

Scotland's Rural College

## **The role of genetics in mainstreaming the production of new and orphan crops to diversify food systems and support human nutrition**

Dawson, IK; Powell, W; Hendre, Prasad; Bancic, JB; Hickey, JM; Kindt, Roeland; Hoad, SP; Hale, Iago; Jamnadass, Ramni

*Published in:*  
New Phytologist

*DOI:*  
[10.1111/nph.15895](https://doi.org/10.1111/nph.15895)

Print publication: 01/10/2019

*Document Version*  
Peer reviewed version

[Link to publication](#)

### *Citation for published version (APA):*

Dawson, IK., Powell, W., Hendre, P., Bancic, JB., Hickey, JM., Kindt, R., Hoad, SP., Hale, I., & Jamnadass, R. (2019). The role of genetics in mainstreaming the production of new and orphan crops to diversify food systems and support human nutrition. *New Phytologist*, 224(1), 37-54. <https://doi.org/10.1111/nph.15895>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 Tansley review in *New Phytologist*

2

3

4

5 **The role of genetics in mainstreaming the production of new and orphan**  
6 **crops to diversify food systems and support human nutrition**

7

8

9

10 **Ian K Dawson<sup>1,2</sup>, Wayne Powell<sup>1</sup>, Prasad Hendre<sup>2</sup>, Jon Bančić<sup>1,3</sup>, John M Hickey<sup>3</sup>,**  
11 **Roeland Kindt<sup>2</sup>, Steve Hoad<sup>1</sup>, Iago Hale<sup>4</sup>, Ramni Jamnadass<sup>2</sup>**

12

13

14 <sup>1</sup> Scotland's Rural College (SRUC), Kings Buildings, West Mains Road, Edinburgh, EH9  
15 3JG, Scotland

16 <sup>2</sup> World Agroforestry (ICRAF), Headquarters, PO Box 30677, Nairobi, Kenya

17 <sup>3</sup> The Roslin Institute, Easter Bush Campus, University of Edinburgh, Midlothian, EH25  
18 9RG, Scotland

19 <sup>4</sup> University of New Hampshire, Durham, NH 03824, USA

20

21

22 Author for correspondence: Ian K Dawson

23 Tel. +44 1904 628 367

24 Email: iankdawson@aol.com

25

26

27 Total count for text main body (Introduction to Acknowledgments inclusive) is 7,399 words  
28 with six colour figures, one table and 133 references. Count for the Summary is 200 words.  
29 Three pieces of supporting information text (in a single file) and one supporting information  
30 table (in Excel).

31

32

33	<b>Contents</b>
34	
35	Summary
36	I. Introduction
37	II. Trends in crop production that inform new and orphan crop promotion
38	III. Genetic improvement objectives for new and orphan crops
39	IV. Approaches for genetic improvement
40	V. Future outlook
41	Acknowledgements
42	References
43	
44	

45 **Summary**

46

47 Especially in low income nations, new and orphan crops provide important opportunities to  
48 improve diet quality and the sustainability of food production, being rich in nutrients, capable  
49 of fitting into multiple niches in production systems, and relatively adapted to low input  
50 conditions. The evolving space for these crops in production systems presents particular  
51 genetic improvement requirements that extensive gene pools are able to accommodate.  
52 Particular needs for genetic development identified in part with plant breeders relate to three  
53 areas of fundamental importance for addressing food production and human demographic  
54 trends and associated challenges, which are: facilitating integration into production systems;  
55 improving the processability of crop products; and reducing farm labour requirements. Here,  
56 we relate diverse involved target genes and crop development techniques. These techniques  
57 include transgressive methods that involve defining exemplar crop models for effective new  
58 and orphan crop improvement pathways. Research on new and orphan crops not only  
59 supports the genetic improvement of these crops, but they serve as important models for  
60 understanding crop evolutionary processes more broadly, guiding further major crop  
61 evolution. The bridging position of orphan crops between new and major crops provides  
62 unique opportunities for investigating genetic approaches for *de novo* domestications and  
63 major crop ‘rewildings’.

64

65 **Keywords:** breeding approaches, crop harvestability, crop integration, crop processability,  
66 model crop exemplars, orthologous genes.

67

68

## 69 **I. Introduction**

70

71 Global food production has homogenised as an ever-narrower range of calorie-rich but  
72 nutritionally-limited and resource-intensive crops has increased in dominance (Khoury *et al.*,  
73 2014). This has enhanced energy availability in diets but endangers human and  
74 environmental health by contributing to hidden hunger (von Grebmer *et al.*, 2014), climate-  
75 related food production shocks (Global Food Security, 2015) and planetary resource  
76 depletion (Rockström *et al.*, 2009). Rediversifying crop production is important to promote a  
77 wider range of healthier foods and more sustainable and stable production systems (von  
78 Grebmer *et al.*, 2014). Efforts to promote diversification however require that policies and  
79 research priorities change (Khoury & Jarvis, 2014; Gillespie & van den Bold, 2017; Willett *et*  
80 *al.*, 2019). In a revised agenda, new and orphan crops rich in valuable micro- and macro-  
81 nutrients, capable of fitting into multiple niches in production systems (where they provide  
82 environmental services as well as direct provisioning services), and relatively adapted to low  
83 input conditions, have an important role (Gruber, 2017; AOCC, 2019; Mustafa *et al.*, 2019).  
84 These plants either are harvested at present from the wild and are candidates for cultivation  
85 (potential new crops) or have already entered the domestication process but are generally  
86 only grown and valued locally or regionally (orphan crops); in both cases, only limited  
87 production research is currently underway on them (Dawson *et al.*, 2018). Despite this  
88 neglect, new and orphan crops have received increased media attention recently (e.g.,  
89 Economist, 2017), based on their potential to address multiple UN Sustainable Development  
90 Goals (UN, 2019) in the low income nations of Africa (AOCC, 2019), Asia (CFF, 2019) and  
91 Latin America (LATINCROP, 2019), and due to Western consumers' interests in new,  
92 healthier foods.

93

94 As well as new and orphan crops' production values, they are attractive candidates for  
95 research by biologists. This is because crop domestication – defined broadly as the genetic  
96 changes involved in bringing a crop into cultivation and in its continued development within  
97 agriculture – has long been recognised as providing fascinating insights into fundamental  
98 evolutionary processes (Darwin, 1859). Clearly, new, orphan and major crops position on a  
99 domestication continuum. Furthermore, the range of locations over which their extant genetic  
100 diversity is distributed also varies. Together, these points mean that a spectrum of these plants  
101 can allow the extrapolation domains of various possible genetic improvement approaches to  
102 be explored, as outlined in Figure 1.

103

104 In addition to their practical and research values, the technical environment for undertaking  
105 new and orphan crop genetic studies has greatly improved in the last decade due to  
106 significant cost reductions in genome characterisation approaches (Varshney *et al.*, 2012).  
107 Along with advances in ‘speed breeding’ (Watson *et al.*, 2018), in participatory improvement  
108 methods (Weltzien & Christinck, 2017) and in statistical approaches that support crop  
109 development (e.g., Meuwissen *et al.*, 2001; Lasky *et al.*, 2018), the landscape for new and  
110 orphan crop genetical study has therefore recently been transformed.

111

112 The above observations all argue for more attention to be paid to new and orphan crops.  
113 Here, we consider how the production of these crops may support human and environmental  
114 health objectives, paying particular attention to the situation in tropical and subtropical low  
115 income nations. Deficits in key dietary nutrients are often high in these countries, but they  
116 also often contain extensive inter- and intra-specific variation in wild and agricultural plants  
117 that could be better utilised for biodiversity-based, sustainable food solutions (Jamnadass *et*  
118 *al.*, 2011). Below, we first address the context of global crop production, considering trends  
119 over the last half century that inform possible new and orphan crop genetic interventions for  
120 initial or wider integration of these plants into agriculture. We then consider genetic  
121 improvement objectives, drawing on existing knowledge of the crop ‘domestication  
122 syndrome’ (Meyer *et al.*, 2012), our own analysis of plant breeders’ perspectives on crop  
123 development needs, and considering other food system stakeholders’ requirements. We  
124 particularly focus on traits and examples of underlying genes to address food production and  
125 human demographic trends and associated challenges in three areas of fundamental  
126 importance: to support the integration of crops into production systems; to increase crop  
127 product processability; and to reduce the farm labour requirements of production. We then  
128 relate approaches for the genetic improvement of new and orphan crops, considering the role  
129 of orthologous gene sequences in trait evolution. As part of this exercise, we illustrate an  
130 approach for defining appropriate genetic improvement pathways for a range of exemplar-  
131 requiring new and orphan crops, based on comparison with a panel of more widely  
132 understood crop models.

133

134 Our intention through this review is to indicate genetics-based research avenues to support  
135 the mainstreaming of new and orphan crops in food production systems. In addition, we  
136 illustrate how research on these plants can contribute to major crop evolution. Clearly, crop

137 improvement is only one aspect to be addressed in mainstreaming production. Further  
138 interdisciplinary work, such as to understand the social and economic drivers of consumer  
139 demand, is also required (Dawson *et al.*, 2018). In addition, policy issues related to the use of  
140 genetic technologies, such as the effective application of the Nagoya Protocol (on access to,  
141 and the fair and equitable sharing of the benefits arising from the utilisation of, genetic  
142 resources), also need to be addressed for new and orphan crops (e.g., Østerberg *et al.*, 2017;  
143 Halewood *et al.*, 2018). These aspects, while outside the scope of the current review, are also  
144 of high importance.

145

## 146 **II. Trends in crop production that inform new and orphan crop promotion**

147

148 In their analysis of global crop production trends, Khoury *et al.* (2014) identified crops that  
149 were relative over-performers ('winners') and under-performers ('losers') over the  
150 approximate half century of 1961 to 2009 in terms of total food supply. To explore the wider  
151 production characteristics of winner and loser crops, we further analysed a representative  
152 selection of them. Our analysis (Fig. 2) indicated that winner crops are more likely to be  
153 produced in lower diversity production systems (tending to monoculture) than are loser crops.  
154 This is consistent with the global reductions in farm production system heterogeneity over  
155 recent decades that have been explored by other authors (e.g., Clay, 2004; Donald, 2004).  
156 Current global production trends thus not only result in lower crop food diversity,  
157 endangering humans' nutritional security, but call into question the continued availability of  
158 agrobiodiversity-related environmental services within farm landscapes and therefore the  
159 sustainability of food production more broadly (Cardinale *et al.*, 2012). Designing new and  
160 orphan crops to better support the maintenance and development of diverse production  
161 systems is therefore a doubly crucial objective. In these systems, the intention should be that  
162 new and orphan crops complement the production of other crops rather than simply substitute  
163 for them, requiring appropriate spatial and temporal integration (Dawson *et al.*, 2019a).

164

165 To help determine where investments in productivity improvements that are generally  
166 considered a fundamental requirement in plant breeding could drive production  
167 diversification with new and orphan crops, we again reviewed available crop production data.  
168 We assessed the relative contributions of yield (production per unit area, with genetic and/or  
169 agronomic contributions possible) and total area planted to changes in global crop output  
170 over the last half century for a panel of 35 exemplar crops (Fig. 3 and Supporting Information

171 1). Our analysis identified a group of nine case study crops where yield contributions to  
172 changes in output appeared markedly lower than the established trend line. A comparison of  
173 these crops with the wider panel revealed that most had relatively low annual global gross  
174 production values in monetary terms, a situation equating to the majority of new and orphan  
175 crops that are used locally and regionally only.

176

177 It seems reasonable to assume that monetary production value is a proxy for historical levels  
178 of investment in plant breeding. Thus, the observed differences in crop performance that  
179 likely relate to breeding investment in our analysis indicate the importance of new breeding  
180 efforts to support new and orphan crop development. Furthermore, such differences in  
181 performance in relation to investment highlight the potential transformative role that new,  
182 cheaper advanced breeding approaches could have in reducing investment barriers to support  
183 significant production gains (Varshney *et al.*, 2012). Our analysis would suggest that  
184 investment in advanced breeding methods is of particular importance for addressing potential  
185 improvement challenges for perennial, vegetatively-propagated crops.

186

### 187 **III. Genetic improvement objectives for new and orphan crops**

188

#### 189 **III.1 New and orphan crop development and the crop domestication syndrome**

190

191 The starting point for new and orphan crop development is a broad understanding of the  
192 ‘domestication syndrome’. This is generally revealed by comparing crops’ phenotypes with  
193 either the extant descendant generations or the archaeological remains of their wild  
194 progenitors (Meyer *et al.*, 2012). Features of the syndrome commonly reported for annual  
195 crops include a reduced ability to disperse seed, more synchronous seed germination,  
196 increased seed size, reduced chemical defences and alterations in reproductive shoot  
197 architecture (Larson *et al.*, 2014). The syndrome is less well defined for perennial crops  
198 (Miller & Gross, 2011) but in the case of fruit trees features include a shift from seed to  
199 vegetative propagation, increased regularity in fruit bearing, enhanced fruit size and  
200 decreased plant stature (Clement, 2004; Goldschmidt, 2013).

