop production. But breeders also  
570 recognized that improving specific culinary qualities was possible but often may not be as high on  
571 the priority list as those traits that deliver the productivity the market requires. Many plant breeders  
572 therefore continued a focus on commodity traits and relegated specific culinary objectives to minor  
573 parts of their work.

574 Within the last 10 years, what were once small projects by plant breeders to modify culinary  
575 traits have blossomed into full-blown breeding programs. One of the primary thought leaders in this  
576 area is the Chef Dan Barber, of Blue Hill and Blue Hill at Stone Barns in New York. Dan was among  
577 the first to realize that partnerships among chefs, farmers, and plant breeders were necessary to be  
578 able to bring a focus on culinary traits to cultivars that could be grown and enjoyed widely. His  
579 efforts with the new seed company Row 7, which are described below, are one of the best examples  
580 of how such partnerships have formed in recent years. The Culinary Breeding Network and Seed to  
581 Kitchen Collaborative are attempts to bring many professionals together to participate in the  
582 development and selection of new vegetable cultivars. As such, it represents a new form of  
583 participatory plant breeding that is rapidly gaining interest in many parts of the world.

584 The origin of the Culinary Breeding Network was in 2011, when Lane Selman, an agricultural  
585 researcher at Oregon State University, observed chefs and plant breeders sharing knowledge during  
586 a taste test of nine different sweet pepper cultivars. At that time, Lane was involved in the  
587 management of vegetable trials for the Northern Organic Vegetable Improvement Collaborative  
588 (NOVIC), a federally funded partnership that uses on-farm trials to identify cultivars of vegetables  
589 that will thrive in organic systems. Farmers were trying to find a replacement for a hybrid sweet  
590 pepper that was no longer being offered for sale in the seed industry. Among the sweet peppers  
591 trialed were several cultivars developed by Frank Morton, breeder and owner of Wild Garden Seed  
592 in Philomath, Oregon. In the field, these plants stood out, and the participants in the trial began to  
593 discuss the various qualities of these peppers. This discussion was followed by more in-depth  
594 discussions among the various stakeholders who could be growing, cooking, eating, and producing  
595 seed of these peppers. A participatory network was thus born.

596 While plant breeders of horticultural crops often taste the breeding lines they are developing,  
597 their evaluations typically lack the sort of analysis that may be common for chefs or other culinary  
598 professionals. For example, many plant breeders “bite test” their breeding materials in the field,  
599 rendering an opinion when comparing among lines but often lacking in the sort of detailed  
600 observation that might be helpful in the culinary arts. When chefs and plant breeders finally started  
601 coming together in these efforts, the conversations that ensued were eye opening. Chefs often  
602 expressed interest in traits breeders had never considered, or would typically throw out. An  
603 expansion of the stakeholders involved in selection made for a much more robust selection process.  
604 Importantly, this sort of participatory breeding has a better chance of resulting in an adopted  
605 cultivar given the involvement of many different stakeholders during cultivar development. And  
606 conversely, as culinary specialists come to appreciate the challenges and limitations of the plant  
607 breeding process, there is a much better overall understanding of what is possible for the future of  
608 our crops. Both the Culinary Breeding Network and the Seed to Kitchen Collaborative combine field  
609 trials with tasting events that allow for such conversations to occur.

610 The goal of the Seed to Kitchen Collaborative (SKC) is to connect farmers, plant breeders and  
611 chefs to develop better cultivars for regional food systems in the Upper Midwest. The collaborative  
612 uses farmer focus groups and surveys to identify traits of interest, and flavor is consistently one of  
613 the top traits from these surveys. Currently, 80 farms are participating in this collaborative  
614 undertaking, and the majority of these farms use information gleaned from trials to find cultivars  
615 that they use in their production systems. Another important aspect of the collaborative initiative is  
616 that it provides an opportunity for independent plant breeders and public sector plant breeders to  
617 trial their newest material. For many specialty crops, organized trailing programs do not exist;  
618 therefore, the collaborative provides a unique outlet for breeding programs.

619 The Row 7 seed company began in 2017 as an effort to bring together breeders and chefs who  
620 want to make produce with better flavor and culinary characteristics. Founders of the Row 7 seed  
621 company, Chef Dan Barber, Professor Michael Mazourek of Cornell University, and Matthew  
622 Goldfarb of Fruition Seed Company, are filling a gap in the seed market that is quite unique. Their  
623 goal is to promote and sell seeds for new vegetable and grain cultivars that might otherwise not have  
624 been sold by any seed company, because their primary characteristics could be their culinary

625 attributes. Row 7's focus is to partner chefs and plant breeders with the aim of creating new cultivars  
626 that would bring a focus on flavor to what may have otherwise been commodity crops [95].

