



REVIEW

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Re-orienting crop improvement for the changing climatic conditions of the 21st century

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Abstract

A 70% increase in food production is required over the next four decades to feed an ever-increasing population. The inherent difficulties in achieving this unprecedented increase are exacerbated by the yield-depressing consequences of climate change and variations and by the pressures on food supply by other competing demographic and socioeconomic demands. With the dwindling or stagnant agricultural land and water resources, the sought-after increases will therefore be attained mainly through the enhancement of crop productivity under eco-efficient crop production systems. 'Smart' crop varieties that yield more with fewer inputs will be pivotal to success. Plant breeding must be re-oriented in order to generate these 'smart' crop varieties. This paper highlights some of the scientific and technological tools that ought to be the staple of all breeding programs. We also make the case that plant breeding must be enabled by adequate policies, including those that spur innovation and investments. To arrest and reverse the worrisome trend of declining capacities for crop improvement, a new generation of plant breeders must also be trained. Equally important, winning partnerships, including public-private sector synergies, are needed for 21st century plant breeding to bear fruits. We also urge the adoption of the continuum approach to the management of plant genetic resources for food and agriculture as means to improved cohesion of the components of its value chain. Compellingly also, the National Agricultural Research and Extension System of developing countries require comprehensive overhauling and strengthening as crop improvement and other interventions require a sustained platform to be effective. The development of a suite of actionable policy interventions to be packaged for assisting countries in developing result-oriented breeding programs is also called for.

Keywords: Plant genetic resources for food and agriculture, PGRFA, Plant breeding, Crop improvement, Climate change, Biotechnology, Marker-aided selection, Genetic transformation, Induced mutations, Phenomics

Introduction

Population growth rates globally have so outstripped the linear rate of increases in food production that the Food and Agriculture Organization of the United Nations (FAO) estimated that 70% more food [1] must be produced over the next four decades in order to nourish adequately a human population projected to exceed 9 billion by the year 2050. The odds for attaining such an unprecedented increase, which would require the raising of the historically linear increases in annual food production by 37% [2], is substantially lessened by the consequences of climate change and variations on crop production systems [3,4].

The scope of the problem

The frequent occurrences of drought and floods, that invariably result in acute food shortages such as the very recent ones in the Horn of Africa [5], are symptomatic of the grave implications of extreme weather conditions for crop production and, hence, food security. Chatham House [6] had, relying on data provided by the United Nation's Intergovernmental Panel on Climate Change (IPCC), concluded that an additional 40 to 170 million more people will be undernourished as a direct consequence of climate change. Indeed, the overwhelming prognosis is that extreme weather events such as heavy precipitation, heat waves, and rising sea levels will occur in many parts of the world during the 21st century [7] with resulting floods, drought, and salinity as the most critical consequences. The strategies for devising solutions

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to these constraints will vary across geographical regions as the types and magnitudes of the problems will vary. For instance, though there is the consensus that rainfall is expected to increase globally overall, some places will actually be receiving less annual rainfalls while the seasonality of rains and hence the timing of the cultivation of crops will also change. More worrisome yet, the frequencies of occurrence and durations of the extreme weather events are also expected to increase. Table 1 summarizes

some of the expected negative impacts on crop production by regions of the world.

This generational challenge of producing enough food for a rapidly growing population under extreme and changing weather conditions is further exacerbated by dwindling agricultural land and water resources. There are no more redundant water resources and arable lands to deploy in augmenting the already over-stretched ones in many parts of the world. Other noteworthy drivers

Table 1 Some expected negative impacts of climate change on crop production by regions^a

Asia

- Crop yields could decrease by up to 30% in Central and South Asia
- More than 28million hectares (ha) in arid and semi-arid regions of South and East Asia will require substantial (at least 10%) increases in irrigation for a 1 °C increase in temperature.

Africa

- One of the most vulnerable continents to climate change and climate variability
- With many semi-arid regions and projected increase of 5% to 8% by the 2080s, likely reduction in the length of growing seasons will render further large regions of marginal agriculture out of production
- Projected reductions in crop yields of up to 50% by 2020
- Fall in crop net revenues by up to 90% by 2100
- Population of 75 to 250 million people at risk of increased water stress by the 2020s and 350 to 600 million people by the 2050s

Australia and New Zealand

- Agricultural production may decline by 2030 over much of southern and eastern Australia, and over parts of eastern New Zealand, due to increased drought and fire
- Change land use in southern Australia, with cropping becoming non-viable at the dry margins
- Production of Australian temperate fruits and nuts will drop on account of reduced winter chill
- Geographical spread of a major horticultural pest, the Queensland fruit fly (*Bactrocera tryoni*), may spread to other areas including the currently quarantined fruit fly-free zone

Europe

- Crop productivity is likely to decrease along the Mediterranean and in south-eastern Europe
- Differences in water availability between regions are anticipated to increase
- Much of European flora is likely to become vulnerable, endangered or committed to extinction by the end of this century

North America

- Increased climate sensitivity is anticipated in the south-eastern USA and in the USA corn belt making yield unpredictable
- Yields and/or quality of crops currently near climate thresholds (for example, wine grapes in California) are likely to decrease
- Yields of cotton, soybeans, and barley are likely to change

Latin America

- Risk of extinctions of important species
- By the 2050s, 50% of agricultural lands in drier areas may be affected by desertification and salinization
- Generalized reductions in rice yields by the 2020s
- Reductions in land suitable for growing coffee in Brazil, and reductions in coffee production in Mexico
- The incidence of the coffee leaf miner (*Perileucoptera coffeella*) and the nematode *Meloidogyne incognita* are likely to increase in Brazil's coffee production area
- Risk of *Fusarium* head blight in wheat is very likely to increase in southern Brazil and in Uruguay

Small islands

- Subsistence and commercial agriculture on small islands will be adversely affected by climate change
- In mid- and high-latitude islands, higher temperatures and the retreat and loss of snow cover could enhance the spread of invasive species including alien microbes, fungi, plants, and animals

^aAdapted from the Second Report on the State of the World's Plant Genetic Resources for Food and Agriculture [38].

for food insecurity include the competing demands on scarce, depleted, and over-used arable lands and scarce food stuff for productions of bioenergy and livestock feeds. Equally confounding current conventional efforts to increase crop production sustainably is the prohibitive economic and environmental costs of the deployment of further agricultural chemicals as means for boosting yields.

The most vulnerable segments of society will be in poor developing countries, particularly in South Asia and sub-Saharan Africa, as they will suffer the most consequences of these changes to their food production systems [8-10]. In fact, Ejeta [11] estimated yield decreases of 10% to 20% for Africa's most important food crops in the coming decades. Similarly, Tester and Langridge [2] inferred that the greatest demand for yield increases as population continues to increase will be in the developing countries of the world though interestingly, Foresight [12] averred that the applications of already existing knowledge and technology could increase yields two- to three-fold in the medium and low income countries of the world.

