Planta (2019) 250:971–977
https://doi.org/10.1007/s00425-019-03200-8

REVIEW

Modernising breeding for orphan crops: tools, methodologies, and beyond

Jean-Marcel Ribaut[1] · **Michel Ragot**[2]

Received: 4 December 2018 / Accepted: 25 May 2019 / Published online: 29 June 2019

Abstract

Main conclusion **In spite of the limited investment in orphan crops, access to new technologies such as bioinformatics and low-cost genotyping opens new doors to modernise their breeding effectively.**

Abstract Innovation in plant breeding is imperative to meet the world's growing demand for staple food and feed crops, and orphan crops can play a significant role in increasing productivity and quality, especially in developing countries. The short breeding history of most orphan crops implies that genetic gain should be achievable through easy-to-implement approaches such as forward breeding for simple traits or introgression of elite alleles at key target trait loci. However, limited financial support and access to sufficient, relevant and reliable phenotypic data continue to pose major challenges in terms of resources and capabilities. Digitalisation of orphan-crop breeding programmes can help not only to improve data quality and management, but also to mitigate data scarcity by allowing data to be accumulated and analysed over time and across teams. Bioinformatics tools and access to technologies such as molecular markers, some of them provided as services via specific platforms, allow breeders to implement modern strategies to improve breeding efficiency. In orphan crops, more marker–trait associations relevant to breeding germplasm are generally needed, but implementing digitalization, marker-based quality control or simple trait screening and introgression will help modernising breeding. Finally, the development of local capacities—of both people and infrastructure—remains a necessity to ensure the sustainable adoption of modern breeding approaches.

Keywords Africa · Crop information system · Data management · Developing countries · Genomics resources · Molecular breeding

Introduction

The practice of plant breeding has undergone unprecedented changes since the beginning of the twenty-first century. Genotyping and phenotyping technologies, genomics and analytics have all contributed to this modernisation, at least for some crops in some regions of the world. While major crops will significantly contribute to the needed global increase in agricultural production, so-called "orphan crops" are globally of localised importance. Orphan crops are often defined as staple crops grown at limited global scale, with limited global economic value—although often with great significance at the local level—and receiving limited breeding resources. Long timelines and fragmented markets tend to deter public or private endeavours from getting involved in orphan-crop breeding, and this is unlikely to change in the foreseeable future. Nonetheless, orphan crops are often vital to the local populations they serve, including both growers and downstream stakeholders, especially in developing countries where they ensure subsistence, provide diverse and nutritious diets (Balderman et al. 2016; Sogbohossou et al. 2018), and allow for an improved response to climate threats by contributing to more diversified agricultural systems and food sources (Tadele 2018). Considering the challenges

---

✉ Jean-Marcel Ribaut
j.ribaut@cgiar.org

Michel Ragot
michelragot@nfgene.com

[1] Integrated Breeding Platform, c/o CIMMYT, km 45 Carretera México-Veracruz, El Batán, Estado de México, Mexico

[2] Nouvelle France Genetics, 15623 Randall Lane, Minnetonka, MN 55345, USA

faced by orphan-crop breeders in delivering the improved varieties that are expected from them, this paper aims to provide (1) an update on the genetic and genomics resources available, (2) a description of the crop information systems and breeding platforms available and (3) possible ways to enhance breeding efficiency using new technologies.

Demand-led validated product profiles and well-defined breeding objectives contribute significantly to breeding effectiveness, helping to define the desired commercial values critical for local markets (Kimani 2017), including for orphan crops. Such product profiles should ensure that the selection strategies deployed for each trait will deliver varieties with significantly improved performance—meeting or exceeding demand—and, as such, with a high probability of being adopted by growers and downstream stakeholders. Furthermore, because the orphan-crop marketplace is rather fragmented, being driven by very specific requirements in terms of local adaptation or end-user preferences, generic technology developments or knowledge accumulation may not generate the required outputs. Rather, specific breeding objectives, such as relative trait priorities and improvement targets, should drive the determination of what technologies or knowledge to develop (Armstead et al. 2009), and where and how these will create value in breeding programmes to satisfy grower and consumer needs (Sogbohossou et al. 2018; Teeken et al. 2018).