201

202 The genes underlying domestication have been partially determined in a range of crops. In an  
203 authoritative review, Meyer and Purugganan (2013) listed 60 genes whose variants were  
204 reported to be involved. Of these, 37 were reported to encode transcription factors (see also



205 Schilling *et al.*, 2018) and 14 to encode enzymes. Loss-of-function alleles were found to be  
206 the most common type of causative change, followed by alleles varying in cis-regulatory  
207 elements altering gene expression. Missense mutations (altering protein function) were  
208 however also not infrequent. Based on Meyer and Purugganan's (2013) compilation, loss-of-  
209 function mutations appeared more often associated with 'domestication' genes (that control  
210 the classic domestication syndrome) and positive change-of-function mutations with  
211 'diversification' genes (which allow crops to adapt to particular uses and agro-ecological  
212 environments). Under this typology, 'domestication' genes may be initial targets for  
213 manipulation in new crop development, while 'diversification' genes may be targets in  
214 orphan crops that have already passed through initial crop development stages. In the rest of  
215 this review, we however generally refer to both these sets of genes as 'domestication-related'  
216 as the distinction between categories is not always clear or useful.

217

218 Around half of the genes compiled by Meyer and Purugganan (2013) were related to fruit and  
219 seed properties. Among these genes, those controlling composition and the palatability and  
220 processability of crop food parts were most prominent. For example, the *WAXY* gene in rice  
221 (*Oryza sativa*) (and orthologues in other crops) controls the amylose versus amylopectin ratio  
222 in grain starch, which determines grain processability (as discussed further later in this  
223 review). In addition, just over one-third of the compiled genes were reported to influence  
224 plant architecture or crop flowering time, both of which are important features for  
225 determining crop integration into production systems. Finally, seven of the identified genes  
226 were related to seed head non-shattering and thus to crop harvesting efficiency and crop  
227 labour requirements. Processability, integration into production systems and the labour  
228 requirements of production have all been identified as important features for new and orphan  
229 development, as we discuss further below. A focus on several of the genes compiled by  
230 Meyer and Purugganan (2013) is therefore of relevance.

231

### 232 III.2. Stakeholders' perspectives on traits for new and orphan crop improvement

233

234 Understanding producers' constraints is crucial for determining sound improvement  
235 objectives for new and orphan crops, but to date little systematic information has been  
236 available. To help remedy this gap, we have gathered information from plant breeders on new  
237 and orphan crop improvement targets for Sub-Saharan Africa, where these plants are  
238 recognised to have a particularly important role to play in supporting human nutrition and

239 sustainable agriculture (AOCC, 2019). Although a survey of breeders' views can only  
240 provide a partial picture of crop development needs since breeders are only one stakeholder  
241 group in crop promotion (along with farmers, consumers, retailers, food processors, etc.;  
242 Dawson *et al.*, 2018), they are perhaps in the best position to grasp sector-wide concerns that  
243 can inform crop improvement targets. In addition, existing contact networks mean that they  
244 are a relatively easy stakeholder group to gather information from.

245  
246 Our survey of breeders' views (described in Supporting Information 2) indicated that crop  
247 pest and/or disease attack was the most frequently mentioned priority genetic or management  
248 constraint for new and orphan crops, while lack of access to suitable planting material was by  
249 far the most mentioned important input constraint (Fig. 4a), echoing concerns on varietal  
250 delivery that we return to later in this review. Consistent with these production constraints,  
251 breeders most mentioned pest and disease tolerance or resistance as the priority trait category  
252 for genetic improvement action, followed by yield *per se* (i.e., production independent of  
253 pests, diseases, etc., that also influence yield). In addition, improved harvestability was the  
254 fifth most mentioned important area for genetic improvement (Fig. 4b).

255  
256 Our survey of breeders also indicated that improvement in crop planting and/or establishment  
257 methods was the most mentioned priority agronomic management intervention required to  
258 support new and orphan crop production, closely followed by soil fertilisation measures. The  
259 proper timing of seasonal field activities was the fourth most mentioned required agronomic  
260 intervention and the diversification of production systems the fifth (Fig. 4c). As expected, the  
261 priority constraints and interventions mentioned by breeders depended on the part of the plant  
262 used for food (Fig. 4d). Significantly, when asked about the likelihood of success of their  
263 suggested priority interventions, breeders considered agronomic management actions to be  
264 more likely to be successful than genetic improvement actions (Fig. 4e). They however  
265 believed both types of action to overall have high potential for success, suggesting a useful  
266 role for a variety of breeder-supported context-specific genetic improvement methods, in  
267 conjunction with agronomic developments. Below, we further consider the results of our  
268 breeders' survey in the context of additional stakeholders' constraints and the global trends  
269 that also inform the efficient production and use of new and orphan crops, under three trait  
270 categories of specific importance.

271  
272 *Traits for greater production integration*

273 Breeders' emphasis on yield, along with knowledge of global crop production and  
274 consumption trends (described in Section II), support the view that diversification of the  
275 world's crop portfolio requires productivity enhancements in new and orphan crops, to enable  
276 them to successfully compete with major crops for farmers' attention (Tadele, 2017).  
277 Diversification is however not only about increasing the range of crops grown, but is  
278 concerned with developing more efficient, sustainable and stable integrated production  
279 systems through approaches such as intercropping (Brooker *et al.*, 2015). An emphasis on  
280 traits that maximise positive crop-crop interactions in terms of yields, sustainability and  
281 stability is therefore crucial for new and orphan crop development. This requirement appears  
282 not to have been fully recognised by the plant breeders included in our survey: while several  
283 breeders indicated the importance of crop diversification as an agronomic management  
284 intervention, less attention was given to this aspect in the trait categories identified for  
285 genetic improvement. This discrepancy could indicate either an inherent difficulty in  
286 intercrop breeding or a conceptual disconnect in breeders' current thinking, perhaps due to  
287 their tendency to work at any one time on only a single crop.

288

289 Insights into plant species' interactions in natural ecosystems may be useful for designing  
290 improved crop-crop interactions. Studies reporting the genetics (and epigenetics; Alonso *et al.*,  
291 2019) of reciprocal helping between plants are however currently relatively scarce;  
292 strategies have though been outlined through which natural genetic variants underlying  
293 mutualisms between pairs of plant species could be characterised (Subrahmaniam *et al.*,  
294 2018). Obvious 'interaction traits', likely to influence resource-use complementarity or  
295 conflict among crops, are those related to plant architecture, growth rate, mycorrhizal  
296 associations and phenology (Vandermeer, 1992; Litrico & Violle, 2015). The currently  
297 cultivated gene pools of orphan crops still contain variation in important interaction traits  
298 because this diversity has not been lost through monoculture breeding as for the advanced  
299 cultivars of major crops (Francis & Smith, 1985); there are therefore significant opportunities  
300 for designing more effective intercrop systems involving them. This depends of course on  
301 suitable breeding methods being made available, a topic we return to below.

302

### 303 *Traits for increased product processability*

304 Our current survey of production constraints only obtained information from plant breeders,  
305 but as already noted it is also important to consult others regarding crop target traits,  
306 including farmers, consumers, retailers and food processors, in order to 'co-construct' more

307 optimal crop development targets. For consumers, traits related to nutritional content, food  
308 acceptability, palatability and cookability are especially important. In new and orphan root  
309 crops and legume seeds in particular, the presence of anti-nutritional compounds such as  
310 phytic acid, saponins, polyphenols, lathyrrogens,  $\alpha$ -galactosides, protease inhibitors,  $\alpha$ -  
311 amylase inhibitors and lectins can be of concern (e.g., Sousa *et al.*, 2015). Reductions in these  
312 compounds mean that foods require less cooking or other processing to remove them and  
313 make consumption safe (Yerra *et al.*, 2015). In turn, this allows poor consumers to make  
314 healthier food choices. This is because the high energy costs for cooking these foods, which  
315 place a large burden on families' finances, are reduced, as are the labour requirements of food  
316 preparation, which fall especially on women (Balmer, 2007). Because a number of anti-  
317 nutritional compounds play important roles in protecting new and orphan crops from pest and  
318 disease attack, however, breeding objectives may focus on altering plant part allocation of  
319 these chemicals (e.g., avoiding the edible portion of the crop) or increasing their lability  
320 during cooking or other processing, rather than their reduction or removal *per se* (Nour-Eldin  
321 & Halkier, 2013).

322

323 With the increasing reliance by growing urban populations in low income nations on  
324 processed foods (Popkin *et al.*, 2012), improvements in a range of processability traits for  
325 new and orphan crops is a priority. This allows the wider incorporation of nutritious new and  
326 orphan crop ingredients in processed food reformulations. Of relevance is the broad physical  
327 properties of ingredients and their chemical compositions, which influence flavour, texture,  
328 stability and overall consumer acceptance (e.g., Sun-Waterhouse *et al.*, 2014). A good  
329 example is the ratio of amylose to amylopectin in cereal starches: this influences the  
330 functional properties of derived processed foods as well as their nutritional and physical  
331 characteristics (Lagassé *et al.*, 2006). The food industry is particularly interested in  
332 identifying novel functional ingredients as surfactants, thickeners and strain-hardening  
333 biopolymers that can support more efficient, healthier processed food production; with their  
334 diverse characteristics, new and orphan crops may present novel opportunities for such uses,  
335 once they have been more fully characterised through tensiometry, rheometry and other  
336 analytical approaches to measure food properties (e.g., Bakare *et al.*, 2016).

337

### 338 *Traits for reduced farm labour requirements*

339 The importance of reducing the labour requirements of new and orphan crop production, and  
340 of coordinating these requirements with other farm activities, is evident from our survey of

341 breeders who indicated the need to improve crop harvestability via genetic means and the  
342 need for attention to the proper timing of seasonal field activities. The significant rural-to-  
343 urban transition currently underway in many low income nations (Kessides, 2005) reinforces  
344 the need for reducing rural labour requirements. At the same time, new concentrations of  
345 available labour in urban areas may support urban and peri-urban food transformation,  
346 reinforcing the importance of improving crop processability traits.

347  
348 Trait categories influencing rural labour requirements and/or the timing of these requirements  
349 include seed and fruit dispersal or retention, seed and fruit size, plant form and crop  
350 phenology. Plant form and phenology are also crucial for crop integration, as described  
351 above, while variation in crop phenology is also important for avoiding seasonal gluts in food  
352 supply that affect market profitability and wastage. Especially for perennial crops, the length  
353 of the plant's juvenile phase is an important factor determining the return to labour. For *de*  
354 *novo* crops, the vision of reducing the labour needed to collect from the wild may serve as an  
355 important stimulus for initial cultivation (Schippmann, 2002), thereby implicating a need to  
356 focus on basic genetic traits related to propagation and *ex situ* establishment ability.

357  
358 III.3. Candidate genes for new and orphan crop priority improvement trait categories

359  
360 Some of the high priority trait categories identified for new and orphan crop improvement,  
361 such as pest and disease resistance and yield *per se*, align with the development profiles of  
362 most major crops. In this section, however, we focus on the three trait categories of specific  
363 importance for driving new and orphan crop development and adoption that were identified  
364 above. Illustrative cases of involved genes, which may present potential targets for  
365 manipulation in crop development, are summarised in Table 1. Specific examples are also  
366 given below.

367  
368 For production system integration, the important feature of flowering time determines the  
369 maturity date of a crop and therefore its intercrop effectiveness (Yu *et al.*, 2015). The genes  
370 controlling flowering pathways have been identified in a range of crops (Nakamichi, 2015)  
371 and the involvement of orthologous sequences across crops has been established (Calixto *et*  
372 *al.*, 2015). Reduced photoperiod sensitivity, resulting from allelic variation in a subset of  
373 these genes, has played an enormous role in the historic range expansion of many major  
374 crops. In barley (*Hordeum vulgare*), for example, a network of ~20 circadian clock-related

375 genes are known to modulate flowering time; the northern expansion of the crop from the  
376 Fertile Crescent was associated with the emergence of day-length insensitive forms (Russell  
377 *et al.*, 2016). The manipulation of related genes in new and orphan crops could similarly  
378 facilitate range expansion and support the development of more effective intercrop  
379 combinations.

380

381 For product processability, examples related to anti-nutritional compounds and starch  
382 chemical composition are illustrative of possible genetic manipulations. In several legumes,  
383 phytates are the primary reserve of phosphorous in the seed, but these chelate iron and zinc  
384 that are essential in human diets (Petry *et al.*, 2015). A low phytic acid mutant isolated in  
385 common bean (*Phaseolus vulgaris*), associated with change in an ABC transporter gene,  
386 demonstrated enhanced iron bioavailability in porridge made from its dried seed, reducing the  
387 cooking time needed to reach acceptable iron absorption levels (Petry *et al.* 2013). Various  
388 orphan crop legume seeds with high phytate levels may have levels similarly reduced through  
389 related mutations. In the case of starch composition, as already noted the ratio of amylose to  
390 amylopectin in rice grain is controlled by the granule-bound starch synthase gene *WAXY*,  
391 while its orthologues have a similar function in other cereals and pseudo-cereals, including  
392 the orphan crops of foxtail millet (*Setaria italica*) and the grain amaranths (e.g., *Amaranthus*  
393 *cruentus*). The waxiness of grain not only affects its attractiveness for consumers, but it  
394 influences the food processing and digestibility characteristics of seed, not always in  
395 beneficial ways for modern diets. For example, waxy grain types may be easier to process,  
396 but they may also have a higher glycaemic index that contributes to type 2 diabetes risk in  
397 humans (Kaur *et al.*, 2016). Trade-offs in reaching breeding objectives for processability  
398 traits are therefore required.

