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Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery

Implementing Genomic Selection in CGIAR Breeding Programs Workshop Participants

Published in:
Nature Genetics

DOI:
[10.1038/ng.3920](https://doi.org/10.1038/ng.3920)

Print publication: 01/01/2017

Document Version
Peer reviewed version

[Link to publication](#)

Citation for published version (APA):

Implementing Genomic Selection in CGIAR Breeding Programs Workshop Participants (2017). Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nature Genetics*, 49(9), 1297 - 1303. <https://doi.org/10.1038/ng.3920>

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1 **Genomic prediction unifies animal and plant breeding programs as platforms**
2 **for biological discovery**

3

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5

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13

14

15 **Abstract**

16 The rate of annual yield increases for major staples must more than double relative to
17 current levels in order to feed a predicted global population of 9 billion by 2050. Controlled
18 hybridization and selective breeding have been used for centuries to adapt plant and
19 animals species for human use. However, achieving higher, sustainable rates of
20 improvement in various species will require renewed genetic interventions and dramatic
21 improvement of agricultural practices. Genomic prediction of breeding values has the
22 potential to improve selection, reduce costs, and provide a platform that unifies breeding
23 approaches, biological discovery, tools and methods. Here we compare and contrast some
24 animal and plant breeding approaches to make a case for bringing the two together by the
25 application of genomic selection. We propose a strategy for the use of genomic selection as
26 a unifying approach to deliver innovative 'step changes' in the rate of genetic gain at scale.

27 **Introduction**

28 The global food price crisis of 2008 highlighted the necessity for innovation in agriculture to
29 address food insecurity in the presence of a changing climate and a growing population.
30 The world population is predicted to reach 9 billion within the next 35 years, requiring a 70-
31 100% increase in food production relative to current levels¹⁻⁴. A burgeoning world
32 population is not the only threat to global food security. Changing life styles, population
33 demographics, competition from subsidized biofuels, deterioration of natural resources,
34 climate change, and dwindling supplies of water will require considerable financial,
35 intellectual and research investment in agriculture, particularly in the developing world^{1,2,4}.
36 Breeding of livestock and crops is one of the key routes through which this increased
37 production, efficiency and sustainability can be delivered.

38 In this Perspective we outline both the opportunities and challenges for the deployment of
39 genomics in breeding programs, drawing attention to the fundamental role that
40 quantitative genetics has played as the intellectual cornerstone of plant and animal
41 breeding for the past century. Access to large scale sequence and phenotype information at
42 unprecedented scales will bring opportunities to unify breeding methods, tools, and
43 technologies across several plant and animal species, which in turn will catalyze the
44 modernization of breeding programs. Furthermore, we postulate that the adoption of these
45 new technologies and approaches at scale will enable breeding programs to be platforms
46 for both the delivery of new products and discovery biology based on genome wide
47 association studies (GWAS) and field validation of novel alleles.

48 **A brief history of plant and animal breeding**

49 Breeding of livestock and crops is as old as agriculture itself. At the heart of all breeding
50 remain such traditional pursuits as designing and analyzing performance trials to rank
51 selection candidates in order of merit, with the aim of maximizing selection gain per unit of
52 resources expended⁵. The history and development of scientific animal and plant breeding
53 can be traced back to contributions of many individuals, but there are a few outstanding

54 contributions, at least from our current scientific perspectives (see Figure 1). These have
55 been extensively reviewed elsewhere and will only be discussed briefly here.

56

57 **Figure 1**

58

59 Despite the conceptual similarities between animal and plant breeding, their theoretical
60 concepts and breeding methods have diverged. This is mainly because of differences in the
61 development and application of new breeding technologies and methods⁵. While the
62 divergence between animal and plant breeding is rather nuanced by species-specific
63 characteristics, e.g. mode of reproduction and number of progeny per reproduction cycle,
64 the two have developed clearly different theoretical concepts, tools and methods. For
65 plants, although breeding can be regarded as starting with domestication, for the vast
66 majority of the past 10,000 years it has consisted of selection only, with no enforced
67 crossing: the sexual mechanism in plants and the need for hybridization has only been
68 generally recognized in the last 250 years⁶. In animals, artificial selection of necessity also
69 involved sex to create progeny and a more structured approach to breeding was adopted
70 earlier with the use of “herd-books” to trace the pedigree of selected animals⁷.