627 Chefs may bring a very useful and interesting perspective to breeding efforts [96]. Chefs readily  
628 admit that the food they prepare is only as good as the ingredients they use, so cultivars with  
629 improved qualities will make their job easier and more satisfying. Sometimes both consumers and  
630 chefs can make an impact on cultivar development. Several examples described by [96] include a  
631 new tomato cultivar developed by a cross between a modern breeding line and an heirloom that was  
632 identified after a taste panel involving 100 consumers, and a squash that was developed by a plant  
633 breeder after extensive dialogue between himself and a chef, who trialed the product in restaurants  
634 during its development. Such collaborative breeding efforts widen the scope of traditional plant  
635 breeding and likely forecast more consumer-friendly cultivars with enhanced culinary qualities.

636

637

## 638 10. Outlook

639 Heirlooms often embody particular shapes, colors, textures, flavors, and productivity traits for  
640 which they have come to be known and sought by farmers and consumers alike. They are  
641 recognized and prized for their specific qualities that have lent uniqueness to the cuisine of many of  
642 the world's cultures. Thus, the wealth of genetic variability encoded in heirloom cultivars of our  
643 crops is one of the treasures of our shared global food system.

644 As modern cultivars and the global seed industry have rapidly replaced heirlooms and the  
645 practice of seed saving, this unique genetic heritage is, however, in danger of being lost. In recent  
646 decades, as our agricultural systems have become even more industrialized, many scientists have  
647 come to recognize that the genetic diversity found in heirloom cultivars is of even greater  
648 importance for our shared food future. Modern crop breeding has improved agricultural  
649 productivity, but simultaneously reduced genetic diversity in our major crops. As our farming  
650 systems become more industrialized and our climate becomes more erratic, enhancing, rather than  
651 shrinking, our crop genetic diversity will be critical for feeding the world's growing population.  
652 Recent efforts to characterize, preserve, and enhance heirlooms abound, bringing these unique types  
653 to the forefront of many modern breeding efforts. Participatory breeding approaches with farmers,  
654 breeders, and chefs are but one example of modern approaches to expanding the diversity found in  
655 heirlooms into modern germplasm pools. Recently molecular research found markers associated  
656 with useful variants in heirloom cultivars that may be further used to introgress such traits into  
657 modern cultivars.

658 Heirloom cultivars are also most closely associated with organic and sustainable farming  
659 systems, and typically do much better in such conditions compared to modern, industrialized  
660 farming systems. As sustainable farming systems gain in popularity in the developed world, the  
661 genetic diversity present in heirloom cultivars may become even more important. However, we  
662 realize that modern farming systems will continue to dominate many sectors of world agriculture.  
663 One of the most important breeding objectives going forward will be therefore to improve the  
664 productivity of heirloom types while retaining their unique qualities.

665 A number of groups have expanded their efforts to preserve traditional heirloom cultivars that  
666 were important cultural touchstones for different ethnic groups around the world. One such  
667 example is the recent attempt to preserve, maintain, and repatriate germplasm of American crops

668 domesticated and bred by Native American tribes. These efforts are closely tied to food sovereignty  
669 movements, which seek to bring particular heirloom types of staple food crops back under the  
670 control of the people who developed them. In such cases, heirloom cultivars represent a vital link to  
671 the past as well as a critical bridge to the future.

672 One of the hallmarks of modern agriculture is the existence of high performing cultivars that  
673 are bred for wide-area adaptation and productivity. These cultivars play a key role in feeding the  
674 world's growing population; but they may not possess the genetic diversity required to sustain the  
675 world's population. Many decades ago, heirloom cultivars appeared to be relics of an earlier age; as  
676 older cultivars that had been improved. However, a renewed interest in heirloom cultivars has  
677 helped foster the sense that they may play an important role in future crop breeding efforts. New  
678 market channels have emerged for heirlooms that have re-energized this unique repository of crop  
679 germplasm. As they possess unique flavors, colors, texture, stress tolerances, and forms, heirlooms  
680 may represent an important collection of traits that can be of immediate value in crop production  
681 and as a source of breeding germplasm for future cultivars. The goal of this review has been to  
682 document some of the unique characteristics of heirlooms with the hope that breeders will identify  
683 useful traits to bring into breeding programs aimed at developing high value cultivars.

684

685

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