Success in attaining the imperative of producing more food under worsening climatic conditions and with a severely constrained natural resources base hinges on enhanced efficiencies, that is achieving more yield per unit of input. This consideration informed the advocacy by Chatham House [6] for the eco-friendly 'knowledge-intensive' 21st century Green Revolution that will replicate the dramatic yield increases of its 20th century 'input intensive' precursor [11,13]. The growing of diverse 'smart' crop varieties that are capable of producing 'more with less' is in accord with this 'greener' perspective and will be critically important to achieving the *sine qua non* of enhanced efficiencies. This will of course require the re-orientation of many aspects of crop production systems with plant breeding and the cultivation of the resulting high yielding, well-adapted, input use-efficient, and resilient crop varieties constituting a major component of the interventions. In line with this perspective, Beddington *et al.* [4] aptly surmised that the concomitant attainment of food security and environmental sustainability would require innovative interventions as main driver for change.

Genetic gains translate to 'smart' crop varieties

Crop yields represent the net result of the intricate interactions between two main critical determinants, of approximately equal contributory effects, namely, the inherent genetic constitution of the crops and agronomic management practices [14]. Indeed, over the past seven decades in the United States, the percentage contribution of genetic gains to total on-farm yield increases in maize ranged between 33% and 94% with an average of about 50% to 60%

[15-17]. Genetic gains, accruable from harnessing the potentials coded into the genetic blueprints of plant genetic resources for food and agriculture (PGRFA), could therefore make significant contributions to attaining this required 70% increases in food production.

Instances of the dramatic effects of genetic gains on crop yields include the development and massive dissemination of high yielding and resilient cereal crop varieties around the world in the course of the aforementioned Green Revolution starting in the late 1960s. The consequent marked increases in food production in many food deficit countries was credited with saving billions of people from starvation especially in Asia [11,13]. More recently, the introduction of high yielding rice varieties, the New Rice for Africa (NERICA), in sub-Saharan Africa has also been credited with substantial increases in the production of the crop in the region [18-21].

Improved crop varieties, that possess superior agronomic and quality traits, are the direct outputs of plant breeding, described by the Columbia Encyclopedia as the science of altering the heritable patterns of plants to increase their value [22]. Foresight [12] had, in recommending the use of new scientific and technological tools to address the significant challenges of producing substantially more food with minimal environmental footprints, specifically identified 'plant breeding using conventional and new techniques to improve yields . . . increase water, nutrient and other input efficiencies' as means to attaining this goal. The World Economic Forum [23] also situated the breeding of new crop varieties at the top of the agenda of its industry partners' coalition of global companies to address food insecurity. This paper contributes to the ongoing discussions on how plant breeding could be rendered more responsive to these challenges. We highlight some of the strategic policy, scientific, technological, and partnership interventions that can aid national programs, especially of developing countries, to have responsive result-oriented crop improvement activities.

Profile of the desired 'smart' crop varieties

FAO [24] posited that 'a genetically diverse portfolio of improved crop varieties, suited to a range of agroecosystems and farming practices, and resilient to climate change' is key to sustainable production intensification. In addition to high yields, the new elite varieties envisioned to address the burgeoning drivers for food insecurity must be adapted to extreme weather conditions and the attendant continually evolving new strains and biotypes of pests and diseases. Extreme and changing patterns of drought and salinity are probably the most critical consequences of climate change and variations for which plant breeding must develop well-adapted varieties. Additionally, the 21st century plant breeding must cater to different prevailing farming systems and conditions - including rain-fed

agriculture that accounts for a significant proportion of global food production in places where erratic rainfall patterns are expected. The new elite varieties must make more efficient use of inputs, and have improved nutritional qualities that meet the myriad dietary preferences of an increasingly more affluent, health-conscious, and generally more discerning consumer. Breeding objectives and strategies must also lead to those crop varieties that fit into ecosystem-based approaches such as conservation agriculture that emphasizes zero tillage. The breeding of multi-purpose crop varieties which biomass are severally suited for use as food, bioenergy substrates, livestock feeds, and fiber will contribute to assuaging the effects of the ever increasing competing demands from these industries on arable lands, water resources, and even foodstuff.

Unlocking the inherent potentials of PGRFA

Deliberate human interventions, including hybridizations and selection pressures, in the last 10,000 years have resulted in the domestication of wild ancestors into the hundreds of thousands of breeds of both plants and animals that now form the basis for food and agriculture [25,26]. An unintended consequence of this human intervention in the otherwise natural process of evolution and speciation has been the narrowing of the genetic base of the plants cultivated for food [2]. The extremely narrow genetic base of crops, as evidenced in the similarities and shared close ancestries of cultivars, imperil food security grievously as a majority of the cultivars of the world's most important food crops would be vulnerable to the same stresses. In Russia, for instance, 96% of all winter wheat varieties are descendants of either one or both of two cultivars, Bezostaya 1 and Mironovskaya 808 [27]. This scenario evokes the specter of the potato blight and ensuing famine in Ireland in the mid-19th century and more recently in the summer of 1970, the major devastation of corn fields by a strain of *Helminthosporium maydis* in the middle and south central part of the United States. With climate change and variations, the threat of wide ranging major crop failures as a result of biotic and abiotic stresses is all too real. This threat can be mitigated by sourcing and/or inducing and deploying new allelic variations in plant breeding.

Widening the sources of heritable variations

Scientists are mindful of the shortcomings in the genetic diversity - and hence, increased vulnerabilities - of crops. Wild relatives of crops, land races, and other non-adapted genetic materials, even if usually low yielding and harboring undesirable traits, should be used more routinely in genetic improvement as means to addressing this shortcoming [2,25]. The investments of efforts in the use of such non-adapted materials in plant breeding have been quite rewarding. Instances include the use of genes located on a translocated chromosome arm of rye in the genetic improvement

of wheat [28]. Gur and Zamir [29] also demonstrated that the introduction of genes from the wild relative of tomato, the drought-tolerant green-fruited *Solanum pennellii*, increased yields by up to 50%. Two centers of the Consultative Group on International Agricultural Research (CGIAR), the International Institute of Tropical Agriculture, Ibadan, Nigeria and the International Center for Tropical Agriculture, Cali, Colombia, have severally used wild relatives of cassava to enhance disease resistance, improve nutritional qualities and extend shelf life of the fresh roots of the crop [30-34]. The legendary contribution of the reduced height gene from the Japanese wheat variety, Norin 10, to the Green Revolution is widely chronicled and certainly, other efforts have yielded significant results as well.

In general, crop wild relatives (CWRs), underutilized crops, and neglected species, that are conserved *ex situ*, on-farm, and *in situ*, are veritable repositories of the beneficial heritable traits lost in the course of domestication [29], including those for adapting to climate change [35]; these can be assembled into the envisaged 'smart' crop varieties. McCouch [25] had aptly surmised that in crop improvement, 'the surest way to succeed in a reasonable amount of time is to have access to a large and diverse pool of genetic variation'. This imperative is at the core of the work of the International Treaty on Plant Genetic Resources for Food and Agriculture (the International Treaty) which aims at the conservation, access, and sustainable use of PGRFA [36,37].