71

72 Following the rediscovery of Mendel’s laws in the early 20th century, plant breeders started
73 selecting and crossing superior individuals, moving on from (in some species at least)
74 developing and maintaining cultivars by (unknowingly) harvesting selfed seed or clonal
75 propagation. The highlights of animal breeding developments over the 20th century have
76 centered on improving exploitation of information from relatives; through selection
77 indices⁸, estimating breeding values as random effects⁹ and statistical methods to estimate
78 these relationships¹⁰. Galton developed the concept of regression (essentially heritability)
79 from which response to selection can be predicted¹¹ and Fisher developed a theory to
80 demonstrate that the mean trait value of polygenic traits can change markedly under
81 selection with only a small change in allele frequencies at individual loci¹².

82

83 Both plant and animal breeders deal with complex traits, but individual mutations with
84 moderate to large effects have been exploited more widely in plant breeding than animal
85 breeding (for example, resistance to yellow (stripe) rust in wheat¹³ and the dwarfing genes
86 in wheat and rice). Most traits in animal breeding, in common with some important plant
87 traits like yield, are typically polygenic. Additionally, plant breeders can usually generate
88 genetically identical individuals or reproducible cultivars and test them in well-designed
89 trials while animal breeders have to rely on unbalanced phenotypic data (usually) from
90 individual animals in different production units. As a result, animal breeders were naturally
91 forced to use complex statistical methods to estimate breeding value whereas plant
92 breeders used well-designed trials to measure phenotype to inform their selection.

93

94 Animal breeders often have to use information from relatives of selection candidates
95 because they have to select for traits that cannot be measured on the candidates
96 themselves (e.g. milk yield in bulls), that have low heritability, or that are measured late in
97 the breeding process. Plant breeders do not generally have the problem of ‘sex-limited’
98 traits and can experimentally increase selection accuracy by growing more plants of the
99 same cultivar. As a result, the merit of a cultivar in a plant breeding program can often be
100 measured to any level of precision that the breeder desires. Reproductive rates and expense
101 make this approach harder for animal breeders to follow. A comparison of typical plant (an
102 inbreeding cereal) and animal breeding approaches is shown in Figure 2.

103

104 **Figure 2**

105

106 Modern quantitative methods, including computer simulation, are pivotal to, and underpin,
107 a host of new technologies and approaches that are of critical importance for the future of
108 plant and animal breeding¹⁴. Many plant breeders view selection as a process of
109 accumulating favorable genes within a single line and use a Mendelian approach to identify
110 and incorporate favorable major genes. In contrast, animal breeders have viewed response
111 to selection as a slow increase in the frequency of favorable alleles in a population,
112 predictable from the ‘breeders’ equation’¹⁵. Animal breeding has therefore deployed a more
113 classical biometrical approach combining phenotype, pedigree and genotype information
114 from records of individuals to build estimates of breeding value to inform selection
115 decisions. Similar approaches are also deployed in outbreeding crops such as maize and
116 forages (e.g. in hybrid breeding¹⁶), though quantitative genetics in plant and animal
117 breeding have developed largely in parallel with difference focuses: for animals on the
118 statistical partition of phenotypic variation in a population into genetic and environmental
119 components, and for plants on the outcome of crosses between two inbred lines¹⁷ with
120 emphasis on identifying “transgressive segregants” with merit exceeding that of the best
121 parent. Furthermore, since the 1980’s plant breeders have utilized various biotechnologies
122 such as transgenics to a much greater degree and perhaps consequently have made much
123 more explicit use of physiology than animal breeders. On the other hand, animal breeders
124 have perhaps more systematically incorporated economics in the definition of their
125 breeding goals than plant breeders. All of this has meant that the fields of plant and animal
126 breeding have diverged somewhat over the decades, leading to inefficiencies, delays in the
127 adoption of technology and a number of missed opportunities.

128

129 The advent of genomic selection has led to the re-emergence of quantitative genetics as a
130 framework for incorporating marker and sequence information to supplement and
131 complement standard phenotype descriptors and pedigree information. Technological
132 changes are now bringing together the biometrical approach of animal breeders and the
133 Mendelian approach of plant breeders. The deployment of modern sequencing methods to
134 identify large numbers of molecular markers, and the emergence of cost-effective high

135 throughput genotyping and phenotyping technologies for crops and animals is not only
136 revolutionizing breeding but offering new incentives for the migration of information and
137 approaches between plant and animal breeding and for the unification of breeding efforts
138 and biological discovery efforts.