399

400 Regarding labour requirements, the standard domestication syndrome trait of seed or fruit  
401 retention is crucial in influencing crop harvestability (Meyer *et al.*, 2012). In addition, fruit  
402 size is an important characteristic, especially for fleshy-fruited crops where the ripe fruit is  
403 eaten whole. This is because larger fruits are easier to harvest to reach the same collected  
404 weight, particularly when the crop is handpicked. The genetic control of fruit size has been  
405 extensively researched in tomato (*Solanum lycopersicum*), the model species for other fleshy-  
406 fruited crops (van der Knaap *et al.*, 2014); some of the identified genes are known to have  
407 orthologues in other plants.

408

## 409 **IV. Approaches for genetic improvement**

410

### 411 IV.1. Available genetic improvement methods for new and orphan crops

412

413 Ideotype targets and an understanding of the inheritance and genetic architecture of defining  
414 traits determine suitable approaches for the genetic improvement of any particular new or  
415 orphan crop (Section III). Especially in low income nations, it is also necessary to consider  
416 how improved varieties will be delivered to farmers. A detailed assessment of planting  
417 material delivery options is outside the scope of this review, but strategies are specific to  
418 breeding approach (Walker *et al.*, 2014). In general, however, an emphasis on working with  
419 farmers in varietal evaluation and in the multiplication of planting stock is a useful means of  
420 building effective bridges between crop breeding and crop production (Weltzien &  
421 Christinck, 2017). This context should be considered when selecting from the possible  
422 breeding and selection options described below.

423

#### 424 *Advanced and conventional breeding*

425 Marker-assisted selection is used widely in major crop development and has begun to be  
426 applied to orphan crops. Examples include the annual orphan crops of foxtail millet (*Setaria*  
427 *italica*; Jia *et al.*, 2013) and pigeonpea (*Cajanus cajan*; Varshney *et al.*, 2017) and,  
428 increasingly, a range of perennial plants (Iwata *et al.*, 2016; Migicovsky & Myles, 2017).  
429 However, the relatively high costs of phenotyping remain a constraint in most cases  
430 (Varshney *et al.*, 2012). This is especially so for perennial crops that require several years of  
431 growth before they can be properly evaluated and that have large life forms that demand  
432 considerable space in field trials.

433

434 Applying genome-wide association scans, Cichy *et al.* (2015) identified genomic regions  
435 associated with variation in the so-called “cooking time trait” in a diversity panel of common  
436 beans. Although perhaps not strictly an orphan crop itself because of relatively high research  
437 investments, common bean can be considered representative of several orphan legumes. The  
438 finding of associations between specific genomic regions and cooking time in legumes is  
439 important because long cooking times limit the more efficient utilisation of the seed as food  
440 (see discussion in Section III.2). Cichy *et al.* (2015) found statistically significant  
441 associations between cooking time and SNPs on three *P. vulgaris* chromosomes, with the  
442 strongest associations on chromosome 6 (Pv06). Proximate coding sequences on Pv06

443 included two cation/H<sup>+</sup> exchanger genes, one homologous to *AtCHX3* and the other to  
444 *AtCHX4* (further information in Table 1). In arabidopsis (*Arabidopsis thaliana*) these genes  
445 are involved in calcium transport, which corresponds with evidence that Ca<sup>2+</sup> plays an  
446 important role in storage-induced increases in common bean's required cooking time (Jones  
447 & Boulter, 1983). Similar to major crops (Liu & Yan, 2019), there is clearly high future  
448 potential for the further application of genome-wide association scans to dissect quantitative  
449 traits for new and orphan crops, if appropriate resources are allocated to phenotyping.

450

451 Genomic selection (Meuwissen *et al.*, 2001) uses phenotypic and genomic data collected  
452 from training populations to predict the breeding value of genome-characterised but un-  
453 phenotyped breeding materials (known as genomic estimated breeding values). To date the  
454 approach has been most effectively adopted for complex trait breeding in animals (Georges *et*  
455 *al.*, 2019), but it is increasingly being used to breed for polygenic traits in plants (Crossa *et*  
456 *al.*, 2017), exploiting cross-sectoral synergies in possible methods (Hickey *et al.*, 2017). As  
457 currently practised, the accuracy of prediction quickly decays as a function of the genetic  
458 distance between the training and experimental germplasm sets; for example, comparisons  
459 across animal breeds can be difficult (Hayes *et al.*, 2009). However, advances are being made  
460 to extend useful comparisons to more distantly related materials by considering sequence  
461 context (Druet *et al.*, 2014) and wider biological priors (e.g., variant annotations, candidate  
462 genes and known causal mutations; MacLeod *et al.*, 2016). The ability to expand  
463 comparisons from relatively well studied crops to genetically-related but under-phenotyped  
464 new and orphan crops could be of key importance.

465

466 The efficacy of genomic selection is currently being tested on cassava (*Manihot esculenta*), a  
467 vegetatively-propagated orphan annual root crop (Wolfe *et al.*, 2017). A further orphan crop  
468 example where the approach is beginning to be explored is finger millet (*Eleusine coracana*),  
469 a seed-propagated annual grain (discussed further below). As for standard marker-assisted  
470 selection, the primary limitation in applying genomic selection to new and orphan crops is the  
471 absence of phenotypic data from relevant training populations (Varshney *et al.*, 2012). The  
472 application of the approach could in theory however be especially effective for slow-maturing  
473 perennial new and orphan crops which are difficult to directly phenotype for key production  
474 traits (Isik *et al.*, 2015). Genomic selection may also be particularly effective when the  
475 underlying biological basis of key traits is poorly understood, as is the case with many new  
476 and orphan crops.



477

478 Along with the advent of new technological approaches for crop genetic improvement there  
479 is an emerging reconsideration of breeding methods that effectively address spatial and  
480 temporal interactions among the different biological components in diverse production  
481 systems (Litrico & Violle, 2015). The identification of target crop-crop interaction traits in  
482 this breeding is partially informed by research on natural systems, as outlined earlier in this  
483 review (Section III.2). In agricultural systems, however, it is also possible to ‘force’ positive  
484 relationships among crop diversity, yield and overall production stability that are unrealisable  
485 naturally due to different balancing trade-offs (Denison *et al.*, 2003). Significant research is  
486 though still required to explore context-appropriate intercrop breeding techniques; the  
487 approaches to intercrop breeding that have been proposed so far have rarely been  
488 implemented (Hamblin *et al.*, 1976; Wright, 1985).

489

490 Theoretically, genomic selection offers clear advantages for intercrop breeding as it can  
491 better manage the expected complex genetics of interaction traits and it reduces the need for  
492 large experimental plots to evaluate crop-crop interactions. In our own research (JB, JH, SH,  
493 IKD, in collaboration with the International Crops Research Institute for the Semi-Arid  
494 Tropics) we are stochastically modelling the effectiveness of intercrop breeding with and  
495 without the application of genomic selection for finger millet and the accompanying legume  
496 crop of groundnut (*Arachis hypogaea*) (Fig. 5). These crops are grown together in East Africa  
497 within low input smallholder production systems that can benefit significantly from  
498 exploiting crop-crop synergies (Yu *et al.*, 2015). Better varietal combinations of finger millet  
499 and groundnut could support higher yielding, more stable and more sustainable agricultural  
500 production in the region. The importance of cereal-legume combinations globally means that  
501 our modelling also has broader application.

502

503 Speed breeding, which reduces the generation interval in breeding programmes by altering  
504 the photoperiod exposure of day length sensitive plants to accelerate their development  
505 (normally through prolonging “long-day” plants’ exposure to light; Ghosh *et al.*, 2018), is  
506 another approach now being applied to orphan crops. Application includes to the long-day  
507 annual legume chickpea (*Cicer arietinum*), for which the number of possible generations per  
508 year has been increased from three to six (Watson *et al.*, 2018). Application has also been  
509 successful with “short-day” annual grain amaranth crops (*Amaranthus* spp.; Stetter *et al.*,  
510 2016). Speed breeding should be especially effective in combination with genomic selection

511 as this allows selection during rapid cycling where full phenotypic data are not collected (Li  
512 *et al.*, 2018a). It has been proposed that the costs of the speed breeding approach for new and  
513 orphan crops in low income nations could be reduced through transportable “speed breeding  
514 capsules”, consisting of shipping containers retrofitted with temperature and light controls,  
515 irrigation systems and greenhouse benches (Chiurugwi *et al.*, 2019).

516

#### 517 *Participatory breeding and selection*

518 “Citizen science” projects that evaluate crop germplasm have been conducted successfully in  
519 high income nations, as illustrated by Würschum *et al.* (2019) who explored genotype-  
520 environment interactions in soybean (*Glycine max*) based on data collected by 1,800  
521 gardeners located across Germany. Even higher potential for participatory experimentation  
522 exists in low income nations where rural populations are greater and include many active  
523 small-scale farmers. If properly supported, these communities can meaningfully evaluate  
524 genetic materials within a range of target environments and cropping systems, and provide  
525 further information on crops’ production and consumption.

526

527 In Central Africa, for example, participatory domestication methods have been successfully  
528 applied to genetically improve new and orphan fruit tree crops including the semi-  
529 domesticated safou (*Dacryodes edulis*) and the incipiently domesticated bush mango  
530 (*Irvingia gabonensis* and *I. wombolu*) (Jamnadass *et al.*, 2011). Here, scientific advances in  
531 tree selection, propagation and fruit processing were combined with local communities’  
532 experiences in tree management. Applying simple selection methods and basic vegetative  
533 propagation approaches resulted in significant yield and quality gains from existing wide  
534 gene pools of these fruit trees and the effective fixation of these polygenic traits (Tchoundjeu  
535 *et al.*, 2006). Vegetative propagation also significantly reduced the interval between crop  
536 establishment and production, and produced smaller, easier to harvest, plants, thereby  
537 increasing returns to farmers’ labour. By linking production to processing and market  
538 development, the participatory tree domestication approach has spread in the Central Africa  
539 region (Asaah *et al.*, 2011).

540

541 Participatory approaches have also been applied in the Middle East and North Africa to  
542 cereals, combining centralised and decentralised breeding through the deployment to farmers  
543 of crop germplasm panels assembled by breeders and scientists (Mustafa *et al.*, 2006). The  
544 participatory approach is considered especially useful for the heterogeneous production

545 conditions common in low income nations and when the preference for specific crop traits is  
546 poorly understood (Bhargav & Meena, 2014). Both of these conditions often apply for new  
547 and orphan crops.

548

#### 549 *Environment-based selection*

550 “Landscape genomic” approaches to crop development are particularly relevant for perennial  
551 plants that exist currently mostly as wild populations adapted over many generations to local  
552 abiotic conditions (Bragg *et al.*, 2015). This is because the ‘*in situ*’ decision making that is  
553 involved avoids the considerable time and effort required to evaluate perennial crop  
554 germplasm in formal field trials. In the approach, genomic data collected from plants growing  
555 in natural populations are correlated with environmental variables using statistical methods  
556 that account for underlying adaptively neutral genetic structure caused by genetic drift (Coop  
557 *et al.*, 2010). Established correlations can then, in theory, be used to screen wider germplasm  
558 panels to determine favourable allele compositions for particular production conditions.

559 Comparisons are facilitated by the large number of georeferenced interpolated environmental  
560 data sets now available digitally, including temperature and precipitation profiles (e.g., Fick  
561 & Hijmans, 2017) and soil types (e.g., ISRIC, 2019). In a landscape genomic analysis  
562 covering the native range of barrel medic (*Medicago truncatula*, a legume), for example,  
563 Guerrero *et al.* (2018) made use of soil maps to identify soil environment as a key driver of  
564 adaption, with a high number of SNPs associated with soil variables, including SNPs in  
565 candidate genes involved in nodulation/symbiotic nitrogen fixation.

566

567 If local adaptation can be assumed to have occurred during orphan crop development and  
568 ecogeographic range expansion, the landscape approach can be applied to orphan crop  
569 landraces as well as to new and orphan crops’ wild germplasm. In this case, meta-analysis of  
570 multiple crops’ progenitors and landraces in the same geographic space could provide  
571 comparative insights into mechanisms of natural and human adaptation. Statistical  
572 approaches are now available that combine the results of multi-common garden genome-wide  
573 association studies, which explore the genetic basis of phenotype-trial site interactions, with  
574 wild and/or landrace sample environment-genomic correlations (Lasky *et al.*, 2018). This can  
575 further facilitate an understanding of causal loci for adaptation and help to define appropriate  
576 strategies for new and orphan crops’ range expansions.

