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Review

Increasing Food Production in Africa by Boosting the Productivity of Understudied Crops

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Abstract: The Green Revolution has enabled Asian countries to boost their crop production enormously. However, Africa has not benefitted from this agricultural revolution since it did not consider local, but important crops grown in the continent. In addition to their versatile adaptation to extreme environmental conditions, African indigenous crops provide income for subsistence farmers and serve as staple food for the vast majority of low-income consumers. These crops, which are composed of cereals, legumes, vegetables and root crops, are commonly known as underutilized or orphan crops. Recently, some of these under-researched crops have received the attention of the national and international research community, and modern improvement techniques including diverse genetic and genomic tools have been applied in order to boost their productivity. The major bottlenecks affecting the productivity of these crops are unimproved genetic traits such as low yield and poor nutritional status and environmental factors such as drought, weeds and pests. Hence, an agricultural revolution is needed to increase food production of these under-researched crops in order to feed the ever-increasing population in Africa. Here, we present both the benefits and drawbacks of major African crops, the efforts being made to improve them, and suggestions for some future directions.

Keywords: African crops; orphan crops; understudied crops; crop improvement; breeding techniques

Abbreviations and Acronyms

AATF: African Agricultural Technology Foundation; **ABNETA**: Agricultural Biotechnology Network in Africa; **ABSPII**: Agricultural Biotechnology Support Project II; **AFLP:** Amplified Fragment Length Polymorphisms; **AGRA**: Alliance for a Green Revolution in Africa; **ASARECA**: Association for Strengthening Agricultural Research in Eastern and Central Africa; **BecA**: Biosciences eastern and central Africa; **BioInnovate**: Bio-resource Innovations Network for Eastern Africa Development; **CAADP**: Comprehensive Africa Agriculture Development Program; **CGA**: Candidate Gene Approach; **CGIAR**: Consultative Group on International Agricultural Research; **CIAT**: International Center for Tropical Agriculture; **CIMMYT:** International Maize and Wheat Improvement Center; **CIP**: International Potato Center; **CIRAD**: Agricultural Research Centre for International Development; **CORAF/WECARD**: West and Central African Council for Agric. Research and Development; **CTA:** Technical Centre for Agricultural and Rural Cooperation; **DZARC**: Debre Zeit Agricultural Research Center; **EIAR**: Ethiopian Institute of Agricultural Research; **FAO**: Food and Agriculture Organization of the United Nations; **FAOSTAT**: FAO statistical database; **FARA**: Forum for Agricultural Research in Africa; **GA**: Gibberellic acid; **GBS**: Genotyping-by-sequencing; **GCP**: Generation Challenge Programme; **GFAR**: Global Forum on Agricultural Research; **GFU**: Global Facilitation Unit for Underutilized Species; **IAA**: indole acetic acid; **IAEA**: International Atomic Energy Agency; **IARCs**: International agricultural research centers; **ICARDA**: International Center for Agricultural Research in the Dry Areas; **ICRISAT**: International Crops Research Institute for the Semi-Arid Tropics; **ICUC**: International Centre for Underutilized-Crops; **IFAD**: International Fund for Agricultural Development; **IFPRI**: International Food Policy Research Institute; **IITA**: International Institute of Tropical Agriculture; **ILRI**: International Livestock Research Institute; **INDEL**: Insertions and Deletions; **IPBO**: Institute of Plant Biotechnology for developing Countries; IRD: Institut de recherche pour le développement; **ISAAA**: International Service for the Acquisition of Agri-biotech Applications; **MAS**: marker-assisted selection; **MoA**: Ministry of Agriculture; **NARS**: National Agricultural Research Systems; **NEPAD:** New Partnership for Africa's Development; **NERICA**: New Rice for Africa; **NGO**: non-governmental organization; **NUE**: nitrogen use efficiency; **ODAP**: β-*N*-Oxalyl-L-α, β-diaminopropanoic acid; **PAEPARD**: Platform for African–European Partnerships on Agric. Research for Development; **PPB**: participatory plant breeding; **PVS**: participatory variety selection; **QTL**: quantitative trait locus; RIL: recombinant inbred line; **RAD**: Restriction-site Associated DNA; **SADC/FANR**: Southern African Development Community/Food, Agric. and Natural Resources; **SNP**: Single Nucleotide Polymorphisms; **SSR**: Simple Sequence Repeats, also known as microsatellites; **TALEN**: Transcription Activator-like Effector Nuclease; **TILLING**: Targeting Induced Local Lesion IN Genomes; **TIP**: Tef Improvement Project.