139

140 **Genomic selection a unifying theme across species**

141 In 2001 a landmark paper¹⁸, which followed earlier work, notably by Lande and Thompson
142 (1990)¹⁹ Nejati-Javaremi *et al.* (1997)²⁰, ²¹Lynch and Walsh (1998)²², Bernardo (1998)²³,
143 Haley and Vischer (1998)²⁴ (who coined the term ‘genomic selection’), and, Whittaker *et al.*
144 (2000)²¹, anticipated the availability of affordable high-density genomic data and proposed
145 statistical methods that enabled this type of data to be used to increase the accuracy of
146 selection. This method came to be called genomic selection. Subsequent modeling showed
147 that genomic selection could have a large impact on genetic progress²⁵ and the technology
148 was quickly adopted across a range of livestock species. Depending on the biology and
149 economics of particular species and the breeding and production systems in which they
150 reside, genomic selection has had different roles to play. In dairy cattle breeding in
151 advanced economies, genomic selection has largely replaced progeny testing, enabling the
152 generation interval to be shortened from five years to two years with consequent increases
153 in rates of genetic gain. For example, in the Netherlands on-farm production levels
154 increased by 21 index points per year in the seven years prior to the adoption of genomic
155 selection in 2008. Since the adoption of genomic selection, on-farm production levels
156 increased by 34 index points per year, a 60% increase. The generation interval of sires of
157 sires, the key pathway through which genetic gain is achieved in dairy cattle breeding
158 programs, has reduced from ~2,500 days to ~1,250 days²⁶. In pig breeding for commercial
159 production systems, genomic selection has resulted in increased accuracy of selection and a
160 better alignment of selection accuracy with the breeding goal, which has driven a 35%
161 increase in rate of genetic gain in the breeding program that supplies the genetics in 25% of
162 the commercially raised pigs globally (W. Herring, personal communication). In other
163 species, such as extensive beef and sheep, genomic selection has provided the technology
164 leap required to enable scientific breeding programs to be much more effective.

165

166 While genomic selection was adopted rapidly across the advanced livestock sectors and at a
167 somewhat slower pace in international seed houses, the uptake has lagged in public sector
168 plant breeding programs and developing world plant and animal breeding programs. Major
169 international seed companies are routinely using genomic selection and many public sector
170 breeding programs are exploring the technology or partially utilizing it, particularly for
171 clonally propagated long-lived perennials²⁷. The explanations for this lag are complex and
172 include the difference between the skills of a typical field-based plant breeder and the skills
173 required to implement genomic selection, the barrier to entry created by the expense of
174 investing in the computational and recording infrastructure and the genotype and
175 phenotypic data required to effectively implement genomic selection, the complexity of the

176 genomes of many plant species, and the fact that plant and animal breeding have diverged
177 somewhat over the decades and that it takes some time for advances in one field to be
178 translated to the other. On the other hand, some argue that plant breeders can derive some
179 of the expected benefits of genomic selection through other technologies and methods. For
180 example, the application of doubled haploid technology²⁸ can reduce generation time
181 significantly and plant breeders can get more reproducible estimates of phenotype by
182 replicating clones and inbreds across generations and sites.

183

184 Effective implementation of genomic selection is expensive and requires specialist skills,
185 creating large barriers to entry. However, because many of the skills and resources are
186 broadly applicable, interdisciplinary and collaborative networks that bring together breeding
187 programs for different plant species as well as animal species could enable widespread
188 adoption of genomic selection across the many small-scale breeding programs in the
189 developing world. This is because, despite the differences between species (within and
190 between plant and animal kingdoms) in terms of their genomes, breeding mechanisms, etc.,
191 they require similar concepts and tools to enable genomic prediction. Thus, plant and
192 animal breeding will benefit from working together to address questions that are common
193 to the two disciplines, e.g. prediction in structured populations⁵. The cross-fertilization of
194 ideas will develop a critical mass around which more can be done per unit of resource, and
195 help to produce a new cadre of better skilled scientists.