Genetic and genomic resources

Until recently, the reality of orphan crops was one of very limited research investments, and very little available knowledge in genetics and genomics. This reality is evolving, often rapidly, as technologies become more affordable and the cost of knowledge generation decreases. Several international initiatives, such as the Generation Challenge Programme (GCP, www.generationcp.org/sunsetblog; Ribaut et al. 2008), provided breeders of a number of orphan crops with access to genetic and genomic technologies and knowledge previously available only for large commercial crops (Varshney et al. 2010). They also offered new perspectives to help modernise orphan-crop breeding (Varshney et al. 2012). Achievements in different crops included characterisation of genetic diversity (Glaszmann et al. 2010), understanding the genetic basis of agronomic traits (Pandey et al. 2014) and identification of elite alleles at target genes (Caniato et al. 2014) for introgression in elite germplasm to impact crop performance (Carvalho et al. 2016). Over the last decade, significant resources have been invested in sequencing orphan-crop genomes (Varshney et al. 2009), and in developing tools aimed at discovering and characterising loci and genes of use in molecular breeding of those sequenced species (Kamei et al. 2016). The African Orphan Crops Consortium (AOCC, http://africanorphancrops.org/), for instance, is working on sequencing 101 traditional African food crops, adding to the list of more than 700 plant species that have already been sequenced according to the US National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov/genome/). The increasing number of diversity panels of orphan crops that have been genotyped using next-generation sequencing (NGS) or high-density SNP arrays opens new perspectives on unlocking these challenging breeding traits through genome-wide association studies (Upadhyaya 2015; Xu et al. 2017; Zhang et al. 2018) or high resolution mapping in multi-parent advanced generation intercross (MAGIC) populations (Herniter et al. 2018; Ongom and Ejeta 2018).

One very significant example of the impact that genetics and genomics have had on an orphan crop's breeding modernisation is that of groundnut, suffering narrow genetic diversity across cultivars. Developments include the construction of chromosome segment substitution line populations to broaden the genetic basis of groundnut by crossing cultivated and wild-relative germplasm (Fonceka et al. 2012) and the sequencing of the diploid ancestor of cultivated groundnut (Bertioli et al. 2016) and of several cultivated species (www.peanutbase.org), leading to the development of a high-density genotyping Arachis array with thousands of SNPs that are polymorphic among cultivated varieties and wild species (Pandey et al. 2017; Clevenger et al. 2018). Those recent achievements are now providing the basis for the identification of elite alleles for target breeding traits via association studies, while introgression lines are being deployed, such as CS-16 (Stalker 2017), now being used as a donor line for introgression of resistance to early leaf spot and rust in popular and elite African germplasm.

Digitalising breeding and providing support

Attempting to modernise breeding without a reliable data-management system in place is a very risky endeavour. Many research projects and breeding programmes fall short of delivering their goals because of poor data quality, lack of documentation, or lost institutional memory. The digitalisation of breeding increases the effectiveness of seed management, data capture, quality control, documentation and analysis. It enables cumulative learning and more accurate selection decisions at all stages of the breeding process (Delannay et al. 2012). It also entails establishing routines to standardise the storage of germplasm information (pedigree, phenotypes and genotypes), metadata (location, climate, etc.), breeding protocols and trait ontology, which in turn enables data mining and sharing of opportunities across a wider range of environments and teams (Leonelli et al. 2017).

A number of crop information systems exist to support the digitalisation of breeding programmes, including for orphan crops. Typically, a crop information system comprises modules for data management, statistical analysis and decision support, accessible through a central workbench interface and interacting with a crop information database that supports the various stages of cultivar development (Ribaut et al. 2012). The Breeding Management System (BMS), key product of the Integrated Breeding Platform (IBP, https://www.integratedbreeding.net), is one such system. The BMS is a flexible system that with a little customisation is suitable to support day-to-day breeding activities for most, if not all crops, making it very attractive for digitalising breeding programmes at an institutional level. Trait dictionaries are accessible via the BMS databases for a large number of crops (Shrestha et al. 2012), including orphan ones. Another system supporting orphan crops is CassavaBase (https://www.cassavabase.org), born as part of the NextGen Cassava breeding project that promises to substantially increase the rate of genetic improvement in cassava breeding. More recently the CassavaBase system has been adapted to support additional orphan crops including yams (https://www.yambase.org) and bananas (https://musabase.org).