1. Types and Significance of African Indigenous Crops

African indigenous crops are also known as orphan crops [1], underutilized crops [2], lost crops [3–5], neglected crops [6] or crops for the future [7]. According to Naylor *et al.* [1] twenty-seven orphan crops within developing countries are annually grown on about 250 million hectares of land. These crops belong to the major groups of crops including cereals, legumes, and root crops. In general, these crops play a key role in the livelihood of the resource-poor farmers and consumers in Africa because they perform better than the major world crops under extreme soil and climate conditions prevalent in the continent. Table 1 shows the list of some of these crops and their desirable and undesirable traits. Brief descriptions are provided below for the most important cereals, legumes and root crops.

Table 1. Major understudied crops of Africa and their desirable and undesirable traits.

Type of crop	Common Name	Botanical name	Desirable property	Undesirable property	Reference
Cereals	Finger millet	*Eleusine coracana*	High in iron & protein, low in glycemic index	Low productivity	[2,8]
	Fonio	*Digitaria exilis*	Fast maturing	Low productivity	[5,8]
	African rice	*Oryza glaberrima*	Resistance to diseases & pests	Lodging & shattering of seed	[5,9]
	Pearl millet	*Pennisetum glaucum*	Drought & heat tolerance	Insect pests & diseases	[10]
	Tef	*Eragrostis tef*	Abiotic stress tolerance, free of gluten	Low productivity & lodging	[11,12]
Leguminous crops	Bambara groundnut	*Vigna subterranea*	Nutritious & drought tolerance	Late maturing	[3]
	Cowpea	*Vigna unguiculata*	Drought tolerance & nutritious	Low productivity & insects	[3]
	Grass pea	*Lathyrus sativus*	Extreme drought tolerance & nutritious	Toxic seeds	[13]
Vegetables	Amaranth	*Amaranthus* spp.	Fast growing & nutritious	Insect pests & diseases	[3]
	Celosia	*Celosia argentea*	High productivity	Sensitivity to nematodes & water-logging	[3,8]
	Dika	*Irvingia gabonensis, I. wombolu*	Rich in oil	Difficulty of kernel removal	[3]
	Okra	*Abelmoschus esculentus*	Tolerance to biotic stresses, fast growing & nutritious	Short shelf-life	[14]

Table 1. *Cont.*

Type of crop	Common Name	Botanical name	Desirable property	Undesirable property	Reference
Oil seeds	Ethiopian Mustard	*Brassica carinata*	Drought tolerance & resistance to insect pests	Poor quality oil	[15]
	Noug	*Guizotia abyssinica*	High oil content	Low productivity, insect pests	[16]
	Sesame	*Sesamum indicum*	Oxidatively stable oil	Low productivity & shattering	[2]
	Vernonia	*Vernonia galamensis*	High in industrial oil		[8,17]
Root crops	Cassava	*Manihot esculentum*	Drought tolerance	Toxic, less nutritious & diseases	[18]
	African yam bean	*Sphenostylis stenocarpa*	High protein content	Late maturing	[3]
	Enset	*Ensete ventricosum*	Drought tolerance	Less nutritious	[19]
	Yam	*Dioscorea* spp	Drought tolerance	Less nutritious	[8]
	Sweet potato	*Ipomoea batatas*	Rich in riboflavin & calcium	Diseases & insect pests	[2]
Fruits	Banana	*Musa* spp.	Healthy & nutritious	Pests & diseases	[20]
	Plantain	*Musa* spp.	Healthy & nutritious	Pests & diseases	[20]