577

#### 578 IV.2. Orthologous gene involvement in new and orphan crop trait evolution

579

580 An understanding of the extent to which the evolution of a common phenotype among  
581 existing crops has involved mutations in orthologous gene sequences as opposed to changes  
582 in different genes is of clear practical relevance for new and orphan crop development  
583 (Pickersgill, 2018). Clearly, the greater the extent of orthologous gene involvement in  
584 common trait evolution in past crop domestications, then the more attractive it is to target  
585 change to related gene sequences in new and orphan crops to drive their domestication  
586 forward. Indeed, the important roles of orthologous gene sequences in crops' domestications  
587 have been widely revealed (Martin & Orgogozo, 2013). For example, orthologous sequences  
588 control at least a portion of variation in flowering time (Calixto *et al.*, 2015), plant height (Jia  
589 *et al.*, 2009), grain stickiness (Meyer & Purugganan, 2013), seed size (Tao *et al.*, 2017), seed  
590 dormancy (Wang *et al.*, 2018) and seed and fruit dispersal or retention (Li & Olsen, 2016)  
591 across various crops (see examples in Table 1). As variation for a number of these traits  
592 underlies new and orphan crop development priorities, focusing on relevant gene  
593 orthologues, defined by comparisons with suitable crop exemplars (further addressed in  
594 Section IV.3), is clearly of value.

595

596 As would be expected, in general the more closely related two crops are then the more likely  
597 they are to share the same underlying genes and genetic architectures for in-common  
598 phenotypes (Lenser & Theißen, 2013). However, orthologous genes are involved in  
599 determining common phenotypes even when crops are evolutionarily distant, as is evident  
600 from some of the examples in Table 1 of our current review. For example, allelic variants in  
601 orthologues of the rice *WAXY* gene control starch composition not only in a range of cereals  
602 and pseudo-cereals from Poaceae to Amaranthaceae (see Box 2 in Meyer & Purugganan,  
603 2013), but even in some non-cereal crops (e.g., Wang *et al.*, 2017). On the other hand,  
604 multiple domestications within a single crop species may involve unrelated genes to reach a  
605 common phenotype (Meyer & Purugganan, 2013), illustrating the breadth of possible  
606 mechanisms involved in crop evolution and that assumptions of orthology should be guarded.

607

608 In general, the literature suggests that the genes associated with initial domestication  
609 processes are more in common across crops than the genes associated with diversification  
610 (Lai *et al.*, 2018; though see discussion in Pickersgill, 2018). This would suggest that the  
611 exploitation of crop-crop orthologous gene relationships could be more beneficial when  
612 domesticating entirely new crops (*de novo* domesticates) rather than when further developing

613 orphan crops that have already passed through initial domestication barriers. Importantly,  
614 however, even if in many cases crops' common phenotypes were reached via alterations in  
615 unrelated genes in past domestications, this does not preclude the targeting of orthologous  
616 sequences in the further domestication of orphan crops, as a transgressive approach from  
617 previous domestication pathways may still prove effective and could be more efficient  
618 (Lenser & Theißen, 2013). Indeed, the use of advanced molecular breeding methods such as  
619 gene editing to effect changes in domestication-related gene orthologues has been shown to  
620 be effective for orphan crops in some circumstances: for example, recent research on the  
621 solanaceous orphan crop groundcherry (*Physalis pruinosa*) using CRISPR/Cas9 to mutate  
622 orthologues of tomato domestication and improvement genes has shown promise  
623 (Lemmon *et al.*, 2018).

624

625 Clearly, the effectiveness of different breeding approaches will depend on the varying  
626 underlying basis of traits' evolution (Østerberg *et al.*, 2017). Applying knockout  
627 CRISPR/Cas9 gene editing to new and orphan crop gene orthologues of known cross-crop,  
628 large effect, initial 'domestication' genes, for which change has often been associated with  
629 loss-of-function mutations, seems advisable. In contrast, application to smaller effect  
630 'optimisation' or 'diversification' genes, where a less clear orthology exists and where  
631 change has more often been associated with gains in function, seems less advisable. The  
632 reduction or removal of anti-nutrients via CRISPR/Cas9 or other mutational (e.g., TILLING)  
633 disruption of dedicated orthologous genes in conserved metabolic pathways (e.g., Emmrich,  
634 2017) could also be particularly effective.

635

#### 636 IV.3. Identifying exemplar crops to inform new and orphan crop domestication pathways

637

638 To determine appropriate genetic improvement pathways for new and orphan crops the  
639 development routes of more widely researched crops should be considered. If orthologous  
640 approaches to improvement are to be best exploited, identifying a given new or orphan crop's  
641 most relevant more widely studied exemplar requires considering the genetic relatedness of  
642 crop pairs. The definition of exemplars also requires consideration of crops' biologies. To  
643 illustrate how appropriate exemplars may be identified on the basis of genetic relatedness and  
644 crop biology, we have compared a group of exemplar-requiring new and orphan crops with a  
645 panel of possible crop models using taxonomy as a proxy for genetic relatedness (as  
646 described in Supporting Information 3; raw data for analysis provided in Supporting

647 Information Table 1). In our analysis, possible exemplars include major crops and new and  
648 orphan crops chosen based on the availability of crop production, trade and food balance data  
649 in FAOSTAT (2019) databases. These data provide some contextual understanding of recent  
650 crop development (e.g., see Fig. 3). The exemplars chosen also represent a range of  
651 production biologies, including perenniality and vegetative propagation. In our comparison,  
652 the exemplar-requiring new and orphan crops we chose are all considered important for  
653 supporting human nutrition in Africa. The results of our analysis, illustrated in Figure 6  
654 (detailed results provided in Supporting Information Table 1), revealed promising pairings  
655 between exemplar-requiring and exemplar crops that were not always intuitive. In addition,  
656 depending on the relative emphasis given to biology and taxonomy in the analysis (adjusting  
657 from a 1:1 biology:taxonomy weighting to 2:1 or 1:2 weightings when calculating paired  
658 crop distances), some change in pairings was evident.

659

660 Greater insights into new and orphan crop genomes are emerging from current sequencing  
661 efforts. As only one example, the African Orphan Crops Consortium is assembling genomes  
662 and resequencing representative germplasm panels for 101 new and orphan crops (AOCC,  
663 2019). These plants represent a prioritised list of exotic and indigenous species to Africa that  
664 are important for meeting human nutritional needs and providing other services that support  
665 farmers' livelihoods on the continent. These other services include those that are not directly  
666 provisioning, such as environmental services, where crop interactions with each other and  
667 with other biotic components of farm landscapes are important. With such sequencing efforts  
668 underway, it is possible to focus more intently on questions of genetic relatedness in efforts to  
669 identify new exemplar crops that have the potential to support transgressive, orthologue-  
670 based approaches to domestication.

671

## 672 **V. Future outlook**

673

674 Comparative research on crops along a domestication continuum allows the value of different  
675 genetic improvement approaches to be determined (Fig. 1). Should more focus, for example,  
676 be placed on environmentally-based *in situ* selection strategies for wild relatives and  
677 progenitors of major crops? And how much more effort should be given to develop *ex situ*  
678 collections of potential new crops, in order to apply advanced and/or conventional breeding  
679 approaches to them? In particular, it is evident that the central bridging positioning of orphan  
680 crops provides unique opportunities for investigating genetic improvement approaches that

681 both support *de novo* domestications and major crop ‘rewildings’ (*sensu* Palmgren *et al.*,  
682 2015). In the case of new domestications, for example, it is important to understand how  
683 effectively crop development can be driven by the knockout of candidate domestication-  
684 related genes, using modern gene editing technologies (Østerberg *et al.*, 2017). If a  
685 comparison of the gene sequences of an orphan crop’s widely prevalent extant wild  
686 progenitors and farmed semi-domesticates indicates that the latter’s development was based  
687 on loss-of-function mutations of fundamental domestication genes, a knockout approach to  
688 domestication could be successfully applied to the wide extant wild germplasm base of  
689 (putative) new crops and could, if desired, be first further practically tested on orphan crops.  
690

691 Further practical testing of the above approach would in addition reveal if there is merit in the  
692 ‘redomestication’ of major crops from their wild relatives and progenitors as a strategy for  
693 efficiently accessing wild gene pools for traits lost in the development of advanced cultivars  
694 but now considered beneficial for addressing agriculture’s sustainability challenges  
695 (Langridge & Waugh, 2019). Recent research using CRISPR/Cas9 gene editing of target  
696 domestication-related genes has shown promise for redomestications, with domesticated  
697 phenotypes that retain important wild attributes achievable starting from crop wild  
698 progenitors in the case of tomato (Li *et al.*, 2018b; Zsögön *et al.*, 2018). It is known that wild  
699 relatives, progenitors and landraces of a number of major crops contain more variation in  
700 traits related to resource use efficiency and a plant’s ability to interact positively with other  
701 crops and non-crop biotic components in complex production systems than do narrowly-  
702 diverse advanced cultivars developed for monoculture (Kapulnik & Kushnir, 1991; Mutch &  
703 Young, 2004; Martín-Robles *et al.*, 2018). Rewilding major crops for these traits (Palmgren  
704 *et al.* 2015), sampling variation at relevant gene sequences whose identification is supported  
705 by new and orphan crop analysis (Jacob *et al.*, 2018), could then be an effective approach for  
706 sustainably intensifying farming, especially when crop interactions are specifically  
707 considered in breeding (Litrice & Violle, 2015). At the same time, ensuring that these once-  
708 cryptic sustainability features are maintained in new and orphan crops as their domestication  
709 either begins or intensifies is clearly important for ensuring more holistic farming system  
710 improvement outcomes (Dawson *et al.*, 2019a).

711

## 712 **Acknowledgements**

713

714 Our thanks to the many colleagues with whom we have had discussions on new and orphan  
715 crop development. SRUC authors of this review gratefully acknowledge Global Challenge  
716 Research Funding on orphan crops (project BB/P022537/1: Formulating Value Chains for  
717 Orphan Crops in Africa, 2017-2019, Foundation Award for Global Agriculture and Food  
718 Systems). World Agroforestry (ICRAF) authors gratefully acknowledge the support of the  
719 CGIAR's funding partners for their work (<https://www.cgiar.org/funders/>).

720

721



722 **References**

723

724 **Alonso C, Ramos-Cruz D, Becker C. 2019.** The role of plant epigenetics in biotic  
725 interactions. *New Phytologist* **221**: 731-737.

726

727 **AOCC. 2019.** *The African Orphan Crops Consortium*. [WWW site] URL

728 <http://africanorphancrops.org/> [accessed 10 January 2019].

729

730 **Asaah EK, Tchoundjeu Z, Leakey RRB, Takou sting B, Njong J, Edang I. 2011.** Trees,  
731 agroforestry and multifunctional agriculture in Cameroon. *International Journal of*  
732 *Agricultural Sustainability* **9**: 110-119.

733

734 **Asano K, Takashi T, Miura K, Qian Q, Kitano H, Matsuoka M, Ashikari M. 2007.**

735 Genetic and molecular analysis of utility of *sd1* alleles in rice breeding. *Breeding Science* **57**:  
736 53-58.

737

738 **Azzi L, Deluche C, Gévaudant F, Frangne N, Delmas F, Hernould M, Chevalier C. 2015.**  
739 Fruit growth-related genes in tomato. *Journal of Experimental Botany* **66**: 1075-1086.

740

741 **Bakare AH, Osundahunsi OF, Olusanya JO. 2016.** Rheological, baking, and sensory  
742 properties of composite bread dough with breadfruit (*Artocarpus communis* Forst) and wheat  
743 flours. *Food Science & Nutrition* **4**: 573-587.

744

745 **Ballaré CL, Pierik R. 2017.** The shade-avoidance syndrome: multiple signals and ecological  
746 consequences. *Plant, Cell & Environment* **40**: 2530-2543.

747

748 **Balmer M. 2007.** Energy poverty and cooking energy requirements: the forgotten issue in  
749 South African energy policy? *Journal of Energy in Southern Africa* **18**: 4-9.

750

751 **Bergonzi S, Albani MC. 2011.** Reproductive competence from an annual and a perennial  
752 perspective. *Journal of Experimental Botany* **62**: 4415-4422.

753

754 **Bhargav DK, Meena HP. 2014.** Participatory plant breeding: farmers as breeders. *Popular*  
755 *Kheti* **2**: 7-14.

756

757 **Bragg JG, Supple MA, Andrew RL, Borevitz JO. 2015.** Genomic variation across  
758 landscapes: insights and applications. *New Phytologist* **207**: 953-967.

759

760 **Brooker RW, Bennett AE, Cong W-F, Daniell TJ, George TS, Hallett PD, Hawes C,**  
761 **Iannetta PPM, Jones HG, Karley AJ et al. 2015.** Improving intercropping: a synthesis of  
762 research in agronomy, plant physiology and ecology. *New Phytologist* **206**: 107-117.

763

764 **Bustos-Korts D, Dawson IK, Russell J, Tondelli A, Guerra D, Ferrandi C, Strozzi F,**  
765 **Nicolazzi EL, Molnar-Lang M, Ozkan H et al. 2019.** Exome sequences and multi-  
766 environment field trials elucidate the genetic basis of adaptation in barley. *The Plant Journal*  
767 (in press).