It is indeed paradoxical that PGRFA is the least tapped resource [38] in the quest for increased food production under worsening climate change and variations scenarios even though there is ample compelling evidence to the contrary. We recommend the harnessing of the widest possible spectrum of the inherent potentials of crops and their relatives as reversal to this trend of sub-optimal use of PGRFA in crop improvement. The accruable benefits from using these non-adapted materials certainly outweigh the additional efforts and costs in time and resources for breaking linkage drags and eliminating unwanted deleterious alleles - the main reason why breeders repeatedly and largely invariably always use the same set of 'safe bet' parents. A large scale global project aimed at collecting and using wild relatives of crops in plant breeding being implemented by the Global Crop Diversity Trust, for instance, is an example of internationally driven multi-stakeholder efforts to redress this shortcoming [39]. Pre-breeding, whereby germplasm curators and plant breeders work together to use heritable variations from non-traditional gene donors to produce populations of intermediate materials that can then be used in breeding, should be adopted universally in achieving this diversification of the genetic base of improved crop varieties. The e-learning course on pre-breeding [40,41] developed by FAO and partners under the auspices of the Global Partnership Initiative for Plant

Breeding Capacity Building (GIPB; [42]), is contributing to capacity development in this novel aspect of crop improvement. Pre-breeding facilitates the broadening of the genetic base of crops through the integration of new alleles of genes into elite novel crop varieties.

Through its Global System on PGRFA [43], FAO makes available relevant policy instruments, information systems, and other mechanisms that facilitate the conservation and sustainable use of PGRFA for food security. These include the World Information and Early Warning System (WIEWS; [44]) which provides online access to 19 databases and 13 organizations, instruments, and entities relevant to PGRFA and the World Information Sharing Mechanism on the implementation of the GPA [45] which provides access to PGRFA information of 71 countries, most of which also have their own portals. FAO's Global System for PGRFA also includes landmark publications such as the Second Report on the State of the World's PGRFA [38] which provides a periodic comprehensive report on not only the status of conservation and use of PGRFA worldwide but also the relevant emerging trends. Most recently in 2011, the Second Global Plan of Action for Plant Genetic Resources for Food and Agriculture (the Second GPA; [46]) was adopted by countries as a global framework to strengthen the capacities of

countries in the conservation of crop diversity and the development and deployment of a genetically diverse portfolio of improved varieties with new traits that meet food and nutritional security needs (Table 2).

All these information repositories are aiding the access to, and use of, genetic variability even across national boundaries. They facilitate access to the 1,750 national, regional, and international genebanks around the world which collectively hold about 7.4 million accessions [38]. These genebanks have been particularly successful with the collection, characterization, evaluation, and conservation of crop germplasm. Complementing the roles of these *ex-situ* gene repositories are about 2,500 botanical gardens which provide refuge for innumerable CWRs *in-situ* and the Svalbard Global Seed Vault, Norway which holds over 400,000 duplicate copies of crop germplasm from around the world [38]. Continued support, through sustained funding and enabling policies, is important for these repositories to be able to avail access to the widest possible genetic variation for improving crops. A major critical weakness in the conservation of PGRFA is the absence of a concerted, possibly global mechanism that mirrors the management of *ex-situ* collections, for *in-situ* conservation. CWRs continue to be lost as their refuges are appropriated

Table 2 Priority Activities of the Second Global Plan of Action on PGRFA^a

Theme	Priority activity
<i>In situ</i> conservation and management	1. Surveying and inventorying plant genetic resources for food and agriculture
	2. Supporting on-farm management and improvement of plant genetic resources for food and agriculture
	3. Assisting farmers in disaster situations to restore crop systems
	4. Promoting <i>in situ</i> conservation and management of crop wild relatives and wild food plants
<i>Ex situ</i> conservation	5. Supporting targeted collecting of plant genetic resources for food and agriculture
	6. Sustaining and expanding <i>ex situ</i> conservation of germplasm
	7. Regenerating and multiplying <i>ex situ</i> accessions
Sustainable use	8. Expanding characterization, evaluation, and further development of specific subsets of collections to facilitate use
	9. Supporting plant breeding, genetic enhancement, and base-broadening efforts
	10. Promoting diversification of crop production and broadening crop diversity for sustainable agriculture
	11. Promoting development and commercialization of all varieties, primarily farmers' varieties/landraces and underutilized species
	12. Supporting seed production and distribution
Building sustainable institutional and human capacities	13. Building and strengthening national programmes
	14. Promoting and strengthening networks for plant genetic resources for food and agriculture
	15. Constructing and strengthening comprehensive information systems for plant genetic resources for food and agriculture
	16. Developing and strengthening systems for monitoring and safeguarding genetic diversity and minimizing genetic erosion of plant genetic resources for food and agriculture
	17. Building and strengthening human capacity
	18. Promoting and strengthening public awareness on the importance of plant genetic resources for food and agriculture

^aAdapted from the Second Global Plan of Action for PGRFA, Food and Agriculture Organization of the United Nations, Rome, Italy [46].

for agricultural production or development projects so time is of essence in this regard.

Induced mutations

In situations where it is either impossible or impractical to source heritable variations from existing germplasm, the induction of allelic variations becomes an appealing option. Mutation, the heritable alteration to the genetic blueprint, has been the main driver for evolution and hence speciation and domestication of both crops and animals. Following the sublime discovery of X-rays and other forms of radiation in the early 20th century and the subsequent demonstration that these could alter the genetic material permanently, scientists have induced mutations in plants using both physical and chemical agents [47-49]. Induced mutation is hence an established crop improvement strategy and is credited with the development of over 3,200 officially released elite crop varieties and ornamental plants being cultivated all over the world [50].

The induction of mutation is a chance event so scientists traditionally enhance their chances of success at inducing useful mutation events by generating massive numbers of putative mutants that are then subsequently screened. This is expensive and time-consuming with the associated sheer drudgery cited as main reason for seeking other means for exploiting heritable variations in crops. Biotechnology applications are now being used to enhance the efficiency levels for producing and evaluating large populations. For instance, the high throughput reverse genetics technique, TILLING, short for Targeted Induced Local Lesions IN Genomes [51-53] permits the efficient screening of large populations of plants for specific mutation events [54-64]. The specificity, and hence efficiency, of TILLING - it identifies mutation events in predetermined genome regions - holds great promise for the use of induced mutations to broaden the genetic base of crops.

Cell and tissue biology techniques are also used to enhance the efficiency of mutation induction. For instance, with doubled haploidy [65,66], homozygosity of the mutated segments of the genome is achieved rapidly while *in vitro* propagation techniques are used to dissociate chimeras quickly (to generate solid homohistonts) and to produce and manage large mutant populations in cost-, time-, and space-efficient manners [67]. The critical importance of other uses of cell biology techniques, for instance, in germplasm conservation, in overcoming hybridization barriers and in the rapid multiplication of disease-free planting materials makes it an indispensable tool in crop improvement in general.

A re-invigorated plant breeding for a changing world

Translating the combinations of the widest possible sources of heritable variations efficiently into crop varieties whose

increased yields, improved nutritional quality attributes and enhanced adaptations to abiotic and biotic stresses exceed those of the prior gains of the 20th century Green Revolution cannot be attained with a business-as-usual mindset. The current yield-centric breeding practices, of oftentimes weak breeding programs, whose objectives are largely conceived solely by the plant breeders, must evolve into participatory, multidisciplinary, and demand-driven programs that, underpinned by nurturing policy environments, make use of the most suitable scientific and technological tools to harness the potentials of PGRFA. Plant-breeding activities must perforce be re-oriented in order to have a reasonable chance of succeeding in the development of the envisaged portfolio of 'smart' crop varieties. We discuss some of the specific attributes that must characterize the result-oriented crop improvement programs of the 21st century.