196

197 Additionally, the skills and resources that would be assembled for genomic selection could
198 serve as powerful platforms for biological discovery and for enabling the dissection of the
199 true relationship between genomes and traits, and increasing the frequency of favorable
200 alleles in breeding programs. For example, the major pig, poultry and cattle breeding
201 programs have assembled data sets with several hundreds of thousands or even millions of
202 individuals with dense genomic and phenotypic information, and results in the public
203 domain suggest that international plant breeding organizations have done the same, at least
204 for maize. Regarding developing world agriculture, while the Consortium of International
205 Agricultural Research Centers (CGIAR) works on a number of plant and animal species, it
206 could synergistically combine its resources and expertise (e.g. for pre-breeding,
207 conventional and molecular breeding, and other research and translation activities) by
208 centrally coordinating activities in genomic selection across its network. This will allow the
209 exchange of knowledge and expertise between programs working on different species to
210 develop deeper and more general insights than what is achievable in the individual
211 programs. We believe that quantitative genetics provides an objective framework for doing
212 this and that four different aspects need to be considered: (i) The breeder's equation; (ii)
213 Unification of biotechnology and quantitative genetics; (iii) Integrating plant and animal
214 breeding concepts and approaches; and (iv) Unification of breeding and biological research.

215

216 **The breeder's equation – opportunities for more gain**

217 The optimal design of any breeding program involves harnessing several scientific disciplines
218 including genetics, statistics, computer science, physiology, molecular biology, logistics,
219 economics, and social science. The breeder's equation, originally introduced by Lush¹⁵
220 provides a framework through which the impact of each of these disciplines, their
221 underlying technologies, and choices about how they are used can be evaluated^{22,29}. The
222 equation models the expected change in a trait in response to selection and can be written
223 as $R = \frac{\delta_g \times i \times r}{L}$, where R is the change in trait mean per year, δ_g is the amount of genetic
224 variation within the population; i is the selection intensity, r is the accuracy of the selection,
225 and L is the generation interval.

226
227 Genomic selection directly addresses the four factors that affect the rate of genetic gain in
228 animal and plant breeding³⁰:

- 229 (i) Breeding is faster because breeders can recycle individuals more quickly if
230 selection is based on genomic estimated breeding value (GEBV), which is
231 generally more effective than that based on phenotype.
- 232 (ii) Selection intensity is greater because breeders can select more individuals
233 genotypically than phenotypically: genotyping cost is typically lower than
234 phenotyping cost so more candidates for selection can be evaluated. This is
235 particularly important in plant breeding.
- 236 (iii) GEBV can be more accurate than estimated breeding value based on phenotype
237 and pedigree alone.
- 238 (iv) Genomic selection tools can also make integration of novel genetic material
239 much more efficient³¹ through application of i-iii above in wide-crosses and pre-
240 breeding programs, and through the use of optimal contribution theory driven by
241 genomic information.

242 243 **Unification of biotechnology and quantitative genetics**

244 The application of biotechnology has had a profound effect on plant and animal breeding; in
245 some cases this has been at the expense of quantitative genetics and selection theory⁵.
246 Genomic selection offers an opportunity to build common grounds between biotechnology
247 and quantitative genetics. Quantitative genetics is the study of the genetics of complex
248 traits that are controlled by a large number of loci and often involve non-genetic factors³².
249 Sequencing and resequencing of crop and animal genomes provide the opportunity to
250 identify genome-wide genomic polymorphisms and correlative relationships between
251 mutations and complex traits. However, causative mutations are more difficult to
252 decipher, particularly in regions of high linkage disequilibrium³³. The potential of
253 CRISPR/Cas 9 for genome editing in theory will provide new ways of validating causative
254 effects particularly for traits that exhibit complex modes of inheritance³⁴. Furthermore,
255 simulation studies³⁵ have recently shown how genome editing technology can be coupled