With the multiplication of different systems, the increasing amount of data being generated by researchers across different disciplines and the astonishing progress in cyber technologies facilitating data storage, access and exchange across systems and databases, crop information systems will soon be at the heart of modular and integrated networks hosted in the cloud, connecting different sources of information and tools to make more educated decisions. This modular approach, building on web services and API calls (Selby et al. 2019), will allow for the integration of a number of sources of metadata (e.g. GIS and agronomic data) with scientific data (e.g. high-throughput phenotyping and genotyping) as well as access to relevant applications and/or modelling predictions to identify target haplotypes (Fig. 1). Such an approach, already adopted by large multinational seed companies, enables the implementation of more sophisticated breeding strategies, with breeders becoming ever more empowered decision makers as they gain access to the knowledge, information and data generated over time by different teams and systems (Cooper et al. 2014).

The BMS has already been deployed as a cloud or LAN instance at over a dozen breeding institutions, as well as several universities in sub-Saharan Africa. Although reliable Internet connectivity via routers and modems remains a major limitation, access to cloud infrastructure is rapidly improving thanks to a boom in IT development in Africa, as shown by the spread of 3G and 4G mobile technology in particular. However, development of and access to new technologies are not sufficient by themselves to prompt individuals or organisations to change their practices or to translate into sustainable adoption. Significant and adequate support of technologies that best meet users' needs are generally a "must have" to bring about a lasting change.

A couple of platforms is also available to provide access to analytical pipelines, modern breeding technologies, breeding material, and related information and services in a centralised and functional manner via a website. Born almost 10 years ago and with more than 5000 registered members

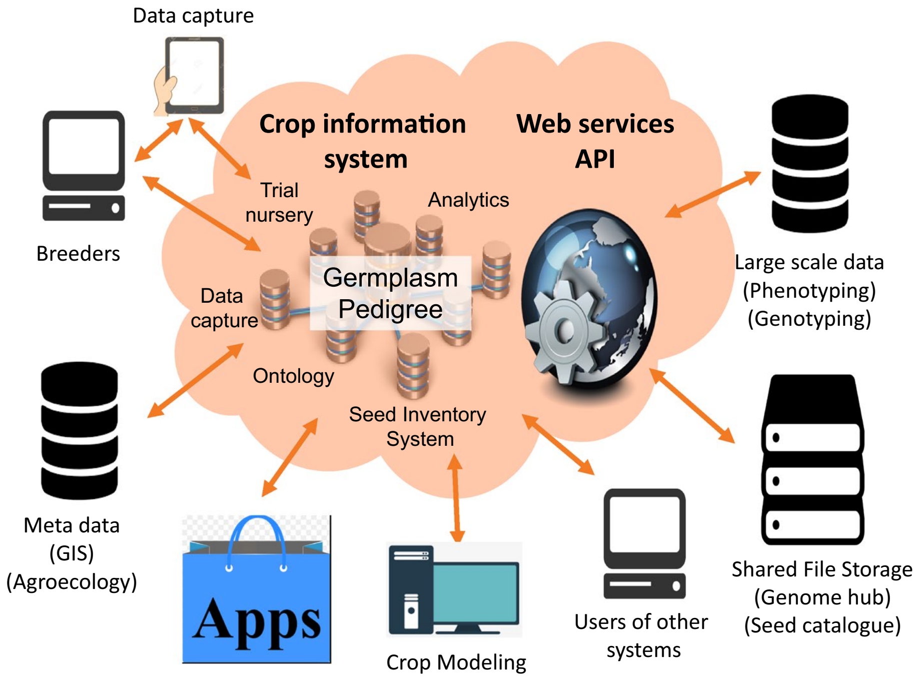

Fig. 1 Modular and integrated cloud breeding network. Crop information system (with a core functionality of germplasm and pedigree management supported by internal modules such as trail/nursery, ontology, data capture, analytics or seed inventory system), integrated into a modular cloud network, allowing breeders to access information, data produced, and functionalities developed by other initiatives via Breeding Application Programming Interface (BrAPI, https://www.brapi.org)

today, the IBP is the oldest of these. The recently born Excellence in Breeding Platform (EiB, http://excellenceinbreeding.org) goes one step further, including training material and support to optimise breeding pipelines and strategies including the implementation of a stage-gate approach and the optimisation of product design and management. The two platforms work in collaboration, offering some common software and services, including genotyping and a number of trait-linked markers to support forward breeding. Genotyping costs for selected SNP markers have recently been significantly reduced thanks to the High Throughput Genotyping Project (HTPG, http://cegsb.icrisat.org/high-throughput-genotyping-project-htpg/) led by ICRISAT, in collaboration with Intertek. HTPG has already generated quite a number of new trait-linked markers, including several for orphan crops. The increasing number of trait-linked markers and the option to screen a genotype with a dozen selected SNPs for little more than a couple of dollars, including DNA extraction, will boost the application of molecular breeding in orphan crops.