Participatory plant breeding

Factoring in the perspectives of the growers and other stakeholders such as consumers, extensionists, vendors, industry, and rural cooperatives in the crop improvement endeavor of developing new varieties is known as Participatory Plant Breeding (PPB; [68]). The need for this paradigm in plant breeding is probably greatest in developing countries relative to the industrialized countries where market forces determine agricultural research and development (R&D) themes including plant-breeding objectives. By having farmers and other end-users involved in the development of varieties, feedback mechanisms are enhanced hence improving the relevance of the breeding activities to the needs of the growers. Farmers' participation in plant breeding can be categorized under the three stages of design, testing, and diffusion [69]. During the design stage, breeding goals are set and variability to be used created while at the testing stage, the breeding materials are evaluated and narrowed down to the few promising ones. The diffusion stage encompasses activities spanning varietal release, on-farm trials under farmer management and the identification of the mechanisms for the dissemination of the seeds and planting materials of the improved varieties.

Farmers, as the custodians of PGRFA, have over the several millennia of selecting from, improving, and exchanging local genetic diversity contributed immensely to the diversity of plants we grow. With the upsurge in the ready availability of modern crop varieties bred in research institutes, the roles of farmers in ensuring diversity and adding value to PGRFA have waned significantly. One effect of this shift is the precariously narrow genetic base of the modern crop varieties. The obvious threat that this poses to food security calls for the systematic re-integration of farmers' knowledge and perspectives in the developing of modern crop varieties. PPB is a veritable and validated means for ensuring this. The International Treaty, through its Article 9, also requires of contracting parties the safeguarding of

farmer's rights to access and benefit from PGRFA. Those rights are not safeguarded when crop varieties that do not meet their food security and nutritional needs and/or do not enhance the resilience of their farming systems are all that are available to them.

In general, PPB facilitates the rapid and enthusiastic adoption of crop varieties [70]. The related Participatory Varietal Selection (PVS) is a means for involving these stakeholders in breeding when elite materials are already available to select from and is relatively more rapid and cost-effective than the more resource-intensive PPB [71]. Ashby [69] identified the impact pathways for PPB and PVS and concluded that their characteristic of producing more acceptable varieties and hence increasing adoption was the most compelling incentive for plant breeders to adopt this paradigm. Indeed, a CGIAR-wide review of plant breeding had recommended that PPB constitute 'an organic part of each center's breeding program' [72].

Novel plant-breeding techniques

The incredible advances in biotechnology demonstrably hold great promise for crop improvement [73]. For instance, molecular breeding, the integration of molecular biology techniques in plant breeding [74], through enhanced efficiencies, has great potentials for changing permanently the science and art of plant breeding. Molecular breeding encompasses both the use of distinguishing molecular profiles to select breeding materials and the applications of recombinant deoxyribonucleic acid (DNA) methods, that is genetic transformation, to add value to PGRFA. There are also a number of other emerging molecular biology-based techniques that hold promise for enhancing the efficiency levels of plant breeding activities. We provide some overview of the use of these technologies and techniques in developing novel crop varieties.

Marker-assisted selection

The increasingly available rapid, efficient, high throughput, and cost-effective molecular biology tools for identifying the sources, and tracing the inheritance, of desired traits are revolutionizing the management of PGRFA in general and plant breeding in particular. Advances in molecular biology, including the ever cheaper sequencing of whole genomes, have resulted in the availability of significant amounts of information on, and hence tools for assaying, the totality of an individual's genetic make-up, that is the genome; this is known as genomics. The related proteomics (the study of proteins) and metabolomics (the study of metabolites), made possible by an ever growing volume of publicly accessible DNA, gene, and protein sequence information, are also novel ways for investigating the heredity of traits. Equally significant, advances in bioinformatics and computational molecular biology which are facilitated greatly by the novel

sophisticated and powerful information technology platforms for storing and analyzing the huge volumes of data generated through these molecular biology strategies, permit the making of valid inferences in the molecular characterization of germplasm, assessments of genetic diversity and for the selections of breeding materials.

The ability to use appropriate molecular approaches in identifying genome segments that discriminate between individuals (that is molecular markers) and to apply statistical algorithms in identifying precisely where these 'landmarks' are located on the genome has changed plant breeding permanently and will be key in developing the 'smart' crops of the 21st century. Molecular markers are now demonstrably the tools of choice for tracing the inheritance of target regions of genomes in breeding materials, a plant breeding methodology known as marker-assisted (or -aided) selection (MAS).

MAS entails the use of environment-neutral molecular markers to trace the inheritance of genes, and hence the trait(s) they control, in a breeding program with or without phenotypic selection [75]. The utility of MAS is greatest for genes whose effects are difficult, time-consuming, or otherwise expensive to evaluate in a population. This may be on account of the phenotypic effects being evident only at maturity, low heritabilities, the absence of the particular stress factor being bred for or as a result of confounding environmental influences on the trait.

The use of MAS is relatively straightforward in breeding for qualitative monogenic traits with clear-cut differences between phenotypes, such as disease resistance in plants, as the genetic mapping of the associated marker results in the mapping of the trait also and vice versa. For quantitative traits, the validation of the trait-marker association through large-scale field experimentations and statistical methods in order to more precisely identify the target genome segments, that is quantitative trait loci (QTL), is additionally required [76,77]. In general, once the marker-trait association has been verifiably established, the transmission of trait genes from parent to offspring is monitored by querying segregating materials for closely linked markers using suitably designed marker-assisted backcrossing, for instance. The utility of MAS in breeding for polygenic traits can also be derived in gene pyramiding, that is the accumulation of two or more genes, say for disease and pest resistance, which seems feasible only with this method [2].

It has been demonstrated that consistently, MAS, either as a standalone strategy or in combination with phenotyping, significantly reduces the number of generations for evaluating segregating breeding materials and generally increases efficiency levels [2,74,75,78-93]. Indeed, it has been demonstrated that MAS permits a seven-fold increase in data handling and ultimately halves the time required for breeding a new crop variety [94]. Nonetheless,

the cost-benefit analysis for adopting MAS relative to phenotypic selection is always a critical consideration that must be borne in mind in devising breeding strategies especially for developing countries.

Already routinely applied in the private sector breeding companies, such as the multinational companies, Monsanto [94]; Pioneer Hi-Bred [95] and Syngenta [96], MAS is yet to take hold in public crop improvement programs mostly on account of high set-up costs and intellectual property rights (IPR) restrictions. This implies that public sector plant breeding is clearly missing out on this singularly promising opportunity to innovate. Thro et al. [97] captured the immense expectations riding on the investments in plant genomics in relation to crop improvement in characterizing plant breeding as the 'translator' of knowledge into improved crop varieties. Public sector plant breeding is yet to assume this 'translator' role in the new dispensation of crop improvement that must be 'knowledge-intensive'.

An encouraging trend, though, is the progressive decline in the cost and the concomitant improvement in the high throughput applicability of molecular biology assays and equipment. It is logical to assume that at some point in the near future, set-up costs would be generally affordable and routine assays sufficiently efficient [98] as to permit wide adoption of MAS in the public sector. The continued successful use of MAS in the private sector is providing the much needed validation and proof of concept for this paradigm. This is critically important as capacity for this breeding methodology will be critical in handling the large populations of new breeding materials to be produced from pre-breeding activities using non-adapted genetic resources, for instance. The Integrated Breeding Platform (IBP) of the Generation Challenge Program of the CGIAR [99] is an example of multi-stakeholder efforts to extend the use of MAS to developing elite varieties of food security crops in developing countries.