256 with genomic selection and double the rate of genetic gain compared with genomic
257 selection conducted in isolation. This novel approach for deploying genome editing in
258 breeding programs, referred to as PAGE (promotion of alleles by genome editing), has
259 considerable potential to accelerate genetic gain in plant and animal improvement
260 programs. In animal breeding, the cost of genotyping and resequencing has reached a point
261 where producers and multipliers, in addition to members of the breeding nucleus (Figure 2),
262 can be genotyped and have sequencing information accurately imputed for a modest
263 investment. The population of genotyped or sequenced animals is therefore of the order of
264 millions (e.g., in Ireland more than one million beef cattle are being genotyped; in major pig
265 and poultry breeding programs similar data sets have been genotyped and are being
266 imputed to whole genome sequence data) and for these, on-farm or slaughterhouse
267 phenotype data are also available. Moreover, in addition, this huge resource can be treated
268 as a genome-wide association mapping panel, which can be used as part of a cascade of
269 technologies³⁶, to detect causative variants of quite small effect with great power, which
270 can then be used as targets for genome editing. Only small numbers of editing events are
271 required to make substantial improvement in genetic gain. In plant breeding, the number of
272 genetically different individuals in production is much smaller (Figure 2), so a directly
273 comparable approach to PAGE in animals may not be so applicable. However, in many minor
274 and so called 'orphan' crops with less advanced breeding programs, cultivars released for
275 production can be quite genetically diverse. If relevant phenotypic data can be collected on
276 individuals, then there may be an opportunity to introduce these methods more rapidly in
277 these cases. This might apply, for example, to some tree species.

278

279 **Integrating plant and animal breeding approaches**

280 The various plant and animal species used in agriculture have different biological systems
281 and are farmed in different environments or within different economic settings. Thus, they
282 require breeding programs that are specifically tailored. However, the underlying principles
283 of breeding programs are common, and generic approaches could be devised for local
284 deployment and adaptation. Recently, Gaynor *et al.*³⁷ proposed the reorganizing of
285 traditional plant breeding programs for inbred or hybrid crops into two distinct parts as a
286 strategy for implementing genomic selection (Figure 3). The first part is a population
287 improvement part that develops improved germplasm. The second part is a product
288 development component that identifies new inbred varieties or parents for hybrids. The
289 first part is highly analogous to a classical animal breeding program based on recurrent
290 selection and could make use of all of the tools and techniques that are well established in
291 that domain. These include optimal contribution theory, economic selection indices, short
292 generation intervals, multiple trait evaluation and selection- techniques that are not widely
293 used in plant breeding. The second part is highly analogous to a classical plant breeding
294 program and could similarly make use of all the tools and techniques that are well
295 established in that domain, supplemented by careful use of genomic selection. Stochastic

296 simulations showed that the program using the two-part strategy generated more than 2.5
297 times the rate of genetic gain of the conventional program and nearly 1.5 times the genetic
298 gain of the best performing program using an alternative genomic selection strategy based
299 on a standard plant breeding program design for the same cost and in the same amount of
300 time (Figure 3). The results also illustrate the synergy that can be realized by integrating
301 plant and animal breeding approaches under the umbrella of a common platform.

302

303 **Figure 3**

304

305 In plant breeding there has been a proliferation of powerful high-throughput phenotyping
306 technologies in recent years which are enabling more accurate characterization of traits
307 and environments along time series³⁸. The expertise in the analysis and utilization of these
308 data, as well as the long-established expertise in the integration of physiological models
309 and quantitative genetics models³⁹, are examples, of which there are many, of the types of
310 thinking, tools, and technology that are common in plant breeding that could be translated
311 into animal breeding.

312

313 **Unification of breeding and biological research**

314 Access to large scale sequence and phenotype information at unprecedented scales will also
315 provide opportunities to unify discovery biology and breeding. In other words, breeding
316 programs will become ‘test beds’ for hypotheses as well as platforms for development and
317 deployment of new varieties and breeds of livestock and fish that deliver multiple benefits.
318 The largest impact of such developments will be in the areas of quantitative or complex
319 traits that have been less amenable to reductionist approaches (as breeders now have ways
320 of predicting the effects of causative factors through genomic selection) and are likely to
321 deliver major benefits for crop and animal improvement programs. In this way, genomic
322 selection may catalyze a unification of breeding methods, tools, and technologies across
323 several plant and animal species, which in turn can advance the modernization of other
324 aspects of breeding programs. These could include the widespread adoption of clearly
325 defined breeding goals, economic selection indices, objective quantification of genetic gains,
326 modeling, new trial design and analysis, and the efficient optimization of resources that
327 underpin both breeding and biological discovery research.