Insights into the modernisation of breeding approaches for orphan crops

Resources allocated to the breeding of orphan crops are not expected to dramatically increase. The modernisation of orphan-crop breeding must, therefore, be achieved through more efficient use of all the relevant data, information and tools available at any point in time. Moreover, orphan crops have had a short breeding history because of the limited resources devoted to them, so some established approaches—that for other crops might have been used in the past and been left behind in the evolution towards more sophisticated breeding methodologies—may still have the potential to make a tremendous impact on the breeding efficiency of orphan ones.

A first step in the modernisation of orphan-crop breeding is to strengthen its current bases: phenotypic data and pedigrees

Phenotypic data have typically been the main source of information in breeding. This is still true for most crops, and much more for orphan crops, where the scarcity of the phenotypic data generated on a yearly basis makes the existing data even more valuable. Phenotyping still, generally, constitutes the biggest expense for low-resourced orphan-crop breeding programmes. Therefore, phenotypic data should be considered an asset and stored in crop information systems in an organised way (along with corresponding metadata) so that they can be retrieved, consolidated, and subsequently used to make better breeding decisions (Fig. 2). Pedigree information is also "staple" information for any breeding programme. Accurate pedigree records can be of tremendous value in selecting parents for breeding populations or, combined with phenotypic data, in predicting performance from genetic correlations among relatives (Bernardo 1995; Piepho et al. 2008). Since few new breeding populations are launched by orphan-crop breeding programmes each year,

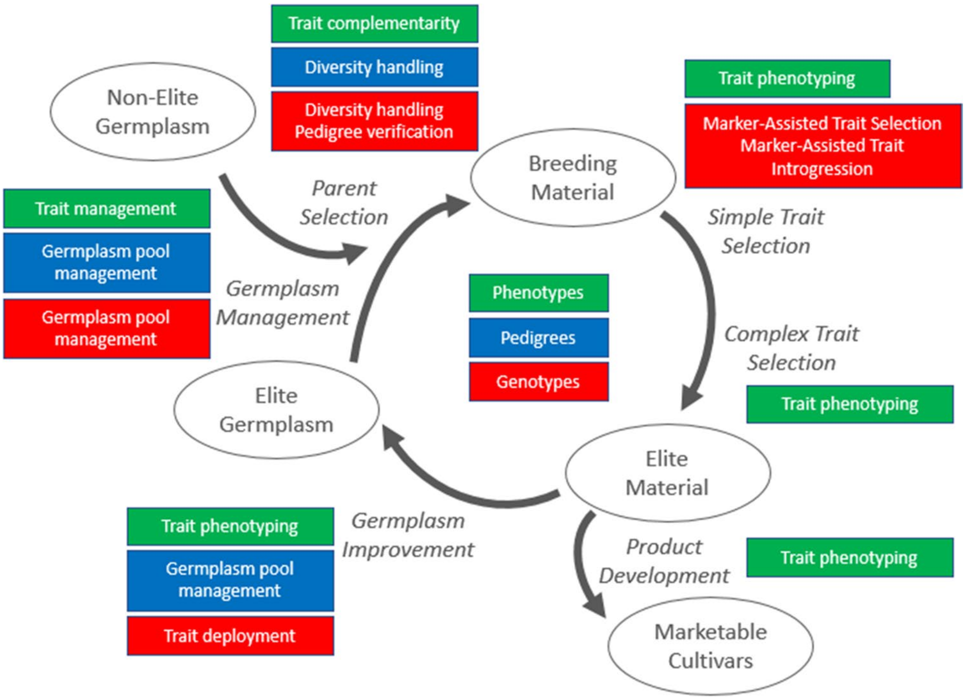

Fig. 2 Orphan-crop breeding modernisation strategies. The figure illustrates the potential impact of using phenotypic, pedigree, or genotypic data more effectively along the different decision-making steps of the breeding cycle. Colours indicate which data type(s) can positively impact each decision-making process if introduced in that process or used in a new way

choosing parental lines accurately—and from different pools in the case of hybrid crops—has a tremendous impact on genetic gain. Furthermore, by allowing access to accurate pedigree information and large amounts of data accumulated over years and across locations, digitalised breeding creates opportunities for breeders to leverage genomic tools and technologies, including in the discovery or validation of agronomically important loci.