768

769 **Calixto, CPG, Waugh R, Brown JWS. 2015.** Evolutionary relationships among barley and  
770 *Arabidopsis* core circadian clock and clock-associated genes. *Journal of Molecular Evolution*  
771 **80**: 108-119.

772

773 **Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A,**  
774 **Mace GM, Tilman D, Wardle DA et al. 2012.** Biodiversity loss and its impact on humanity.  
775 *Nature* **486**: 59-67.

776

777 **CFF. 2019.** *Crops for the Future. Facilitating the wider use of underutilised crops.* [WWW  
778 site] URL <http://www.cffresearch.org/> [accessed 16 April 2019].

779

780 **Chakrabarti M, Zhang N, Sauvage C, Muños S, Blanca J, Cañizares J, Diez MJ,**  
781 **Schneider R, Mazourek M, McClead J et al. 2013.** A cytochrome P450 regulates a  
782 domestication trait in cultivated tomato. *Proceedings of the National Academy of Sciences*  
783 *USA* **110**: 17125-17130.

784

785 **Chiurugwi T, Kemp S, Powell W, Hickey LT. 2019.** Speed breeding orphan crops.  
786 *Theoretical and Applied Genetics* **132**: 607-616.

787

788 **Cichy KA, Wiesinger JA, Mendoza FA. 2015.** Genetic diversity and genome-wide  
789 association analysis of cooking time in dry bean (*Phaseolus vulgaris* L.). *Theoretical and*  
790 *Applied Genetics* **128**: 1555-1567.  
791

792 **Clay JW. 2004.** *World agriculture and the environment: a commodity-by-commodity guide*  
793 *to impacts and practices.* Washington DC, USA: Island Press.  
794

795 **Clement CR. 2004.** Fruits. In: Prance GT, Nesbitt M, eds. *The cultural history of plants.*  
796 London, UK: Routledge, 77-95.  
797

798 **Comadran J, Kilian B, Russell J, Ramsay L, Stein N, Ganal M, Shaw P, Bayer M,**  
799 **Thomas W, Marshall D et al. 2012.** Natural variation in a homolog of *Antirrhinum*  
800 *CENTRORADIALIS* contributed to spring growth habit and environmental adaptation in  
801 cultivated barley. *Nature Genetics* **44**: 1388-1392.  
802

803 **Coop G, Witonsky D, Di Rienzo A, Pritchard JK. 2010.** Using environmental correlations  
804 to identify loci underlying local adaptation. *Genetics* **185**: 1411-1423.  
805

806 **Crossa J, Pérez-Rodríguez P, Cuevas J, Montesinos-López O, Jarquín D, de los Campos**  
807 **G, Burgueño J, González-Camacho JM, Pérez-Elizalde S, Beyene Y. 2017.** Genomic  
808 selection in plant breeding: methods, models, and perspectives. *Trends in Plant Science* **22**:  
809 961-975.  
810

811 **Darwin C. 1859.** *On the origin of species by means of natural selection, or the preservation*  
812 *of favoured races in the struggle for life.* London, UK: John Murray.  
813

814 **Dawson IK, Hendre P, Powell W, Sila D, McMullin S, Simons T, Revoredo-Giha C,**  
815 **Odeny DA, Barnes AP, Graudal L et al. 2018.** *Supporting human nutrition in Africa*  
816 *through the integration of new and orphan crops into food systems: placing the work of the*  
817 *African Orphan Crops Consortium in context.* ICRAF Working Paper No. 276. Nairobi,  
818 Kenya: The World Agroforestry Centre.  
819

820 **Dawson IK, Park SE, Attwood SJ, Jamnadass R, Powell W, Sunderland T, Carsan S.**  
821 **2019a.** Contributions of biodiversity to the sustainable intensification of food production.  
822 *Global Food Security* (under review).  
823

824 **Denison RF, Kiers ET, West SA. 2003.** Darwinian agriculture: when can humans find  
825 solutions beyond the reach of natural selection? *The Quarterly Review of Biology* **78**: 145-  
826 168.  
827

828 **Doebley J, Stec A, Hubbard L. 1997.** The evolution of apical dominance in maize. *Nature*  
829 **386**: 485-488.  
830

831 **Druet T, Macleod IM, Hayes BJ. 2014.** Toward genomic prediction from whole-genome  
832 sequence data: impact of sequencing design on genotype imputation and accuracy of  
833 predictions. *Heredity* **112**: 39-47.  
834

835 **Economist. 2017.** *No crop left behind: improving the plants that Africans eat and breeders*  
836 *neglect*. The Economist. [WWW document] URL [http://www.economist.com/news/science-and-](http://www.economist.com/news/science-and-technology/21731614-nutrition-and-genetics-africa-improving-plants-africans-eat-and)  
837 [technology/21731614-nutrition-and-genetics-africa-improving-plants-africans-eat-and](http://www.economist.com/news/science-and-technology/21731614-nutrition-and-genetics-africa-improving-plants-africans-eat-and) [accessed 5  
838 December 2018].  
839

840 **Emmrich PMF. 2017.** Genetic improvement of grass pea (*Lathyrus sativus*) for low  $\beta$ -L-  
841 ODAP content. PhD thesis. Norwich, UK: John Innes Centre.  
842

843 **FAOSTAT. 2019.** *Food and Agriculture Organization of the United Nations Statistics*  
844 *Division portal*. [WWW site] URL <http://faostat3.fao.org/> [accessed 15 January 2019].  
845

846 **Fick SE, Hijmans RJ. 2017.** WorldClim 2: new 1-km spatial resolution climate surfaces for  
847 global land areas. *International Journal of Climatology* **37**: 4302-4315.  
848

849 **Foster J, Kim HU, Nakata PA, Browse J. 2012.** A previously unknown oxalyl-CoA  
850 synthetase is important for oxalate catabolism in *Arabidopsis*. *The Plant Cell* **24**: 1217-1229.  
851

852 **Francis CA, Smith ME. 1985.** Variety development for multiple cropping systems. *Critical*  
853 *Reviews in Plant Sciences* **3**: 133-168.

854

855 **Frary A, Nesbitt TC, Grandillo S, Knaap E, Cong B, Liu J, Meller J, Elber R, Alpert**  
856 **KB, Tanksley SD. 2000.** *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit  
857 size. *Science* **289**: 85-88.

858

859 **Gamuyao R, Chin JH, Pariasca-Tanaka J, Pesaresi P, Catausan S, Dalid C, Slamet-**  
860 **Loedin I, Tecson-Mendoza EM, Wissuwa M, Heuer S. 2012.** The protein kinase Pst11  
861 from traditional rice confers tolerance of phosphorus deficiency. *Nature* **488**: 535-539.

862

863 **Georges M, Charlier C, Hayes B. 2019.** Harnessing genomic information for livestock  
864 improvement. *Nature Reviews Genetics* **20**: 135-156.

865

866 **Ghosh S, Watson A, Gonzalez-Navarro OE, Ramirez-Gonzalez RH, Yanes L, Mendoza-**  
867 **Suárez M, Simmonds J, Wells R, Rayner T, Green P et al. 2018.** Speed breeding in  
868 growth chambers and glasshouses for crop breeding and model plant research. *Nature*  
869 *Protocols* **13**: 2944-2963.

870

871 **Gillespie S, van den Bold M. 2017.** Agriculture, food systems, and nutrition: meeting the  
872 Challenge. *Global Challenges* **1**: Article 1600002. URL  
873 <https://onlinelibrary.wiley.com/doi/epdf/10.1002/gch2.201600002>

874

875 **Gruber K. 2017.** The living library. *Nature* **544**: S8-S10.

876

877 **Goldschmidt EE. 2013.** The evolution of fruit tree productivity: a review. *Economic Botany*  
878 **67**: 51-62.

879

880 **Guerrero J, Andrello M, Burgarella C, Manel S. 2018.** Soil environment is a key driver of  
881 adaptation in *Medicago truncatula*: new insights from landscape genomics. *New Phytologist*  
882 **219**: 378-390.

883

884 **Guseman JM, Webb K, Srinivasan C, Dardick C. 2017.** *DRO1* influences root system  
885 architecture in *Arabidopsis* and *Prunus* species. *The Plant Journal* **89**: 1093-1105.

886

887 **Halewood M, Chiurugwi T, Sackville Hamilton R, Kurtz B, Marden E, Welch E,**  
888 **Michiels F, Mozafari J, Sabran M, Patron N *et al.* 2018.** Plant genetic resources for food  
889 and agriculture: opportunities and challenges emerging from the science and information  
890 technology revolution. *New Phytologist* **217**: 1407-1419.  
891

892 **Hamblin J, Rowell JG, Redden R. 1976.** Selection for mixed cropping. *Euphytica* **25**: 97-  
893 106.  
894

895 **Hayes BJ, Bowman PJ, Chamberlain AC, Verbyla K, Goddard ME. 2009.** Accuracy of  
896 genomic breeding values in multi-breed dairy cattle populations. *Genetics Selection*  
897 *Evolution* **41**: Article 51. URL <https://doi.org/10.1186/1297-9686-41-51>  
898

899 **Hickey JM, Chiurugwi T, Mackay I, Powell W, Eggen A, Kilian A, Jones C, Canales C,**  
900 **Grattapaglia D, Bassi F *et al.* 2017.** Genomic prediction unifies animal and plant breeding  
901 programs to form platforms for biological discovery. *Nature Genetics* **49**: 1297-1303.  
902

903 **Isik F, Kumar S, Martínez-García PJ, Iwata H, Yamamoto T. 2015.** Acceleration of  
904 forest and fruit tree domestication by genomic selection. *Advances in Botanical Research*  
905 **74**: 93-124.  
906

907 **ISRIC. 2019.** *ISRIC – world soil information*. [WWW site] URL <https://www.isric.org/>  
908 [Lasted accessed 14 December 2018].  
909

910 **Iwata H, Minamikawa MF, Kajiye-Kanegae H, Ishimori M, Hayashi T. 2016.** Genomics-  
911 assisted breeding in fruit trees. *Breeding Science* **66**: 100-115.  
912

913 **LATINCROP. 2019.** *LATINCROP. An integrated strategy for the conservation and use of*  
914 *underutilized Latin American agrobiodiversity* [WWW site] URL <http://www.laticrop.org/>  
915 [accessed 16 April 2019].  
916

917 **Lin Z, Li X, Shannon LM, Yeh C-T, Wang ML, Bai G, Peng Z, Li J, Trick HN,**  
918 **Clemente TE *et al.* 2012.** Parallel domestication of the *Shattering1* genes in cereals. *Nature*  
919 *Genetics* **44**: 720-724.  
920

921 **Jacob P, Avni A, Bendahmane A. 2018.** Translational research: exploring and creating  
922 genetic diversity. *Trends in Plant Science* **23**: 42-52.  
923

924 **Jamnadass RH, Dawson IK, Franzel S, Leakey RRB, Mithöfer D, Akinnifesi FK,**  
925 **Tchoundjeu Z. 2011.** Improving livelihoods and nutrition in sub-Saharan Africa through the  
926 promotion of indigenous and exotic fruit production in smallholders' agroforestry systems: a  
927 review. *International Forestry Review* **13**: 338-354.  
928

929 **Jia G, Huang X, Zhi H, Zhao Y, Zhao Q, Li W, Chai Y, Yang L, Liu K, Lu H et al. 2013.**  
930 A haplotype map of genomic variations and genome-wide association studies of agronomic  
931 traits in foxtail millet (*Setaria italica*). *Nature Genetics* **45**: 957-961.  
932

933 **Jia Q, Zhang J, Westcott S, Zhang X-Q, Bellgard M, Lance R, Li C. 2009.** GA-20  
934 oxidase as a candidate for the semidwarf gene *sdw1/denso* in barley. *Functional &*  
935 *Integrative Genomics* **9**: 255-262.  
936

937 **Jones PMB, Boulter D. 1983.** The analysis of development of hardbean during storage of  
938 black beans (*Phaseolus vulgaris L*). *Plant Foods for Human Nutrition* **33**: 77-85.  
939

940 **Kaur B, Ranawana V, Henry J. 2016.** The glycaemic index of rice and rice products: a  
941 review, and table of GI values. *Critical Reviews in Food Science and Nutrition* **56**: 215-236.  
942

943 **Kessides C. 2005.** *The urban transition in Sub-Saharan Africa: implications for economic*  
944 *growth and poverty reduction*. Africa Region, Working Paper Series No. 97. Washington DC,  
945 USA: The World Bank.  
946

947 **Khoury CK, Bjorkman AD, Dempewolf H, Ramirez-Villegas J, Guarino L, Jarvis A,**  
948 **Rieseberg LH, Struik PC. 2014.** Increasing homogeneity in global food supplies and the  
949 implications for food security. *Proceedings of the National Academy of Sciences USA* **111**:  
950 4001-4006.  
951

952 **Khoury CK, Jarvis A. 2014.** *The changing composition of the global diet: implications for*  
953 *CGIAR research*. CIAT Policy Brief No. 18. Cali, Colombia: Centro Internacional de  
954 Agricultura Tropical.