328 **Conclusions**

329 The greatest and most immediate opportunity for the application of genomic selection is in
330 the developing world where the demands and needs are greatest⁴⁰. The recently launched
331 Excellence in Breeding Platform of the CGIAR (see URLs) is designed to create economies of
332 scale, unify breeding ideas, technology, resources and demand and capacity across species
333 and systems to modernize breeding programs that are focused on meeting the needs of
334 small holder farmers in the developing world. This approach is summarized in Figure 4 and
335 embraces many of the concepts outlined in this article and is designed to deliver innovative

336 'step changes' in the rate of genetic gain for crops, livestock and fish of relevance to the
337 developing world.

338

339 **Figure 4**

340

341 The successful implementation of genomic selection for the delivery of public goods for the
342 developed and developing world will require a strategic approach to the design of breeding
343 programs, greater collaboration, new partnerships that span the public and private sector,
344 and new skills. However, the impact of genomic selection may extend beyond the creation
345 of new varieties and improved livestock to include an integrative framework for
346 simultaneous delivery of both scientific discoveries and new products for the developing
347 world. This may represent the biggest incentive for enhanced and global coordination of
348 funding to support modern plant and animal breeding programs.

349

350 **URLs-**

351 <http://excellenceinbreeding.org>

352

353 **Acknowledgements-**

354 The Implementing Genomic Selection in CGIAR Breeding Programs Workshop was funded by
355 the CGIAR Consortium and UK Biotechnology and Biological Sciences Research Council
356 (BBSRC), it was held at the CGIAR Consortium Offices in Montpellier, France.

357

358 **Author Contributions-**

359 T.C., I.M., J.H. and W.P. jointly developed the ideas and wrote the paper.

360

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440

441 **Figure Legends-**

442

443 **Figure 1 Some key milestones of selective animal and plant breeding**

444

445 **Figure 2 Comparison of animal and plant breeding approaches.** In some areas plant and
446 animal breeders have adopted similar approaches. All breeding programs can be thought of
447 as having two basic components: (i) a recurrent selection component that seeks to increase
448 the frequency of favorable alleles in a population that in turn increases the mean of the
449 population; and (ii) a product development component that seeks to extract genotypes
450 from this improved population for a farmer to grow. A major difference between animal and
451 plant breeding has been that the former places greater emphasis on population
452 improvement with product development consisting primarily of multiplication of stock
453 which is not recycled into the breeding nucleus, whereas in the latter greater emphasis is
454 placed on selection of an improved product, in the form of a recognizable plant variety,
455 which is often also the source of parents for the next breeding cycle. That is, while varieties
456 (often protected by plant breeders' rights) are the focus in plant breeding, the concept is
457 almost irrelevant in animals.
458

459

459 **Figure 3 A variant of the two-part breeding program design for plant breeding**

460

461 **Figure 4** Capturing new opportunities to accelerate the pace of genetic gain based on
462 efficient and targeted access to genetic diversity, coordinated phenotyping across
463 environments, cost effective sequencing, genomic prediction and genome editing
464