A second step in the modernisation of orphan-crop breeding programmes is the introduction of new technologies or knowledge that creates value

With genomic tools and technologies increasingly being made available for orphan crops, whole-genome genotyping with generic, non-trait-linked markers is now accessible for most orphan crops through simple and low-cost platforms.

An immediate application of whole-genome genotyping is marker-based quality testing of genetic materials at key stages of a breeding programme (e.g. parents and their crossed progeny). Such a step is critical to ensure the accuracy of pedigrees, and of the corresponding breeding decisions (Fig. 2).

Furthermore, because of their short breeding history, orphan crops are likely to still contain large-effect favourable or deleterious alleles that have not yet been fixed or eliminated, respectively. The availability of knowledge about these loci, and of tools to manipulate their allele frequencies, can be mobilised to develop trait-linked markers. Those markers can then be used to very effectively select for favourable alleles or against deleterious ones (Fig. 2) at loci involved in simple (Knapp 1998) or, in the case of orphan crops, even moderately complex traits, such as resistances to pests, plant architecture, or nutritional composition. Trait-linked markers can also be used to successfully introduce new traits into elite or popular cultivars (Ragot et al. 1995). These relatively simple approaches have a high probability of resulting in significant genetic gain for target traits in the short to medium term.

A word of caution is needed, however. Allelic effects observed in upstream research and discovery projects do not necessarily hold true in target breeding material because of different allelic compositions, genetic background effects, or environmental effects. Research and discovery projects designed to be genetically relevant to specific breeding programmes can be expected to have a much more significant impact on simple to moderately complex orphan-crop traits than projects with inaccurately defined breeding targets. High levels of impact should be easily ensured by connecting academic institutions that run such research and discovery projects with specific breeding programmes from the onset.

Lastly, using markers to identify and manipulate loci involved in complex traits, such as most abiotic stresses, remains a major challenge. Therefore, and despite some promising results (Ozimati et al. 2018), the development of predictive models and their implementation in genomic selection (Dawson et al. 2013; Gaspare et al. 2018), for which the availability of sufficient good-quality phenotypic data is often the limiting factor (Perez-de-Castro et al. 2012), still remains a rather distant prospect for most orphan crops in Africa.

Reality check and challenges

In spite of the recent research investments mentioned above (often driven by major crops), many orphan crops remain orphan from a breeding perspective because they are not being sufficiently supported with funding. Modernising breeding for orphan crops requires more than just access to genetic and genomic resources, bioinformatics and technological platforms that link phenotypes to genotypes, though these remain critical components (Ribaut et al. 2010).

While digitalising breeding reduces the technical challenges to data sharing, institutional memory and collaboration, it does not remove the institutional, social, or behavioural barriers that prevent change (Eisenberg 2006). Among other factors, competition around discovery and publication, conflicting interests, capacity gaps, lack of common standards, and widespread norms all still discourage scientific collaboration and the open sharing of resources (Campbell and Bendavid 2003; Shibayama et al. 2012; Fusi et al. 2018). Modernising breeding for orphan crops may be less about technology than about creating a responsive and enabling environment to fuel people's eagerness to explore and implement best breeding practices for effective delivery.

The emerging new generation of African breeders represents a tremendous opportunity to empower such a cultural change (Diop et al. 2013). Several African universities have, with the support of international funding and collaborations, developed excellent PhD programmes in crop improvement. As a consequence, the level of education and expertise in breeding has increased significantly in a number of countries (Suza et al. 2016). The next challenge will be to retain the best and brightest young minds, and to create a growth setting for innovative scientists and plant breeders who see a future in African agriculture and want to work on the potential for sub-Saharan Africa to feed itself (van Ittersum et al. 2016). "Brain drain" remains a major challenge for Africa in general, and low salaries combined with limited opportunities to implement what they have learned at universities is one of the major challenges faced by young breeders (Davies and Ribaut 2017).

Conclusions

In short, the tools and the methodologies exist, and the opportunities to modernise the breeding of orphan crops are real. However, resources allocated to orphan-crop breeding are thin and practical limitations on the implementation of modern technologies, such as the production of reliable phenotypic data, remain major bottlenecks.