1.1. Cereals

Cereals are rich sources of nutrients for both humans and animals. African cereals, particularly millets, have got high amounts of vitamins, calcium, iron, potassium, magnesium and zinc [21]. The straws and crop residues of cereals are also the main sources of livestock feed for farmers in developing countries. Crops such as finger and pearl millets were recently shown to have an anti-proliferative property, and might have a potential in the prevention of cancer initiation [22]. This anti-proliferative property is associated with the presence and content of phenolic extracts.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is dominantly cultivated as a food crop in the semi-arid areas of Asia and Africa due to its extreme tolerance to moisture deficit [10]. It is annually cultivated on about 16 million ha in Africa alone [23]. Finger millet (*Eleusine coracana* Gaertn.) is one of the important food crops in the semi-arid regions of Asia and Africa due to its adaptation to unfavorable climatic and soil conditions especially drought [2,8]. The seeds of finger millet contain valuable amino acids especially methionine [5], which is lacking in the diets of hundreds of millions of the poor who live on starchy staples such as cassava. Finger millet is also a popular food among diabetic patients because of its low glycemic index and slow digestion [24]. Tef [*Eragrostis tef* (Zucc.) Trotter] is a cereal crop mainly grown in the Horn of Africa, and its annual cultivation in Ethiopia alone accounts for over 2.8 million ha of land [25]. The crop is tolerant towards abiotic stresses, especially to poorly drained soils where other crops such as maize and wheat do not withstand [11]. In addition, tef is considered a healthy food since the seeds do not contain gluten [12,26], the cause for celiac disease. Fonio (*acha*) [*Digitaria exilis* (Kippist) Stapf. and *D. iburua* Stapf] is widely cultivated for human food in the semi-arid regions of West Africa. Fonio is not only drought-tolerant but also a very fast-maturing crop [5,8]. The seeds of fonio are nutritious, especially in methionine and cysteine, the two amino acids essential for human health, but deficient in major cereals such as wheat, rice and maize [27]. African rice (*Oryza glaberrima* Steudel) is mostly cultivated in West Africa especially in drought-prone areas and on impoverished soils [5,9]. Due to its early maturing property, African rice is the source of food during food shortage particularly just before other crops are harvested.

1.2. Leguminous Crops

Legumes are the major source of protein for consumers. Due to their ability to fix atmospheric nitrogen and convert it to the available form for plants, legumes contribute towards improving the soil. Bambara groundnut [*Vigna subterranean* (L.) Verdc.] is grown for human consumption and is the third most important grain legume in Africa after cowpea and groundnut [28]. The seeds of bambara groundnut are known as a complete food because they contain adequate quantities of protein (19%), carbohydrate (63%), and fat (6.5%) [3]. Cowpea [*Vigna unguiculata* (L.) Walp.] is grown on about 10 million hectares of land in the world, mainly in Africa. The crop is tolerant towards drought and heat, and it also performs better than many other crops on sandy soils with low levels of organic matter and phosphorus [29]. Since cowpea has got a quick growth bringing about rapid ground cover, it is a useful crop in controlling erosion [30]. Grass pea (*Lathyrus sativus* L.) is grown for human and livestock consumption in Asia, Africa and Europe. In Africa, it is cultivated in Egypt, Ethiopia, Morocco and Algeria [13]. The plant is extremely tolerant towards drought and is considered as an insurance crop since it produces reliable yields when all other crops fail. Like other grain legumes, grass pea is a source of protein particularly for resource-poor farmers and consumers.

1.3. Vegetables

There are many indigenous or locally important vegetables in Africa. Among these, the following have benefits in some agronomic and/or nutritional traits: amaranthus (*Amaranthus caudatus* L.) matures fast and is nutritious [3]; dika [*Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill] is rich in oil [3]; okra [*Abelmoschus esculentus* (L.) Moench] is fast maturing and nutritious [14]; and the Ethiopian mustard (*Brassica carinata* A. Braun), which is used both as a leafy vegetable and an oil crop, is tolerant towards drought and insect pests [15].