465

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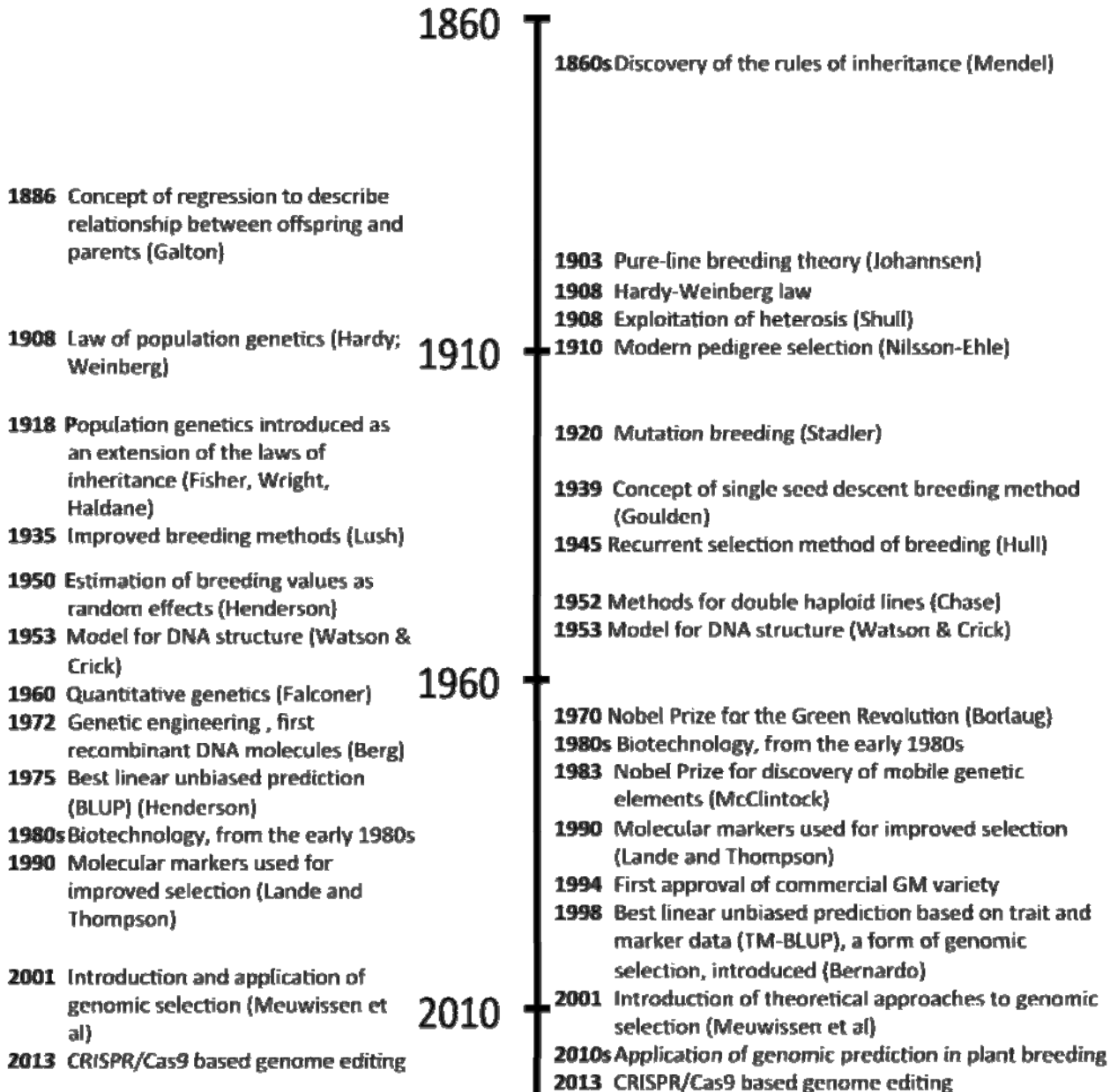
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524 World Agroforestry Centre, ICRAF House, United Nations Avenue, Gigiri, Nairobi,
525 Kenya
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Animals