Given that inherent scarcity of phenotypic data, the modernisation of orphan-crop breeding programmes must focus on first accumulating and integrating quality phenotypic data generated over time, and second leveraging that data in the most effective possible way. Data accumulation and integration can be achieved through the digitalisation of breeding programmes, and several tools exist that are within reach of orphan-crop breeders. Digitalisation helps increase data quality, as do molecular markers when used to verify pedigrees to ensure that actions reflect decisions. Digitalisation of orphan-crop breeding programmes also helps fastening breeding (e.g. data capture and parental selection) and supporting the discovery of new and leverage existing genetic information. Marker–trait associations discovered or validated in specific breeding materials through the mobilisation of accumulated phenotypic and pedigree information can be used to effectively conduct forward or backcross breeding in orphan crops. The increasing number of such marker–trait associations currently available could expand even further and faster if research projects aimed at discovering such associations were based on germplasm relevant to orphan-crop breeding programmes.

In addition, providing resources to support sustainable access to, and adoption of, relevant technologies—ensuring that both infrastructure and human resources are in place—will have an even greater impact on orphan-crop productivity in the medium to long term. Finally, in improving breeding efficiency it is critical to start with better, targeted definition and documentation of breeding objectives and product profiles in alignment with consumer and market demand, all the while considering socioeconomic and agro-ecological challenges. These should in fact be the key drivers in identifying the most suitable breeding strategy to achieve real impact in the fields of orphan-crop producers.

Author contribution statement J-MR and MR contributed significantly to this paper, from the first draft to the final version.

Acknowledgements The authors would like to thank Valerie Boire, Eloise Phipps and Jan Erik Backlund for their constructive review. It is relevant to underline that the Bill and Melinda Gates Foundation has supported partially or entirely a number of the initiatives reported in this paper, including CassavaBase, Excellence in Breeding, High Throughput Genotyping Project and the Integrated Breeding Platform.

References

Armstead I, Huang L, Ravagnani A, Robson P, Ougham H (2009) Bioinformatics in the orphan crops. Brief Bioinform 10:645–653. https://doi.org/10.1093/bib/bbp036

Baldermann S, Blagojević L, Frede K, Klopsch R, Neugart S, Neumann A, Ngwene B, Norkeweit J, Schröter D, Schröter A, Schweigert FJ, Wiesner M, Schreiner M (2016) Are neglected plants the food for the future? Cr Rev Plant Sci 35:106–119. https://doi.org/10.1080/07352689.2016.1201399

Bernardo R (1995) Genetic models for predicting maize single-cross performance in unbalanced yield trial data. Crop Sci 35:141–147

Bertioli DJ, Cannon SB, Froenicke L et al (2016) The genome sequences of arachis duranensis and arachis ipaensis, the diploid ancestors of cultivated peanut. Nat Genet 48:438–446. https://doi.org/10.1038/ng.3517

Campbell EG, Bendavid E (2003) Data-sharing and data-withholding in the genetics and the life sciences: results of a national survey of technology transfer officers. J Health Care Law Policy 6:241–255

Caniato FF, Hamblin MT, Guimaraes CT, Zhang Z, Schaffert RE, Kochian LV, Magalhaes JV (2014) Association mapping provides insights into the origin and the fine structure of the sorghum aluminum tolerance locus, AltSB. PLoS One 9:e87438

Carvalho G, Schaffert RE, Malosetti M et al (2016) Back to acid soil fields: The citrate transporter SbMATE is a major asset for sustainable grain yield for sorghum cultivated on acid soils. G3 6:475–484. https://doi.org/10.1534/g3.115.025791

Clevenger JP, Korani W, Ozias-Akins P, Jackson S (2018) Haplotype-based genotyping in polyploids. Front Plant Sci 9:564. https://doi.org/10.3389/fpls.2018.00564

Cooper M, Messina CD, Podlich D, Totir LR, Baumgarten A, Hausmann NJ, Wright D, Graham G (2014) Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction. Crop Pasture Sci 65:311–336. https://doi.org/10.1071/CP14007

Davies WJ, Ribaut J-M (2017) Stress resilience in crop plants: strategic thinking to address local food production problems. Food Energy Secur 6:12–18. https://doi.org/10.1002/fes3.105

Dawson JC, Endelman JB, Heslot N, Crossa J, Poland J, Dreisigacker S, Manès Y, Sorrells ME, Jannink JL (2013) The use of unbalanced historical data for genomic selection in an international wheat breeding program. F Crop Res 154:12–22. https://doi.org/10.1016/j.fcr.2013.07.020