955  
956 **Kotoda N, Iwanami H, Takahashi S, Abe K. 2006.** Antisense expression of *MdTFL1*, a  
957 *TFL1*-like gene, reduces the juvenile phase in apple. *Journal of the American Society for*  
958 *Horticultural Science* **131**: 74-81.  
959  
960 **Lagassé SL, Hatcher DW, Dexter JE, Rossnagel BG, Izydorczyk MS. 2006.** Quality  
961 characteristics of fresh and dried white salted noodles enriched with flour from hull-less  
962 barley genotypes of diverse amylose content. *Cereal Chemistry* **83**: 202-210.  
963  
964 **Lai X, Yan L, Lu Y, Schnable JC. 2018.** Largely unlinked gene sets targeted by selection  
965 for domestication syndrome phenotypes in maize and sorghum. *Plant Journal* **93**: 843-855.  
966  
967 **Langridge P, Waugh R, 2019.** Harnessing the potential of germplasm collections. *Nature*  
968 *Genetics* **51**: 200-201.  
969  
970 **Larson G, Piperno DR, Allaby RG, Purugganan MD, Andersson L, Arroyo-Kalin**  
971 **M, Barton L, Climer Vigueira C, Denham T, Dobney K et al. 2014.** Current perspectives  
972 and the future of domestication studies. *Proceedings of the National Academy of Sciences*  
973 *USA* **111**: 6139-6146.  
974  
975 **Lasky JR, Forester BR, Reimherr M. 2018.** Coherent synthesis of genomic associations  
976 with phenotypes and home environments. *Molecular Ecology Resources* **18**: 91-106.  
977  
978 **Lemmon ZH, Reem NT, Dalrymple J, Soyk S, Swartwood KE, Rodriguez-Leal D, Van**  
979 **Eck J, Lippman ZB. 2018.** Rapid improvement of domestication traits in an orphan crop by  
980 genome editing. *Nature Plants* **4**: 766-770.  
981  
982 **Lenser T, Theißen G. 2013.** Molecular mechanisms involved in convergent crop  
983 domestication. *Trends in Plant Science* **18**: 704-714.  
984  
985 **Li H, Rasheed A, Hickey LT, He Z. 2018a.** Fast-forwarding genetic gain. *Trends in Plant*  
986 *Science* **23**: 184-186.  
987



988 **Li L-F, Olsen KM. 2016.** To have and to hold: selection for seed and fruit retention during  
989 crop domestication. *Current Topics in Developmental Biology* **119**: 63-109.  
990

991 **Li T, Yang X, Yu Y, Si X, Zhai X, Zhang H, Dong W, Gao C, Xu C. 2018b.**  
992 Domestication of wild tomato is accelerated by genome editing. *Nature Biotechnology*  
993 **36**: 1160-1163.  
994

995 **Litrice I, Violle C. 2015.** Diversity in plant breeding: a new conceptual framework. *Trends*  
996 *in Plant Science* **20**: 604-613.  
997

998 **Liu H-J, Yan J. 2019.** Crop genome-wide association study: a harvest of biological  
999 relevance. *The Plant Journal* **97**: 8-18.  
1000

1001 **MacLeod IM, Bowman PJ, Vander Jagt CJ, Haile-Mariam M, Kemper KE,**  
1002 **Chamberlain AJ, Schrooten C, Hayes BJ, Goddard ME. 2016.** Exploiting biological  
1003 priors and sequence variants enhances QTL discovery and genomic prediction of complex  
1004 traits. *BMC Genomics* **17**: Article 144. URL <https://doi.org/10.1186/s12864-016-2443-6>  
1005

1006 **Mai CD, Phung NTP, To HTM, Gonin M, Hoang GT, Nguyen KL, Do VN, Courtois B,**  
1007 **Gantel P. 2014.** Genes controlling root development in rice. *Rice* **7**: Article 30. URL  
1008 <https://doi.org/10.1186/s12284-014-0030-5>  
1009

1010 **Martin A, Orgogozo V. 2013.** The loci of repeated evolution: a catalog of genetic hotspots  
1011 of phenotypic variation. *Evolution* **67**: 1235-1250.  
1012

1013 **Martín-Robles N, Lehmann A, Seco E, Aroca R, Rillig MC, Milla R. 2018.** Impacts of  
1014 domestication on the arbuscular mycorrhizal symbiosis of 27 crop species. *New Phytologist*  
1015 **218**: 322-334.  
1016

1017 **Meuwissen TH, Hayes BJ, Goddard ME. 2001.** Prediction of total genetic value using  
1018 genome-wide dense marker maps. *Genetics* **157**: 1819-1829.  
1019

1020 **Meyer RS, DuVal AE, Jensen HR. 2012.** Patterns and processes in crop domestication: an  
1021 historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196:**  
1022 29-48.  
1023

1024 **Meyer RS, Purugganan MD. 2013.** Evolution of crop species: genetics of domestication  
1025 and diversification. *Nature Reviews Genetics* **14:** 840-852.  
1026

1027 **Migicovsky Z, Myles S. 2017.** Exploiting wild relatives for genomics-assisted breeding of  
1028 perennial crops. *Frontiers in Plant Science* **8:** Article 460. URL  
1029 <https://doi.org/10.3389/fpls.2017.00460>  
1030

1031 **Miller AJ, Gross BL. 2011.** From forest to field: perennial fruit crop domestication.  
1032 *American Journal of Botany* **98:** 1389-1414.  
1033

1034 **Mustafa MA, Mayes S, Massawe F. 2019.** Crop diversification through a wider use of  
1035 underutilised crops: a strategy to ensure food and nutrition security in the face of climate  
1036 change. In: Sarkar A, Sensarma SR, vanLoon GW, eds. *Sustainable solutions for food*  
1037 *security: combating climate change by adaptation*. Springer Nature Switzerland AG, Cham,  
1038 Switzerland, 125-149.  
1039

1040 **Mustafa Y, Grando S, Ceccarelli S. 2006.** *Assessing the benefits and costs of participatory*  
1041 *and conventional barley breeding programs in Syria*. Aleppo, Syria: The International Center  
1042 for Agricultural Research in the Dry Areas.  
1043

1044 **Nakamichi N. 2015.** Adaptation to the local environment by modifications of the  
1045 photoperiod response in crops. *Plant Cell Physiology* **56:** 594-604.  
1046

1047 **Nour-Eldin HH, Andersen TG, Burow M, Madsen SR, Jørgensen ME, Olsen CE,**  
1048 **Dreyer I, Hedrich R, Geiger D, Halkier BA. 2012.** NRT/PTR transporters are essential for  
1049 translocation of glucosinolates defence compounds to seeds. *Nature* **488:** 531-534.  
1050

1051 **Nour-Eldin HH, Halkier BA. 2013.** The emerging field of transport engineering of plant  
1052 specialized metabolites. *Current Opinion in Biotechnology* **24:** 263-270.  
1053

1054 **Palmgren MG, Edenbrandt AK, Vedel SE, Andersen MM, Landes X, Østerberg JT,**  
1055 **Falhof J, Olsen LI, Christensen SB, Sandøe P et al. 2015.** Are we ready for back-to-nature  
1056 crop breeding? *Trends in Plant Science* **20**: 155-164.  
1057

1058 **Panzeri D, Cassani E, Doria E, Tagliabue G, Forti L, Campion B, Bollini R, Brearley**  
1059 **CA, Pilu R, Nielsen E et al. 2011.** A defective ABC transporter of the MRP family,  
1060 responsible for the bean *lpa1* mutation, affects the regulation of the phytic acid pathway,  
1061 reduces seed *myo*-inositol and alters ABA sensitivity. *New Phytologist* **191**: 70-83.  
1062

1063 **Petry N, Boy E, Wirth JP, Hurrell RF. 2015.** The potential of the common bean (*Phaseolus*  
1064 *vulgaris*) as a vehicle for iron biofortification, *Nutrients* **7**: 1144-1173.  
1065

1066 **Petry N, Egli I, Campion B, Nielsen E, Hurrell R. 2013.** Genetic reduction of phytate in  
1067 common bean (*Phaseolus vulgaris* L.) seeds increases iron absorption in young women. *The*  
1068 *Journal of Nutrition* **143**: 1219-1224.  
1069

1070 **Pickersgill B. 2018.** Parallel vs. convergent evolution in domestication and diversification of  
1071 crops in the Americas. *Frontiers in Ecology and Evolution* **6**: Article 56. URL  
1072 <https://doi.org/10.3389/fevo.2018.00056>  
1073

1074 **Popkin BM, Adair LS, Ng SW. 2012.** Now and then: the global nutrition transition: the  
1075 pandemic of obesity in developing countries. *Nutrition Reviews* **70**: 3-21.  
1076

1077 **Østerberg JT, Xiang W, Olsen LI, Edenbrandt AK, Vedel SE, Christiansen A, Landes**  
1078 **X, Andersen MM, Pagh P, Sandøe P et al. 2017.** Accelerating the domestication of new  
1079 crops: feasibility and approaches. *Trends in Plant Science* **22**: 373-384.  
1080

1081 **Remigereau M-S, Lakis G, Rekima S, Leveugle M, Fontaine MC, Langin T, Sarr A,**  
1082 **Robert T. 2011.** Cereal domestication and evolution of branching: evidence for soft selection  
1083 in the *Tb1* orthologue of pearl millet (*Pennisetum glaucum* [L.] R. Br.). *PLoS ONE* **6**:  
1084 e22404. URL <https://doi.org/10.1371/journal.pone.0022404>  
1085

1086 **Russell J, Mascher M, Dawson IK, Kyriakidis S, Calixto C, Freund F, Bayer M, Milne**  
1087 **I, Marshall-Griffiths T, Heinen S et al. 2016.** Adaptation of barley to different

1088 environments revealed in the exomes of a range-wide collection of landraces and wild  
1089 relatives. *Nature Genetics* **48**: 1024-1030.

1090

1091 **Schilling S, Pan S, Kennedy A, Melzer R. 2018.** MADS-box genes and crop domestication:  
1092 the jack of all traits. *Journal of Experimental Botany* **69**: 1447-1469.

1093

1094 **Schippmann U, Leaman DJ, Cunningham AB. 2002.** The impact of cultivation and  
1095 gathering of medicinal plants on biodiversity: global trends and issues. In: *Biodiversity and*  
1096 *the ecosystem approach in agriculture, forestry and fisheries. Satellite event on the occasion*  
1097 *of the Ninth Regular Session of the Commission on Genetic Resources for Food and*  
1098 *Agriculture*. Rome, 12-13 October 2002. Rome, Italy: Food and Agriculture Organization of  
1099 the United Nations, Inter-Departmental Working Group on Biological Diversity for Food and  
1100 Agriculture.

1101

1102 **Sheehan MJ, Kennedy LM, Costich DE, Brutnell TP. 2007.** Subfunctionalization of  
1103 *PhyB1* and *PhyB2* in the control of seedling and mature plant traits in maize. *The Plant*  
1104 *Journal* **49**: 338-353.

1105

1106 **Sousa DO, Carvalho AF, Oliveira JT, Farias DF, Castelar I, Oliveira HP, Vasconcelos**  
1107 **IM. 2015.** Increased levels of antinutritional and/or defense proteins reduced the protein  
1108 quality of a disease-resistant soybean cultivar. *Nutrients* **7**: 6038-6054.

1109

1110 **Stetter MG, Zeitler L, Steinhaus A, Kroener K, Biljecki M, Schmid KJ. 2016.** Crossing  
1111 methods and cultivation conditions for rapid production of segregating populations in three  
1112 grain amaranth species. *Frontiers in Plant Science* **7**: Article 816. URL  
1113 <https://doi.org/10.3389/fpls.2016.00816>

1114

1115 **Studer AJ, Wang H, Doebley JF. 2017.** Selection during maize domestication targeted a  
1116 gene network controlling plant and inflorescence architecture. *Genetics* **207**: 755-765.

1117

1118 **Subrahmaniam HJ, Libourel C, Journet E-P, Morel J-B, Munos S, Niebel A, Raffaele S,**  
1119 **Roux F. 2018.** The genetics underlying natural variation of plant-plant interactions, a beloved  
1120 but forgotten member of the family of biotic interactions. *The Plant Journal* **93**: 747-770.