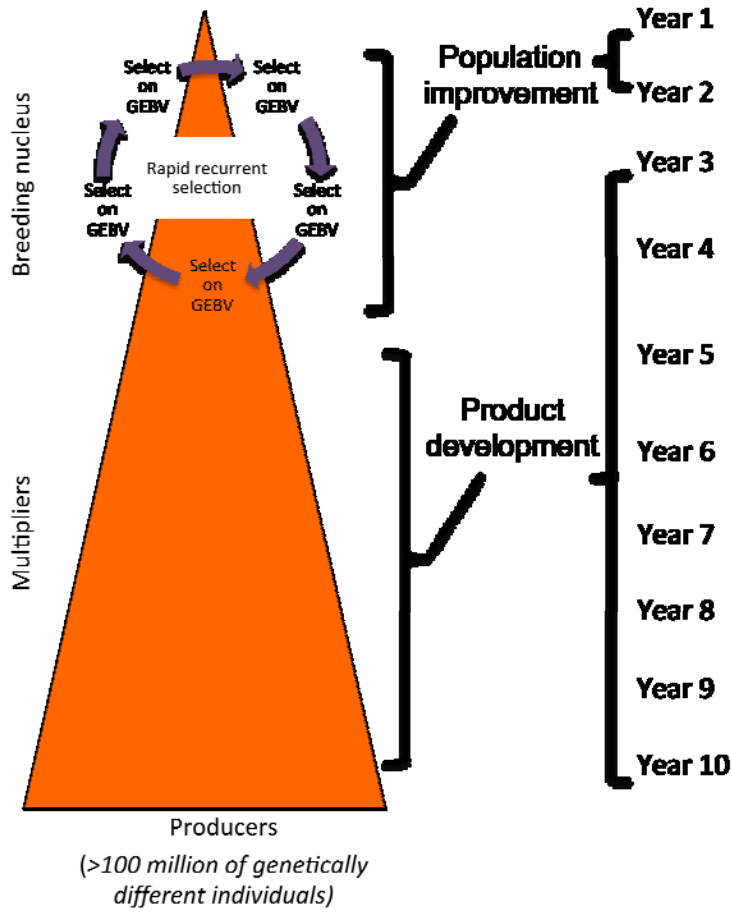
Plants

Domestication ~12000 years ago

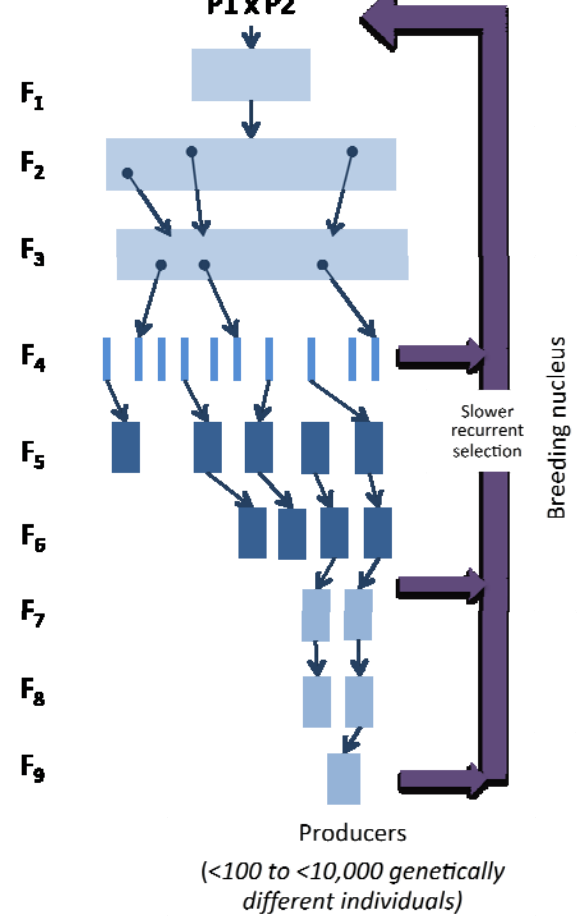
Domestication ~ 12000 years ago



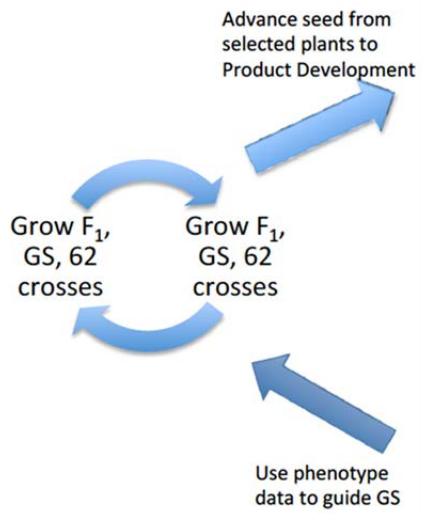
Animal breeding



Plant breeding



Population Improvement



Product Development

Year	Generation		Number of Plants	Action
1	F_1		124 half-sib families	Increase in greenhouse
2	F_2		1000 plants per family	Bulk 50 plants per family
3	F_3		1000 plants per family	Bulk 50 plants per family
4	F_4		1000 plants per family	Derive new lines from 50 plants per family
5	$F_{4:5}$		6200 headrows	Advance 1000 lines
6	PYT, $F_{4:6}$		1000 lines	Yield trial, genotype
7	AYT, $F_{4:7}$		100 lines	Yield trial
8	EYT, $F_{4:8}$		10 lines	Yield trial
9	EYT, $F_{4:9}$		10 lines	Yield trial
10	$F_{4:10}$		1 line	Release variety