Delannay X, McLaren G, Ribaut J-M (2012) Fostering molecular breeding in developing countries. Mol Breeding 29:857–873. https://doi.org/10.1007/s11032-011-9611-9

Diop NN, Okono F, Ribaut J-M (2013) Evaluating human resource capacity for crop breeding in national programs in Africa and South and Southeast Asia. Creat Educ 4:72–81. https://doi.org/10.4236/ce.2013.410A011

Eisenberg RS (2006) Patents and data-sharing in public science. Ind Corp Change 15:1013–1031

Fonceka D, Tossim HA, Rivallan R et al (2012) Construction of chromosome segment substitution lines in peanut (*Arachis hypogaea* L.) using a wild synthetic and QTL mapping for plant morphology. PLoS One 7:e48642. https://doi.org/10.1371/journal.pone.0048642

Fusi F, Manzella D, Louafi S, Welch E (2018) Building global genomics initiatives and enabling data sharing: insights from multiple case studies. OMICS 22:237–247. https://doi.org/10.1089/omi.2017.0214

Gaspare W, Liu S, Conaty W, Zhu QH, Gillespie V, Llewellyn D, Stiller W, Wilson L (2018) Historical datasets support genomic selection models for the prediction of cotton fiber quality phenotypes across multiple environments. G3 8:1721–1732. https://doi.org/10.1534/g3.118.200140

Glaszmann JC, Killian B, Upadhyaya HD, Varshney RK (2010) Accessing genetic diversity for crop improvement. Curr Opin Plant Biol 13:167–173. https://doi.org/10.1016/j.pbi.2010.01.004

Herniter IA, Muñoz-Amatriaín M, Lo S, Guo YN, Close TJ (2018) Identification of candidate genes controlling black seed coat and pod tip color in cowpea (*Vigna unguiculata* [L] Walp). G3 8:3347–3355. https://doi.org/10.1534/g3.118.200521

Kamei CLA, Severing EI, Dechesne A, Furrer H, Dolstra O, Trindade LM (2016) Orphan crops browser: a bridge between model and orphan crops. Mol Breed 36:9. https://doi.org/10.1007/s11032-015-0430-2

Kimani PM (2017) Principles of demand-led plant variety design. In: Persley GJ, Anthony VM (eds) The business of plant breeding: market-led approaches to new variety design in Africa. CABI, Wallingford, pp 1–25

Knapp SJ (1998) Marker-assisted selection as a strategy for increasing the probability of selecting superior genotypes. Crop Sci 38:1164–1174

Leonelli S, Davey RP, Arnaud E, Parry G, Bastow R (2017) Data management and best practice for plant science. Nat Plants 3:1–4. https://doi.org/10.1038/nplants.2017.86:1-4

Ongom P, Ejeta G (2018) Mating design and genetic structure of a multi-parent advanced generation intercross (MAGIC) population of sorghum (*Sorghum bicolor* (L) Moench). G3 8:331–341. https://doi.org/10.1534/g3.117.300248

Ozimati A, Kawuki R, Esuma W, Kayondo IS, Wolfe M, Lozano R, Rabbi I, Kulakow P, Jannink JL (2018) Training population optimization for prediction of cassava brown streak disease resistance in west african clones. G3 8:3903–3913. https://doi.org/10.1534/g3.118.200710

Pandey MK, Upadhyaya HD, Rathore A et al (2014) Genomewide association studies for 50 agronomic traits in peanut using the 'reference set' comprising 300 genotypes from 48 countries of the semi-arid tropics of the world. PLoS One 9:1–14. https://doi.org/10.1371/journal.pone.0105228

Pandey MK, Agarwal G, Kale SM et al (2017) Development and evaluation of a high density genotyping'Axiom_Arachis' array with 58 K SNPs for accelerating genetics and breeding in groundnut. Sci Rep 7:40577. https://doi.org/10.1038/srep40577

Perez-de-Castro AM, Vilanova S, Cañizares J, Pascual L, Blanca JM, Diez MJ, Prohens J, Pico B (2012) Application of genomic tools in plant breeding. Curr Genom 13:179–195. https://doi.org/10.2174/138920212800543084

Piepho HP, Möhring J, Melchinger AE, Büchse A (2008) BLUP for phenotypic selection in plant breeding and variety testing. Euphytica 161:209–228