1121

1122 **Sun-Waterhouse D, Zhao M, Waterhouse GIN. 2014.** Protein modification during  
1123 ingredient preparation and food processing: approaches to improve food processability and  
1124 nutrition. *Food and Bioprocess Technology* **7**: 1853-1893.  
1125

1126 **Tadele Z. 2017.** Raising crop productivity in Africa through intensification. *Agronomy* **7**:  
1127 Article 22. URL <https://doi.org/10.3390/agronomy7010022>  
1128

1129 **Taketa S, Amano S, Tsujino Y, Sato T, Saisho D, Kakeda K, Nomura M, Suzuki T,**  
1130 **Matsumoto T, Sato K et al. 2008.** Barley grain with adhering hulls is controlled by an ERF  
1131 family transcription factor gene regulating a lipid biosynthesis pathway. *Proceedings of the*  
1132 *National Academy of Sciences USA* **105**: 4062-4067.  
1133

1134 **Tao Y, Mace ES, Tai S, Cruickshank A, Campbell BC, Zhao X, Van Oosterom EJ,**  
1135 **Godwin ID, Botella JR, Jordan DR. 2017.** Whole-genome analysis of candidate genes  
1136 associated with seed size and weight in *Sorghum bicolor* reveals signatures of artificial  
1137 selection and insights into parallel domestication in cereal crops. *Frontiers in Plant Science*  
1138 **8**: Article 1237. URL <https://doi.org/10.3389/fpls.2017.01237>  
1139

1140 **Tchoundjeu Z, Asaah E, Anegbeh PO, Degrande A, Mbile P, Facheux C, Tsobeng A,**  
1141 **Atangana AR, Ngo-Mpeck ML, Simons AJ. 2006.** Putting participatory domestication into  
1142 practice in West and Central Africa. *Forests, Trees and Livelihoods* **16**: 53-69.  
1143

1144 **Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005.** The pseudo-response  
1145 regulator *Ppd-H1* provides adaptation to photoperiod in barley. *Science* **310**: 1031-1034.  
1146

1147 **Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K,**  
1148 **Kanno N et al. 2013.** Control of root system architecture by *DEEPER ROOTING 1* increases  
1149 rice yield under drought conditions. *Nature Genetics* **45**: 1097-1102.  
1150

1151 **UN. 2019.** *United Nations Sustainable Development Goals*. United Nations. [WWW site]  
1152 URL <https://sustainabledevelopment.un.org/> [accessed 15 January 2019].  
1153

1154 **van der Knaap E, Chakrabarti M, Chu YH, Clevenger JP, Illa-Berenguer E, Huang Z,**  
1155 **Keyhaninejad N, Mu Q, Sun L, Wang Y et al. 2014.** What lies beyond the eye: the

1156 molecular mechanisms regulating tomato fruit weight and shape. *Frontiers in Plant Science*  
1157 **5**: Article 227. URL <https://doi.org/10.3389/fpls.2014.00227>  
1158

1159 **Vandermeer J. 1992.** The ecology of intercropping. Cambridge, UK: Cambridge University  
1160 Press.  
1161

1162 **Varshney RK, Ribaut J-M, Buckler ES, Tuberosa R, Rafalski JA, Langridge P. 2012.**  
1163 Can genomics boost productivity of orphan crops? *Nature Biotechnology* **30**: 1172-1176.  
1164

1165 **Varshney RK, Saxena RK, Upadhyaya HD, Khan AW, Yu Y, Kim C, Rathore A, Kim**  
1166 **D, Kim J, An S et al. 2017.** Whole-genome resequencing of pigeonpea accessions identifies  
1167 genomic regions associated with domestication and agronomic traits. *Nature Genetics* **49**:  
1168 1082-1088.  
1169

1170 **von Grebmer K, Saltzman A, Birol E, Wiesmann D, Prasai N, Yin S, Yohannes Y,**  
1171 **Menon P, Thompson J, Sonntag A. 2014.** *2014 Global hunger index: the challenge of*  
1172 *hidden hunger*. Bonn, Germany: Deutsche Welthungerhilfe, with Washington DC, USA:  
1173 International Food Policy Research Institute; and Dublin, Ireland: Concern Worldwide.  
1174

1175 **Walker T, Alene A, Ndjeunga J, Labarta R, Yigezu Y, Diagne A, Andrade R, Muthoni**  
1176 **Andriatsitohaina R, De Groote H, Mausch K et al. 2014.** *Measuring the effectiveness of*  
1177 *crop improvement research in sub-Saharan Africa from the perspectives of varietal output,*  
1178 *adoption, and change: 20 crops, 30 countries, and 1150 cultivars in farmers' fields*. Report  
1179 of the Standing Panel on Impact Assessment. Rome, Italy: CGIAR Independent Science and  
1180 Partnership Council Secretariat.  
1181

1182 **Wang M, Li W, Fang C, Xu F, Liu Y, Wang Z, Yang R, Zhang M, Liu S, Lu S et al.**  
1183 **2018.** Parallel selection on a dormancy gene during domestication of crops from multiple  
1184 families. *Nature Genetics* **50**: 1435-1441.  
1185

1186 **Wang Y, Li Y, Zhang H, Zhai H, Liu Q, He S. 2017.** A soluble starch synthase I gene,  
1187 *IbSSI*, alters the content, composition, granule size and structure of starch in transgenic sweet  
1188 potato. *Nature Scientific Reports* **7**: Article 2315. URL [www.nature.com/articles/s41598-017-](http://www.nature.com/articles/s41598-017-02481-x)  
1189 02481-x

1190  
1191 **Wang Z-Y, Zheng F-Q, Shen G-Z, Gao J-P, Snustad DP, Li M-G, Zhang J-L, Hong M-**  
1192 **M. 1995.** The amylose content in rice endosperm is related to the post-transcriptional  
1193 regulation of the *waxy* gene. *The Plant Journal* **7**: 613-622.  
1194  
1195 **Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey M-D, Md Hatta MA,**  
1196 **Hinchliffe A, Steed A, Reynolds D et al. 2018.** Speed breeding is a powerful tool to  
1197 accelerate crop research and breeding. *Nature Plants* **4**: 23-29.  
1198  
1199 **Weltzien E, Christinck A. 2017.** Participatory breeding: developing improved and relevant  
1200 crop varieties with farmers. In: Snapp S, Pound B, eds. *Agricultural systems: agroecology*  
1201 *and rural innovation for development*. 2nd edition. Cambridge, Massachusetts, USA:  
1202 Academic Press, 259-301.  
1203  
1204 **Willett W, Rockström J, Loken B, Springmann M, Lang T, Vermeulen S, Garnett T,**  
1205 **Tilman D, DeClerck F, Wood A et al. 2019.** Food in the Anthropocene: the EAT–  
1206 *Lancet* Commission on healthy diets from sustainable food systems. *The Lancet* **393**: 447-  
1207 492.  
1208  
1209 **Wolfe MD, Del Carpio DP, Alabi O, Ezenwaka LC, Ikeogu UN, Kayondo IS, Lozano R,**  
1210 **Okeke UG, Ozimati AA, Williams E et al. 2017.** Prospects for genomic selection in cassava  
1211 breeding. *Plant Genome* **10**: Article 0015. URL  
1212 <https://dl.sciencesocieties.org/publications/tpg/abstracts/10/3/plantgenome2017.03.0015>  
1213  
1214 **Wright AJ. 1985.** Selection for improved yield in inter-specific mixtures or intercrops.  
1215 *Theoretical and Applied Genetics* **69**: 399-407.  
1216  
1217 **Würschum T, Leiser WL, Jähne F, Bachteler K, Miersch M, Hahn V. 2019.** The soybean  
1218 experiment ‘1000 Gardens’: a case study of citizen science for research, education, and  
1219 beyond. *Theoretical and Applied Genetics* **132**: 617-626.  
1220  
1221 **Yamagishi N, Kishigami R, Yoshikawa N. 2014.** Reduced generation time of apple  
1222 seedlings to within a year by means of a plant virus vector: a new plant-breeding technique

1223 with no transmission of genetic modification to the next generation. *Plant Biotechnology*  
1224 *Journal* **12**: 60-68.

1225

1226 **Yerra S, Putta S, Kilari EK. 2015.** Detoxification of ODAP in *Lathyrus sativus* by various  
1227 food processing techniques. *Pharmaceutical and Biological Evaluations* **2**: 152-159.

1228

1229 **Yu Y, Stomph T-J, Makowski D, van der Werf W. 2015.** Temporal niche differentiation  
1230 increases the land equivalent ratio of annual intercrops: a meta-analysis. *Field Crops*  
1231 *Research* **184**: 133-144.

1232

1233 **Zsögön A, Čermák T, Naves ER, Notini MM, Edel KH, Weinl S, Freschi L, Voytas**  
1234 **DF, Kudla J, Peres LEP. 2018.** *De novo* domestication of wild tomato using genome  
1235 editing. *Nature Biotechnology* **36**: 1211-1216.

1236

1237



1238 **Supporting Information**

1239

1240 **Supporting Information 1.** Approach for analysing production contributors to changes in  
1241 global crop output.

1242

1243 **Supporting Information 2.** Approach for surveying plant breeders to identify new and  
1244 orphan crop production constraints.

1245

1246 **Supporting Information 3.** Approach for comparing exemplar-requiring new and orphan  
1247 crops with model crops.

1248

1249 **Supporting Information Table 1.** Supporting data for 30 new and orphan crops requiring  
1250 exemplar models and 30 exemplar crops.

1251

1252 **Figure legends**

1253

1254 **Figure 1.** Schematic of the distribution of genetic diversity for new, orphan and major crops,  
1255 with related improvement method options. The distribution of genetic resources (triangles  
1256 and rectangle) varies by the category of plant, with implications for the application of  
1257 different genetic improvement methods. For example, whereas major crops are well  
1258 represented in gene banks globally, new crops are not; but in their case significant genetic  
1259 variation is often still extant in the wild, though sometimes this variation is threatened  
1260 (Dawson *et al.*, 2018). Orphan crops occupy an intermediate position in the distribution of  
1261 genetic resources across location categories and in their position on the domestication  
1262 continuum. This positioning provides unique opportunities for orphan crops in investigating  
1263 the extrapolation domains of a range of crop genetic improvement approaches, for *de novo*  
1264 domestications and major crop ‘rewildings’ (rewilding *sensu* Palmgren *et al.*, 2015: the  
1265 reestablishment of beneficial wild type properties in crops).

1266

1267 **Figure 2.** The diversity of farming systems in which winner and loser crops in the global  
1268 food system are produced, based on data for 20 crops. The relationship between the diversity  
1269 (summarised as intercrop or retained natural diversity; y-axis) of typical production systems  
1270 and the relative change in food importance over the last half century (x-axis) for crops is  
1271 shown. Crops were assigned numeric scores for production system diversity (ranging  
1272 between 0 and 2, where 0 = lowest diversity, typically monoculture production) and change  
1273 in food importance (positive scores = more important, negative scores = less important) by  
1274 Dawson *et al.* (2018), where further information on method can be found. Briefly, in the case  
1275 of food importance, scores were based on the longitudinal trend analysis of Khoury *et al.*  
1276 (2014) of FAOSTAT annual global food supply balance sheets, with crops showing a wide  
1277 range of changes in relative food importance over the last half century being chosen as  
1278 representative samples. Point size represents current global production area, based on a 2009-  
1279 2013 mean (for reference purposes, the actual value for wheat, the crop with the largest  
1280 production area, is 220 million ha). A linear regression indicates a trend toward lower  
1281 diversity systems for increasingly important crops.

1282

1283 **Figure 3.** The relationship between production contributors (yield and total area) and changes  
1284 in global output for 35 crops for the period 1961 to 2013. Our analysis is described in  
1285 Supporting Information 1. Briefly, values on the y-axis are the slope coefficients of linear

1286 regressions of yield (production per unit area) and total production area contributions to crop  
1287 output over the annual time series 1961 to 2013 for each of the 35 crops. Values of  $>$  and  $<$  0  
1288 on the  $y$ -axis indicate relatively greater contributions from yield than total area and vice versa  
1289 to global output over the time series, respectively. Values on the  $x$ -axis are changes in total  
1290 global output over the 1961 to 2013 period. Point size represents current annual global gross  
1291 production value, based on a 2009-2013 mean (for reference purposes, the actual value for  
1292 paddy rice, the crop with the largest value, is 191 billion USD [in constant 2004-2006 USD]).  
1293 As expected, a linear regression indicates an overall negative relationship between increases  
1294 in output and the proportional contribution of yield to output for our crop panel, showing that  
1295 in general crop yields were unable to keep pace with output increases over the last half  
1296 century, in particular when output increases were very large. A group of nine crops where  
1297 yield contributions to changes in output appear markedly low (well below the trend line) are  
1298 encircled (dashed red line). With the exception of apple, these crops are characterised by  
1299 relatively low production values ( $<$  USD 10 billion, compared to the mean for the total crop  
1300 panel of USD 25 billion). Eight of the encircled crops are also perennial. In addition, six are  
1301 (generally) propagated vegetatively under cultivation (cloves, coconut and sunflower being  
1302 the seed-propagated exceptions). In a global context of limited land availability and  
1303 increasing sustainability needs, moving such below-trend crops closer to the trend line may  
1304 be an important measure for diversifying crop production.