Genetic transformation

Recombinant DNA technology, involving the use of molecules containing DNA sequences derived from more than one source to create novel genetic variation, has become an important crop improvement option. This is known as genetic modification (or transformation) with the new variants referred to as transgenics or simply genetically modified organisms (GMOs). The procedures involve the incorporation of exogenous DNA or ribonucleic acid (RNA) sequences, using either biolistics or vectors, into the genome of the recipient organism which, as a result, expresses novel and agronomically useful traits. Though transgenic varieties of only four crops, maize, soybean, canola, and cotton, harboring two transformation events, that is herbicide tolerance and insect resistance or their combinations,

have been grown commercially since the first approvals in 1996, James [100] estimated that there had been a 94-fold increase in hectareage in the 16 years of the commercialization of genetically modified (GM) crops (from 1.7 million hectares in 1996 to 160 million hectares in 2011). Grown in 29 countries (19 developing and 10 industrial), the author estimated the value of the GMO seed market at US\$13.2 billion in 2011 while the produce for GM maize, soybean, and cotton were valued in excess of US\$160 billion for the same year.

In spite of the low numbers of commercial GM crops and the transformation events that confer the modified agronomic traits, four and two, respectively, the development and deployment of GM crops signal a trend in crop improvement that can no longer be ignored. This is more so as approvals for the importation of GM crops and release to the environment had been approved in 31 other countries [100]. Tester and Langridge [2] pointed out that, though the major contributions to crop improvement for this decade will be non-GM, the production and evaluation of GM crops remained an actively researched theme with only political and bioethical considerations (both driven mostly by public negative perceptions for the technology) constituting the main hindrances to wider access to the technology by growers in more countries.

Technically, the drawbacks to more widespread development of GM varieties include the lack of efficient genotype-independent regeneration systems for most crops. Also, the lingering technical difficulties with the stacking of transformation events severely limits the utility of genetic transformation in breeding for polygenic traits such as resistance to the abiotic stresses, for example salinity and drought, being caused by climate change and variations. However, the successful stacking of genes conferring insect resistance and herbicide tolerance [100] is indicative of progress in addressing this constraint. Also, research efforts must target the increasing of the range of agronomic traits being improved through this method; the two transformation events in commercial varieties are simply inadequate for GM technology to become a dominant crop improvement method.

Probably the most limiting of all factors, however, is the associated intellectual property rights (IPR) protections that restrict access to the technology. Such IPR regimes have made GMOs remain the exclusive preserve of multinational plant breeding and seed companies in developed countries that effectively use patents to restrict access to several technologies relevant to the R&D efforts for the production of the transgenic crops. These constraints must be addressed in order that this technology be used fully in realizing its possible contributions to the development of the 'smart' crop varieties of this century. With GMO crops currently grown in developing

countries, for example about 60 million hectares in South America in 2011 and with millions of small holder farmers cultivating transgenic cotton in both India and China [100-102], it is plausible to expect that the IPR regimes will be changing in the future. Another hindrance to wider adoption of the GM technology is the absence of biosafety regulatory frameworks as specified by the Cartagena Protocol on Biosafety to the Convention on Biological Diversity [103] in many countries.

Efforts to address the constraints that impede both the use of the GM technology in R&D and the cultivation of GMOs have been significant as well. For instance, the African Agricultural Technology Foundation (AATF; [104]), based in Nairobi, Kenya, is acquiring and deploying proprietary agricultural technologies in sub-Saharan Africa. In one instance, AATF obtained 'a royalty-free, nonexclusive license to Monsanto technology, a *Bacillus thuringiensis* (Bt) gene (cry-1Ab)' which is being used in the development of cowpea varieties with resistance to the cowpea pod borer [105]. Similarly, the US-based Public Sector Intellectual Property Resource for Agriculture (PIPRA; [106]), assists 'foundations, not-for-profit organizations, universities, international aid agencies, and governments' in dealing with IPR issues in order to enable access to proprietary technologies. Also, Cambia, an Australian private, non-profit research institute, publishes relevant patents, white papers, and provides tutorials as means 'to provide technical solutions that empower local innovators to develop new agricultural solutions' [107]. The activities of these organizations underscore the seriousness of the impediments that IPR protections pose for innovations in agriculture and the countervailing efforts to extend the reach of the technologies and applications especially into the public goods and commons R&D domains.

Emerging biotechnology techniques of relevance to plant breeding

The integration of biotechnologies into crop improvement is a very dynamic field of endeavor that is changing continually. A snapshot of the status of emerging technologies is provided by Lusser et al. [108] in response to a request by the European Commission 'to provide information on the state of adoption and possible economic impact of new plant breeding techniques'. The authors identified eight new such techniques and concluded that the new varieties ensuing from these techniques might be released within 3 years. These new techniques and their features are:

- Zinc finger nuclease (ZFN): Single mutations or short indels are generated or new genes are introduced into pre-determined target sites of the genome
- Oligonucleotide directed mutagenesis (ODM): Targeted mutations of one or a few nucleotides are induced
- Cisgenesis and intragenesis: GMOs are produced by the insertion of hereditary materials derived from the species itself or from a cross-compatible species and are contiguous and unchanged (cisgenesis) or the inserted DNA may be a new combination of DNA fragments but must still be from the species itself or from a cross-compatible species
- RNA-dependent DNA methylation (RdDM): Still being refined, modified gene expressions are epigenetic with the new phenotypes inherited only over a few generations
- Grafting (on GM rootstock): Desired improvements are achieved by the grafting of non-transgenic scions onto GM rootstock
- Reverse breeding: A combination of recombinant DNA techniques and cell biology procedures is used to generate suitable transgene-free homozygous parental lines rapidly for reconstituting elite heterozygous genotypes
- Agro-infiltration: Used mostly in research settings, for example to study plant-pathogen interaction in living tissues, to select parental lines or to evaluate the efficacy of transgenes, a liquid suspension of *Agrobacterium* sp. containing the desired gene(s) is used to infiltrate plant tissues, mostly leaves, so that the genes are locally and transiently expressed at high levels
- Synthetic genomics: Large functional DNA molecules that are synthesized without any natural templates are used for constructing viable minimal genomes which can serve as platforms for the biochemical production of chemicals such as biofuels and pharmaceuticals

Lusser et al. [108] concluded that ODM, cisgenesis/intragenesis, and agro-infiltration were the most commonly used techniques with the crops developed using them having reached the commercial development phase. On the other hand, the ZFN technology, RdDM, grafting on GM rootstocks, and reverse breeding were the less used techniques in breeding. The authors further projected that the first commercial products derived from these technologies that will be released for production would be herbicide resistant oilseed rape and maize using ODM and fungal resistant potatoes, drought tolerant maize, scab resistant apples, and potatoes with reduced amylose content developed using cisgenesis and/or intragenesis.