Ragot M, Biasiolli M, Delbut MF, Dell'Orco A, Malgarini L, Thevenin P, Vernoy J, Vivant J, Zimmermann R, Gay G (1995) Marker-assisted backcrossing: a practical example. In: Berville A, Tersac M (eds) Les colloques, vol 72. INRA, Paris, pp 45–46

Ribaut J-M, Monneveux P, Glaszman JC, Leung H, Van Hintum T, de Vicente C (2008) International programs and the use of modern biotechnologies for crop improvement. In: Moore P, Ming R (eds) Genomics of tropical crop plants. Springer, New York, pp 21–63

Ribaut J-M, de Vicente MC, Delannay X (2010) Molecular breeding in developing countries: challenges and perspectives. Curr Opin Plant Biol 13:213–218. https://doi.org/10.1016/j.pbi.2009.12.011

Ribaut J-M, Delannay X, McLaren G, Okono F (2012) Molecular breeding platforms in world agriculture. In: Robert AM (ed) Encyclopedia of sustainability science and technology. Springer, Berlin, pp 6692–6720

Selby P, Abbeloos R, Backlund JE et al (2019) BrAPI—an application programming interface for plant breeding applications. Bioinformatics 5:190. https://doi.org/10.1093/bioinformatics/btz190

Shibayama S, Walsh JP, Baba Y (2012) Academic entrepreneurship and exchange of scientific resources: material transfer in life and materials sciences in japanese universities. Am Sociol Rev 77:804–830. https://doi.org/10.1177/0003122412452874

Shrestha R, Matteis L, Skofic M, Portugal A, McLaren G, Hyman G, Arnaud E (2012) Bridging the phenotypic and genetic data useful for integrated breeding through a data annotation using the crop ontology developed by the crop communities of practice. Front Physiol 3:326. https://doi.org/10.3389/fphys.2012.00326

Sogbohossou EOD, Achigan-Dako EG, Maundu P et al (2018) A roadmap for breeding orphan leafy vegetable species: a case study of *Gynandropsis gynandra* (Cleomaceae). Hortic Res 5:2. https://doi.org/10.1038/s41438-017-0001-2

Stalker HD (2017) Utilizing wild species for peanut improvement. Crop Sci 57:1102–1120. https://doi.org/10.2135/cropsci2016.09.0824

Suza WP, Gibson P, Edema R, Akromah R, Sibiya J, Madakadze R, Lamkey KR (2016) Plant breeding capacity building in Africa. Nat Clim Change 6:976. https://doi.org/10.1038/nclimate3139

Tadele Z (2018) African orphan crops under abiotic stresses: challenges and opportunities. Scientifica, Article ID 1451894. https://doi.org/10.1155/2018/1451894

Teeken B, Olaosebikan O, Haleegoah J, Oladejo E, Madu T, Bello A, Parkes E, Egesi C, Kulakow P, Kirscht H, Tufan HA (2018) Cassava trait preferences of men and women farmers in Nigeria: implications for breeding. Econ Bot 72:263–277

Upadhyaya HD (2015) Establishing core collections for enhanced use of germplasm in crop improvement. J Crop Breed and Gen 1:1–12. http://oar.icrisat.org/id/eprint/10058

van Ittersum MK, van Bussel LGJ, Wolf J et al (2016) Can sub-saharan Africa feed itself? PNAS 113:14964–14969. https://doi.org/10.1073/pnas.1610359113

Varshney RK, Close TJ, Singh NK, Hoisington DA, Cook DR (2009) Orphan legume crops enter the genomics era! Curr Opin Plant Biol 12:202–210

Varshney RK, Glaszmann JC, Leung H, Ribaut J-M (2010) More genomic resources for less studied crops. Trends Biotechnol 28:452–460

Varshney R, Ribaut J-M, Buckler ES, Tuberosa R, Rafalski JA, Langridge P (2012) Can genomics boost productivity of orphan crops. Nat Biotechnol 30:1172–1176

Xu P, Wu X, Muñoz-Amatriaín M et al (2017) Genomic regions, cellular components and gene regulatory basis underlying pod length variations in cowpea (Unguiculata V, Walp L). Plant Biotechnol J 15:547–557. https://doi.org/10.1111/pbi.12639

Zhang S, Chen X, Lu C et al (2018) Genome-wide association studies of 11 agronomic traits in cassava (*Manihot esculenta* Crantz). Front Plant Sci 9:503. https://doi.org/10.3389/fpls.2018.00503