1305

1306 **Figure 4.** Results of a survey of new and orphan crop production constraints, based on  
1307 responses given by 53 African plant breeders on 30 specific plants of nutritional importance  
1308 in Sub-Saharan Africa. The survey is described in Supporting Information 2. (a) Priority  
1309 production constraints, classified as genetic/management or input constraints. Crop pest or  
1310 disease attack followed by storage problems were the most mentioned high priority genetic  
1311 and/or management constraints and lack of access to suitable planting material followed by  
1312 lack of crop-specific knowledge the most mentioned priority input constraints. (b) Key traits  
1313 for genetic improvement of new and orphan crops. Pest and disease tolerance or resistance  
1314 followed by yield (*per se*, i.e., independent of other production factors affecting yield, such as  
1315 pest and disease attack) were the traits most mentioned as priorities for improvement (the  
1316 apparent discrepancy between pie charts [a] and [b], where ‘yield’ as a unique feature is  
1317 identified less often in the former case, appears to reflect yield in pie chart [a] being  
1318 subsumed into [improved] ‘planting material’). Improvement in harvestability was the fifth  
1319 most mentioned category. (c) Key agronomic management interventions for new and orphan

1320 crop production. Improvements in planting and/or establishment methods followed by soil  
1321 fertilisation measures were the most mentioned priority interventions. Seasonal timing of  
1322 field activities (such as planting, weeding and harvesting) was the fourth most mentioned  
1323 category for intervention, with the fifth being interventions to diversify production systems.  
1324 (d) Variation in priorities by plant primary food product for specific constraints and  
1325 interventions identified by breeders (letters in parentheses as identified in pie charts [a] to  
1326 [c]). Values are shown as proportions of all responses, by food product category (F = fruit, L  
1327 = leaf, R = root, S = seed; for further information on these findings, see Supporting  
1328 Information 2). (e) Breeders' views of the potential for successful intervention in genetic  
1329 improvement and in adopting new management practices. Here, breeders were asked to rate  
1330 the potential for each of the key traits for genetic improvement or priority management  
1331 interventions they had identified in (b) and (c), respectively, which were given equal weight  
1332 as categories in analysis.

1333

1334 **Figure 5.** Intercrop breeding for finger millet and groundnut improvement. A proposed  
1335 design with three example cycling/selection methods currently being explored via stochastic  
1336 modelling is given: Base = non-genomic selection breeding approach with recurrent selection  
1337 of parents based on their phenotypes at general intercropping ability (GIA) 1 and GIA 2  
1338 stages; GSPYT = genomic selection applied at the monoculture preliminary yield trial (PYT)  
1339 stage to select new parents; and GSDH = genomic selection applied at the doubled haploid  
1340 (DH, homozygous plant) stage to select new parents. Both of the shown example genomic  
1341 selection scenarios currently being tested include advancement of individuals based on their  
1342 genomic estimated breeding values (GEBV) in PYT and GIA 1 stages; in the GSDH  
1343 scenario, this is additionally done in the DH stage. At the GIA 2 stage, only the individuals of  
1344 the respective species with the best overall combining ability are advanced to specific  
1345 intercropping ability (SIA) stage 1. Probe = an outstanding genotype of the alternate species  
1346 used in combined test plots to evaluate intercropping ability.

1347

1348 **Figure 6.** Nearest exemplar crops, based on biologies and taxonomies, for 30 new and orphan  
1349 crops in need of breeding method models. Crops chosen as exemplars are shown on the left  
1350 of the figure and model-requiring new and orphan crops on the right. Connecting lines  
1351 between crop pairs signify the minimum (Gower) distances between each model-requiring  
1352 new or orphan crop and exemplar crops (analysis described in Supporting Information 3; raw  
1353 data and detailed results provided in Supporting Information Table 1). If analysis revealed

1354 more than one exemplar crop equally close to a model-requiring new or orphan crop, then  
1355 multiple pairings are shown. To ease visualisation, the 30 exemplar-requiring new and orphan  
1356 crops we chose are divided into three groups of ten crops, with different coloured connector  
1357 lines indicating minimum distances between crop pairs for each group. Solid connector lines  
1358 represent an initial 1:1 biology:taxonomy weighting in the distance analysis. If there were  
1359 differences in crop pairings when 2:1 or 1:2 biology:taxonomy weightings were subsequently  
1360 applied, these are indicated by dashed connectors. Thirty exemplar crops, five of which were  
1361 new or orphan crops and 25 of which were other crops, were chosen as the panel of  
1362 exemplars because of the availability of production data for these crops in FAOSTAT. These  
1363 exemplars are drawn from the crops (or crop groups) chosen for production trend analysis in  
1364 Figure 3. Additional exemplars not specifically named in Figure 3 represent cases in which  
1365 data were grouped for crops in the earlier figure (pooled reporting), but where component  
1366 crops could be treated separately in current crop-crop comparisons.  
1367

1368 **Table 1.** Illustrative genes for important new- and orphan crop-specific trait categories that  
 1369 may be targets for crop development

Trait category	Examples of relevant genes/pathways
<b><i>Production integration</i></b>	
Plant architecture	<p>Major genes determining plant height are some of the best studied in the crop literature. In barley, for example, mutations in the <i>SEMI-DWARF1 (sdw1)</i> gene encoding the enzyme gibberellin 20-oxidase 3, which is involved in gibberellin biosynthesis, reduce plant stature (Jia <i>et al.</i>, 2009). Mutations in the orthologous gene in rice, <i>SD1</i>, have been crucial in modern semi-dwarf rice variety development, one of the most important crop breeding interventions associated with the Green Revolution (Asano <i>et al.</i>, 2007).</p> <p>Several genes that regulate plant branching architecture have been identified, including <i>TEOSINTE BRANCHED1 (Tb1)</i>, which belongs to the TCP family of transcriptional regulators, in maize (<i>Zea mays</i>) (Studer <i>et al.</i>, 2017). Orthologues include <i>Pgtb1</i> in pearl millet (<i>Pennisetum glaucum</i>) (Remigereau <i>et al.</i>, 2011). The expression of <i>Tb1</i> in maize is higher than in its progenitor (teosinte), conferring reduced branching (Doebley <i>et al.</i>, 1997).</p> <p>Genes determining root architecture in rice include <i>DEEPER ROOTING 1 (DRO1)</i> and <i>PHOSPHORUS-STARVATION TOLERANCE 1 (PSTOL1)</i> (Mai <i>et al.</i>, 2014). <i>DRO1</i>, a member of the IGT gene family, effects the root gravitropic response, via a modulation of epidermal cell elongation. It increases the angle between roots and the horizontal, inducing deeper rooting. The introduction of <i>DRO1</i> into a shallow-rooting rice cultivar enabled the resulting line to avoid drought (Uga <i>et al.</i>, 2013). Orthologues appear to control root development in a range of other plants (Guseman <i>et al.</i>, 2017). The <i>PSTOL1</i> gene, which encodes a receptor-like cytoplasmic kinase, is absent from modern rice varieties. Inserted into modern lines, it enhances early root growth, conferring greater root length and root surface area, and contributing to increased phosphorous uptake (Gamuyao <i>et al.</i>, 2012)</p>
Seasonal phenology	<p>Gene networks controlling flowering are well researched, especially in cereals. In barley, for example, variation at the <i>PHOTOPERIOD-H1 (HvPPD-H1)</i> gene, which encodes a pseudo-response regulator, and at the earliness <i>per se</i> gene <i>CENTRORADIALIS (HvCEN)</i>, which encodes a phosphatidylethanolamine-binding protein, controls the days to heading trait (Russell <i>et al.</i>, 2016). Causal variation at both these genes has been explored (Turner <i>et al.</i>, 2005 and Comadran <i>et al.</i>, 2012, respectively) and the magnitude of the effect of different haplotypes has been determined across multiple environments, allowing genotype-environment interactions to be characterised (Bustos-Korts <i>et al.</i>, 2019)</p>
Light competition	<p><i>PHY</i> genes encoding phytochrome photoreceptors and involved in plant growth regulator biosynthesis are involved in response to plant competition that changes the red to far red light ratio (Ballaré &amp; Pierik, 2017). In maize, <i>PHYB1</i> and <i>PHYB2</i> genes encode phytochromes of the PHYB family that contribute differently to the shade avoidance response (Sheehan <i>et al.</i>, 2007)</p>

### **Product processability**

Anti-nutritional compounds

Biosynthetic and degradation pathways are known in model plants and have been studied in some orphan crops (especially legumes). Changes in single genes are able to influence both absolute level and organ allocation within the plant (Nour-Eldin & Halkier, 2013). Targeting the genes of specialised transport proteins essential for the transport of secondary metabolites, such as orthologues of *ARABIDOPSIS THALIANA GLUCOSINOLATE TRANSPORTER-1 (GTR1)* and *GTR2* that are essential for the transport of glucosinolate defence compounds, could eliminate anti-nutrients from edible plant parts (Nour-Eldin *et al.*, 2012).

In common bean, an ethyl methanesulphonate mutant with significantly lowered phytic acid levels in seeds is affected in an MRP type ABC transporter gene, *Pvmp1*, that is required for phytic acid accumulation and is orthologous to arabidopsis (*Arabidopsis thaliana*) *AtMRP5/AtABCC5* and maize *ZmMRP4* (Panzeri *et al.*, 2011).

In grass pea (*Lathyrus sativus*), the biosynthetic pathway of the neurotoxin  $\beta$ -N-oxaly-L- $\alpha$ ,  $\beta$ -diaminopropanoic acid (ODAP), which is a structural analogue of endogenous glutamate neurotransmitters, is not fully understood. But candidate genes for targeting, including a gene similar to that coding for an oxalyl-CoA synthetase in arabidopsis named *ACYL-ACTIVATING ENZYME3 (AtAAE3)* that could catalyse the penultimate reaction step in the biosynthesis of ODAP (Foster *et al.*, 2012), are currently under evaluation (Emmrich, 2017)

The “cooking time trait”

Genome-wide association scans have identified SNPs associated with cooking time on a number of common bean chromosomes (Pv02, Pv03, and Pv06). Proximate sequences of interest on Pv06 included two similar to arabidopsis *Cation/H(+) Antiporter 3 (AtCHX3)* and *AtCHX4* that transport calcium, a mineral known to influence cooking time for dry beans (Cichy *et al.*, 2015)

Processability traits for food formulation

Variation in the amylose to amylopectin ratio in cereal starches that affects consumer preference-, digestion- and processing-related traits has been identified with mutations at the rice *WAXY* gene *GRANULE BOUND STARCH SYNTHASE I (OsGBSS1)* and at orthologous sequences in a range of grains (Meyer & Purugganan, 2013). Mutations at *WAXY* that affect transcript processing and reduce GBSS activity confer the sticky (waxy) rice phenotype (low amylose to amylopectin ratio) (Wang *et al.*, 1995).

Ease of hull removal is an important physical property of grain that can influence its processability (e.g., ability to mill). In barley, the free-threshing (naked) phenotype is controlled by the *Nud* gene on chromosome 7H that encodes an ethylene response factor (ERF) family transcription factor involved in lipid biosynthesis. Deletion or low expression of the *Nud* gene results in the naked phenotype (Taketa *et al.*, 2008)

### **Labour costs production**

Seed/fruit retention	The loss of seed and fruit dispersal mechanisms, which greatly facilitates harvesting efficiency, are key domestication syndrome traits (Meyer & Purugganan, 2013). Orthology is observed for some genes across crops, such as for <i>Shattering1 (Sh1)</i> , which encodes a YABBY transcription factor that provides shattering resistance in maize, sorghum ( <i>Sorghum bicolor</i> ) and rice. In domesticated sorghum, for example, a range of different types of mutations in <i>SbSh1</i> have led to reduced gene function and a reduction in shattering (Lin <i>et al.</i> , 2012). A wide range of other genes influencing loss of dispersal ability have been identified in various seed and fleshy-fruited crops, and the effects and identities of many other candidate sequences are under consideration (Li & Olsen, 2016)
Fruit size	The genetic control of fruit size has been intensively researched in tomato, where the <i>FRUITWEIGHT2.2 (FW2.2)</i> gene, which codes for a negative regulator of cell proliferation that may function as a metal cation transporter, has an important function, accounting for up to 30% of the difference in fruit weight between domesticated tomato and its wild relatives (Frary <i>et al.</i> , 2000). Variation at orthologues of tomato <i>FW2.2</i> also effect fruit size in a range of other crops (Azzi <i>et al.</i> , 2015). Other tomato fruit-growth-related genes have been identified, including <i>FW3.2 (SIKLUH)</i> that encodes for a cytochrome P450 enzyme which may also play a role in regulating fruit mass in other crops (Chakrabarti <i>et al.</i> , 2013)
Length of juvenile stage (unit time return to labour)	For perennial crops especially, the length of the juvenile phase of the plant is an important factor in determining labour returns. In various perennials, this has been shown to be controlled by orthologues of the arabidopsis <i>TERMINAL FLOWER 1 (AtTFL1)</i> gene that encodes a phosphatidylethanolamine-binding protein which acts as a floral repressor (Bergonzi & Albani, 2011). Transgenic apple ( <i>Malus domestica</i> ) expressing <i>MdTFL1</i> antisense RNA, with reduced <i>MdTFL1</i> function, was shown to exhibit accelerated flowering (Kotoda <i>et al.</i> , 2006). The use of an <i>Apple latent spherical virus</i> vector to simultaneously promote the expression of the arabidopsis <i>FLOWERING LOCUS T</i> gene and silence <i>MdTFL1</i> , through embryo inoculation immediately after germination, resulted in early flowering of the resultant apple seedlings, with the cross-pollination of these early-flowering plants producing fruits with seeds (Yamagishi <i>et al.</i> , 2014).