The clearly identified needs for the further fine-tuning of technical impediments to the routine adoptions and use of these new techniques notwithstanding, it would

appear that policy regulations that are expensive to comply with and public perceptions, rather than the ability to innovate, are holding back the unleashing of the incredible advances of science and technology in crop improvement. Considering that Blakeney [109] opined that 'the right to patent agricultural innovations is increasingly located within a political context', it is plausible that the magnitude of the worsening threats to global food security may ultimately serve as the critical inducement for policy-makers, interest groups, and leaders of thought and industries to unravel the thorny issues that constrain the scope of the integration of biotechnology into crop improvement.

High throughput phenotypic evaluations

The selections of few promising individuals out of large populations of segregating materials can be a very daunting task. With MAS, the volume of assays that can be carried out and data points generated per unit time has increased substantially. For the workflow to be wholly efficient, the assessments of the phenotypes must also keep pace with high throughput molecular assays. Indeed, for molecular data used in breeding to be reliable, the corresponding phenotypic data for which inferences are made, must also be accurate [110]. Phenomics, the study of phenomes - the sum total of an individual's phenotype is the term that describes the novel high throughput measurements of the physical and chemical attributes of an organism. Somewhat imprecisely named in this seeming analogy to genomics, it is defined by Houle *et al.* [111] as 'the acquisition of high-dimensional phenotypic data on an organism-wide scale'. High throughput imaging of parts of a living plant, for example roots and leaves, using thermal infra-red, near infra-red, fluorescence, and even magnetic resonance imaging permit non-destructive physiological, morphological, and biochemical assays as means for dissecting complex traits such as drought and salinity tolerances into their component traits [112,113]. Though significant technical challenges, such as data management, still require addressing, phenomics facilities are increasingly being set up with a number of them providing high throughput phenotyping services to requestors. These new facilities include the High Resolution Plant Phenomics Centre in Canberra and the Plant Accelerator in Adelaide, both in Australia [114]; LemnaTec in Wuersele [115] and Jülich Plant Phenotyping Centre in Jülich [116] both in Germany; and Ecotron [117] and Ecophysiology Laboratory of Plant Under Environmental Stress (LEPSE; [118]) both in Montpellier, France. In Canada, there is the The Biotron Experimental Climate Change Research Centre in London, Ontario [119]. The high set-up costs and technical know-how may impede the access of developing countries to such platforms for some considerable time.

Overarching policy environment for the PGRFA management continuum

The benefits of value addition to PGRFA, that is improved crop varieties that meet the needs of the growers, can be derived sustainably, especially for the most at-risk food insecure countries in the developing world, only with the comprehensive strengthening of, and forging of linkages between, the three components of the PGRFA value chain: (1) conservation; (2) plant breeding; and (3) the delivery of high quality seeds and planting materials to growers. This is the 'PGRFA continuum' [120], the seamless dovetailing of the three components, as distinct from targeting the strengthening of any of the three in isolation. Based on the cohesion in this value chain - that characterizes the activities of private sector commercial breeding companies and the PGRFA management of some emerging countries such as Brazil, China, and India [94] - it is logical to conclude that the real value of crop germplasm lies in its use in plant breeding. Pragmatically also, the efforts invested in breeding come to naught if there is no effective delivery system for the seeds and planting materials underscoring therefore the need to interlock all three components.

The successful implementation of the Second GPA [46] also envisages the adoption of this continuum approach. The 18 priority activities (Box 1) of the GPA provide a most practical template for countries for concerted interventions at the three components of the PGRFA value chain. These PAs are subdivided into four main themes: *in-situ* conservation and management; *ex-situ* conservation; sustainable use; and building sustainable institutional and human capacities.

The sustainable use of PGRFA encompasses activities relating to direct utilization of PGRFA by farmers and to their uses in crop improvement. The International Treaty, especially in its Article 6, equally requires of contracting parties not only to conserve their genetic resources but to use them (for value addition) and to deliver the improved varieties efficiently. FAO [121] opined that 'any weakness in this continuum truncates the value chain and effectively scuttles all the efforts to grow the most suitable crop varieties'. It is in this vein that FAO and partners are working with developing countries to articulate National PGRFA Strategies for institutionalizing the continuum approach to managing PGRFA [120]. The strategy identifies priority crops and relevant stakeholders; prescribes time-bound action plans across the continuum and enunciates governance mechanisms and means for monitoring implementation. Nurturing policy environments, especially those that enable countries adopt the continuum approach to the management of PGRFA, are critically important for reaping the most sustainable benefits from PGRFA, namely, the improved crop varieties.

FAO's normative activities provide support for the implementations of the International Treaty and the Second GPA and for developing the necessary policies, and legislations as means for attaining this goal.

Winning partnerships

The reorientation of crop improvement in order to be responsive to the drivers of food insecurity, especially in developing and emerging economies, will require a wider range of partnerships beyond the traditional National Agricultural Research and Extension Systems (NARES). FAO [38] reported the prevailing trend whereby the private sector (multinational and local commercial plant breeding and seed companies) is increasingly developing and deploying elite crop varieties especially in instances where markets, favorable policy regimes, and legal frameworks that spur investments are in place. In tandem, public investment in crop breeding programs is contracting implying therefore that the breeding and dissemination of elite varieties of crops that fall outside of the business remit of the private sector could, as is increasingly the case, be neglected to the detriment of food security. Equally important is the role of non-governmental organizations and myriad civil society actors in the provision of agricultural extension services in developing countries. These burgeoning dynamics must influence the articulation of policies and the building of collaborations and wide-ranging partnerships. For such partnerships to succeed, local knowledge must be integrated just as relevant private and public sector entities including the NARES, centers of the CGIAR, and regional R&D networks are assembled. The safeguarding of intellectual property rights, including plant variety protection, and the respect of patents are means for attracting private sector investments. Public-private partnerships, for example the ongoing joint activities between Syngenta and public African NARES [122,123], are particularly important for technology transfer, a critical vehicle for increasing the access of developing countries to novel biotechnologies that impact on crop improvement, for instance. On the other hand, public sector investments in food security must be ensured as the private sector, especially in developing countries, do not cater for all crops that are important for food security. Partnerships must also be cross-sectoral, for instance between ministries responsible for the environment, science and technology, commerce, education, and the ministry of agriculture. This ensures access to the full spectrum of PGRFA that may be needed for value addition while also ensuring a means for delivering the planting materials efficiently to the growers in gainful manners.

National capacities for crop improvement

The GIPB surveyed 81 countries for capacities in plant breeding and related biotechnologies [124] and subsequently conducted in-depth analysis of the plant-breeding and seed systems sectors of six of the countries: Ghana, Kenya, Malawi, Bangladesh, Thailand, and Uruguay [125]. The findings reflected the deduction by FAO [38] that, in general, the scope of funding, staffing and hence, activities per capita, of publicly-funded plant-breeding programs were either dwindling progressively or had stagnated over time. In Africa, instances of up to a 10-fold decrease in funding of plant breeding activities have occurred between 1985 and 2001 [126,127]. The worrisome global trend of ageing and retiring plant breeders that were not being replaced by younger ones was captured in these surveys also; over 40% of plant breeders in the countries surveyed were aged 50 years and above. Indeed, to compound the problem, too few new plant breeders are being trained in universities in both developed and developing countries [127-129]. It would appear though that there was no perceptible downward trend in the award of plant breeding degrees in the USA between 1995 and 2000 [130] implying that this problem might either have been more acute in developing countries [128] or had assumed a global dimension only in the last decade. Currently, there is a general consensus however that the current capacity for plant breeding is inadequate to deal with the generational challenges of food insecurity with Knight [131] encapsulating the sense of despair in the somberly titled article, 'A Dying Breed'.

The training of future plant breeders is generally considered a major component of the preparedness for sustained food security and has been the subject of copious analyses and studies. For instance, the symposium 'Plant Breeding and the Public Sector: Who Will Train Plant Breeders in the U.S. and around the World?' held at Michigan State University in the US was aimed at charting a course for addressing this critical constraint through the devising of curricula, raising awareness, and fostering partnerships [126,132-139]. The symposium concluded that future plant breeders, at PhD level, must in addition to possessing skills in the traditional disciplines of experimental design, applied statistics, Mendelian (transmission) genetics, population and quantitative genetics, and principles and practice of plant breeding also be trained in myriad areas ranging from subjects in the biological sciences including plant physiology, ecology, pathology, entomology, molecular biology, and genomics through business management to law, especially IPR [137]. More recently, Repinski *et al.* [129] in analyzing a very wide ranging Delphi study for articulating the curriculum of the future plant breeder came to the same conclusions regarding the need for broadening the scope of the curriculum to reflect the realities of modern breeding techniques and the fact that a significant

number of plant breeders work in the private sector where legal and policy issues are critically important. Multidisciplinary teams, staffed by personnel with specialized skills in these areas, will compensate for the reality that no one plant breeder will be adept at sufficient levels of skill in all these disciplines.

Granted, most private sector plant breeders graduated from publicly-funded institutions ([132] estimated that most private sector breeders in the US attended publicly-funded land grant universities, for instance) but the public sector's role in the training of plant breeders is very critical and must be considered a contribution to public good [133] that cannot be ceded wholly to the private sector without compromising the future of plant breeding and hence food security. While the role of the private sector is also critical in this regard, in the provision of fellowships, for instance [139], it should not be expected to play the leading role as funding could not be guaranteed this way.

The centers of the CGIAR are also considered valuable partners in the training of plant breeders [133]. With improved funding, these centers, appropriately located in developing countries and working on food security crops, could provide the much-needed training facilities that many developing country governments cannot provide. The IBP, for instance, is spearheading the training of plant breeders from developing countries in molecular breeding techniques. The African Centre for Crop Improvement (ACCI; [139]) at the University of Kwazulu-Natal, South Africa and the West Africa Centre for Crop Improvement (WACCI;) at the University of Ghana, Legon, Ghana, both funded under the auspices for the Alliance for a Green Revolution in Africa, are producing highly skilled plant breeders that are trained in Africa to work on African food security crops. Both universities partner with Cornell University, Ithaca, New York in the US in this endeavor. This is a very laudable model that is bridging the gap created by the continued inability of countries to establish and fund training facilities adequately.

Conclusions and future perspectives

There is a compelling urgency to institute measures that ensure that farmers worldwide, but especially the small-scale farmers that produce the majority of the food in food insecure countries, can grow the portfolio of suitable crop varieties that are amenable to the eco-efficient production systems of the sustainable crop production intensification (SCPI) paradigm needed to feed the world in the 21st century. The major hindrances to the attainment of SCPI include: inadequate investment; sub-optimal human resources; inability to innovate as evidenced in prevailing inadequate deployment of appropriate science and technology; weak institutions; sub-optimal R&D infrastructure; and poor policy regimes. Crop improvement, by fostering genetic gains that aid food production through enhanced

productivities, is a very critical component of SCPI. We make the case therefore that plant breeding, by translating the potentials inherent in PGRFA into 'smart' crop varieties, can engender a most significant impetus for sustained food security even as human population increases and extremely inclement weather conditions constrain crop production. To achieve this, plant breeding must be re-oriented in a number of very critical ways.

Broadened genetic diversity of crops

Firstly, the extremely narrow genetic base of crops, which puts food security at risk, must be broadened at both the intra- and inter-specific levels. Conserved PGRFA, *ex-situ* and *in-situ*, and the heritable diversity available on-farm, including in landraces, must be explored to source the novel alleles that confer enhanced productivities. FAO through its Global PGRFA System, the International Treaty and the Global Crop Diversity Trust; the CGIAR centers, regional networks, and the NARES around the world must continue to invest considerable efforts to ensure that breeders have access to the genetic variations they require for their work. Some harmonization of the information dissemination mechanisms is called for to ensure enhanced efficiencies. International norms are now being leveraged to facilitate the sourcing of these much needed genetic variations even across national boundaries. Induced mutations, an established scientific method that has been used for almost one century to mimic nature, is increasingly important for inducing the unmasking of novel alleles of genes to which plant breeders do not otherwise have access. The current constraints to crop productivities deny humanity the limitless space and time for the natural process of spontaneous mutations to make these novel heritable variations available. Pre-breeding is critical in achieving this broadened genetic base of crops. The introduction of new genes and their variants into crops from novel sources will be critical to replicating the impacts of the Green Revolution as the current generational challenges demand.

Defining the breeding objectives

A second area for re-orienting plant breeding is in the 'what'. What should be the breeding objectives? Without de-emphasizing yield, resistances to biotic and abiotic stresses of import in climate change adaptation, enhanced nutritional quality traits, and the multipurpose use of crop biomass (including for bioenergy, livestock feed, and fiber) are key objectives. Also, the amenability to low-input eco-efficient farming systems will increasingly constitute standard breeding objectives. The enthusiastic adoption of NERICA in sub-Saharan Africa is an example of the efficacy of the alignment of breeding objectives to addressing the constraints

posed by empirically determined drivers. In general, market forces which reflect end-user preferences will be the main driver in the definition of breeding objectives.

Innovating for result-oriented plant breeding

Thirdly, the 'how' of plant breeding will probably attract the most innovative interventions. How should crops be bred? Increased use of the immensely powerful biotechnologies that have revolutionized the biological sciences is imperative. Demonstrably, MAS, supported by the tools of genomics and the other -omics and information technology platforms, permits high throughput evaluations of breeding materials. Genetic transformation and the resulting GM crops are increasingly cultivated around the world; the technology holds promise and countries need capacity building in order to, at the minimum, make evidence-based decisions as to its adoption. Equally, the other emerging biotechnologies such as ZFN, ODM, transgenesis and cisgenesis, RdDM, grafting on GM stock, reverse breeding, agro-infiltration, and synthetic genomics, though requiring further refinements to varying degrees, will also become quite important in the very near future. Countries will increasingly require support in navigating the IPR regimes that govern access to these technologies and the regulatory issues pertaining to their adoptions. As massive numbers of new breeding materials are generated through pre-breeding, MAS must be complemented by phenomics in order that reliable predictions of the breeding values can be made. Private sector plant breeding and seed companies have taken the lead in leveraging these innovations in producing highly successful crop varieties and provide models for re-tooling the public sector crop improvement programs.

Policy and strategic interventions

A fourth consideration is the 'where' in the agricultural R&D environment for situating plant breeding. Certainly, an enabling environment is required for breeding to be relevant and, hence, thrive. The erstwhile piecemeal interventions at the three components of the PGRFA value chain, namely, conservation, breeding, and dissemination of seeds and planting materials is, simply, inadequate. A result-oriented plant breeding must have access to the widest possible source of heritable variations just as it needs an effective mechanism to deliver high quality seeds and planting materials to the growers. This is the PGRFA continuum that significantly enhances the ability of plant breeding to deliver need-based outputs. We posit that not only all three individual components but their intervening linkages must be strengthened in tandem. A National PGRFA Strategy helps to institutionalize this paradigm that demonstrably mirrors the operations of the highly successful private sector crop improvement multinationals.

Winning partnerships for the reinvigorated crop improvement

The 'who' of the 21st century plant breeding is the fifth critical consideration. Who are the main stakeholders in the crop improvement component of the PGRFA management continuum? The increasingly pivotal roles of the private sector must be factored into policy-making and in the development of strategies. The private sector is not only marketing seeds and planting materials but also breeding the new varieties; its continued participation in these activities must be encouraged especially where comparative advantages are demonstrated. Enabling policy, legal, and market environments that spur innovation and investments of capital are key to fostering the much needed public-private partnerships required for operating at scale. A healthy balance must be struck between IPR (and the innovations and investments that they encourage) and the imperative of contributing to public good. The roles of the International Convention for the Protection of New Varieties of Plants, that is UPOV, and various national, regional, and global industry interest groups will be critically important in this regard.

Capacity enhancements for the 21st century plant breeder

A sixth consideration is the 'by whom'. What is the profile of the 21st century plant breeder? In fact, the 'plant breeder' is the multidisciplinary team that makes use of the most appropriate scientific and technological tools in generating new crop varieties and the germplasm curators, farmers, and seed marketers that they work with. Technically, the multidisciplinary team driving a breeding program will include persons skilled in the traditional disciplines of plant breeding as well as those with in-depth knowledge of various ancillary biotechnological techniques. Skills in information technology, business management, law, and so on will also be required in such teams. Aside from private sector plant breeding and seed companies, such a suite of expertise does not exist in most public sector breeding concerns. The training of the future plant breeder, though mentioned often now, is still not receiving as much attention, in terms of funding, facilities, skilled trainers, and the number of available opportunities, which it deserves. Capacity building will require wide-ranging public-private partnerships in order that the curriculum being developed can be effective. The role of the CGIAR centers will remain critical. The regional training hubs, ACCI and WACCI, provide models worth emulating and scaling up. The highly successful land grant universities scheme of the United States demonstrates the lasting impacts that concerted investment of resources in training can have.

Strengthening the NARES

Finally, the re-oriented crop improvement programs require a sustaining platform, in this case, the NARES. As we have indicated, the continued decline in funding for agricultural R&D has led to weakened NARES; breeding programs are ill-staffed and poorly equipped while extension systems have become moribund in many developing countries. Equally disturbing is the dearth of reliable mechanisms for the dissemination of high quality seeds and planting materials of improved varieties. Indeed, while the work of the CGIAR centers in filling this gap cannot but be commended, the manifest over dependence of many NARES on these centers can only be injurious in the long run. For one thing, the mandates of these centers preclude work on many important food security crops. United in the recognition of the imperative for re-orienting agriculture, development organizations including FAO, the World Bank, the International Fund for Agricultural Development (IFAD), the CGIAR, and so on have severely recommitted their resolves to stamp out hunger. The strengthening of the NARES, the ultimate bulwark between hunger and the populace in many developing countries, must be at the top of the agenda. Bold initiatives underpinned by political will have strengthened and re-oriented agriculture in the past. For instance, the contributions of the land grant universities, including the extension services, to the food security of the US are legendary. Many national governments sadly lack the political will to strengthen their NARES as means for ending hunger. Support to national governments must therefore include mechanisms that contribute to fostering the nurturing policy environments for investments to bear fruit. In the final analysis, the ultimate responsibilities for crop improvement, just as in safeguarding food security in general, lies with national governments and by extension, their NARES. These responsibilities may be abdicated only at the peril of food security and at the certain risk of consequent instability and retarded development. The well-funded and adequately staffed Embrapa, Brazil's Agricultural Research Corporation, for instance, demonstrates very clearly the recent significant impacts that government policies can have on the viability of a country's agricultural R&D sector.

The coalescence of the consequences of climate change and variations with other critical demographic, economic, social, and industrial pressures pose unprecedented monumental risks to food security and people's general well-being. Unarguably, crop improvement and its outputs of 'smart' crop varieties can contribute to mitigating these threats. Multilateral organizations, civil society, and national governments must ride the momentum of the current reinvigorated attention to food security and strengthen capacities for crop improvement in innovative manners. Countries need assistance with suites of actionable policy interventions that leverage validated technologies and strategies in aid of result-oriented crop improvement. Such

policy items or measures that countries can adopt in strengthening the three components of, and the linkages between, the PGRFA continuum in tandem are not readily available in forms amenable to ease of dissemination. The re-orienting of crop improvement would require the packaging of validated measures into a 'toolbox' to act as a one-stop shop for actionable intervention instruments. The work of the GIPB and similar multi-stakeholder platforms in articulating and assembling such tools serve as examples of multi-stakeholder efforts that deserve continued support especially in order to operate successfully at scale.

Abbreviations

AATF, African Agricultural Technology Foundation; ACCL, African Centre for Crop Improvement; Bt, *Bacillus thuringiensis*; CBD, Convention on Biological Diversity; CGIAR, Consultative Group on International Agricultural Research; CWRs, crop wild relatives; DNA, deoxyribonucleic acid; FAO, Food and Agriculture Organization of the United Nations; GIPB, Global Partnership Initiative for Plant Breeding Capacity Building; GM, genetically modified; GMO, genetically modified organism; GPA, Global Plan of Action for Plant Genetic Resources for Food and Agriculture; IBP, Integrated Breeding Platform of the Generation Challenge Program of the CGIAR; IFAD, International Fund for Agricultural Development; IFPRI, International Food Policy Research Institute; IPCC, United Nation's Intergovernmental Panel on Climate Change; MAS, Marker-Assisted (or, Aided) Selection; NARES, National Agricultural Research and Extension Systems; NERICA, New Rice for Africa; ODM, Oligonucleotide directed mutagenesis; PGRFA, Plant Genetic Resources for Food and Agriculture; PIPRA, Public Sector Intellectual Property Resource for Agriculture; PPB, Participatory Plant Breeding; PVS, Participatory Varietal Selection; R&D, research and development; QTL, quantitative trait loci; RdDM, RNA-dependent DNA methylation; RNA, ribonucleic acid; SCPI, sustainable crop production intensification; TAC, Technical Advisory Committee of the Consultative Group on International Agricultural Research; TILLING, Targeted Induced Local Lesions IN Genomes; UPOV, International Convention for the Protection of New Varieties of Plants; WACCI, West Africa Centre for Crop Improvement; WIEWS, World Information and Early Warning System; ZFN, Zinc finger nuclease.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

CM conceived of the study, developed the outline for a publication, conducted literature reviews, coordinated inputs and drafted the manuscript. EPG conducted literature reviews and contributed to the design and draft of the manuscript. KG conducted literature reviews and contributed to the design and draft of the manuscript. All authors read and approved the manuscript.

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