1.4. Oil Seeds

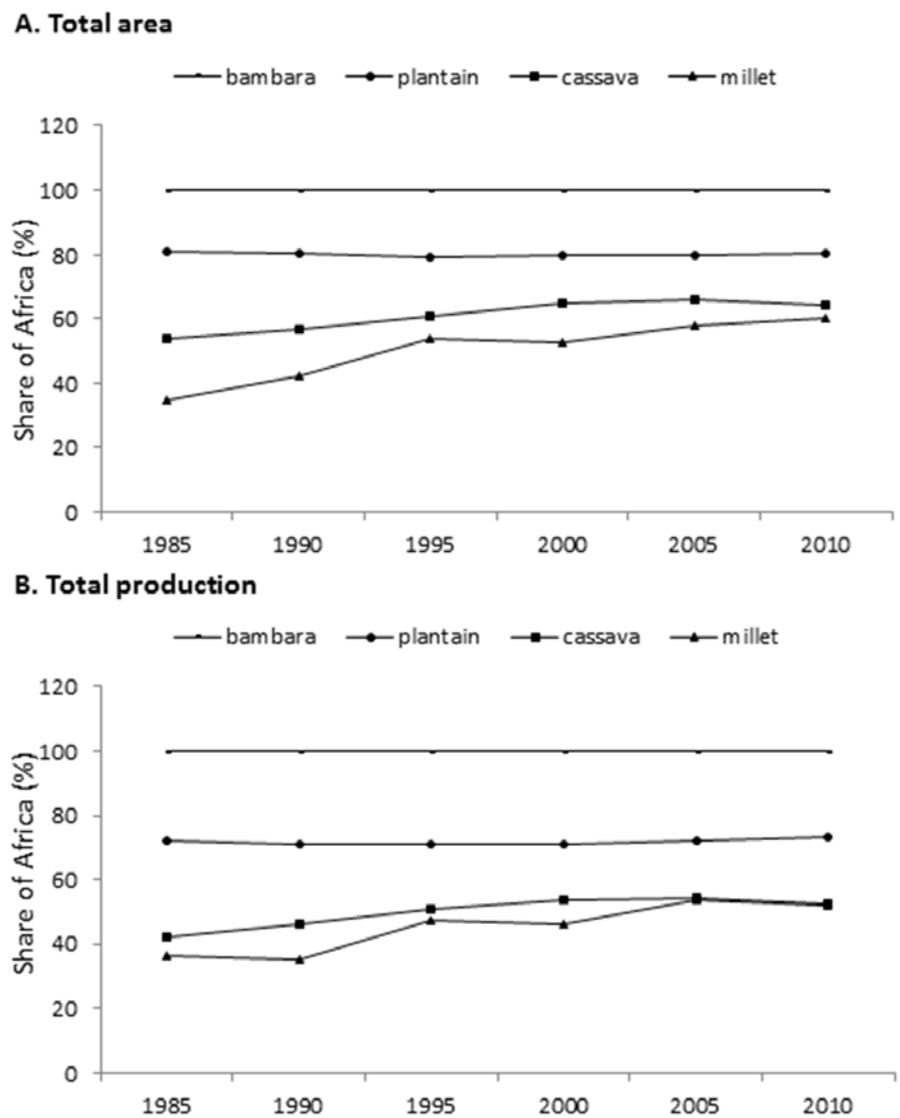
Among locally grown oil crops, the oil from noug [*Guizotia abyssinica* (L.f.) Cass.] and sesame (*Sesamum indicum* L) are used for human consumption while the one from vernonia [*Vernonia galamensis* (Cass.) Less.] is used in industry.

1.5. Root Crops

Among the root crops grown in Africa, cassava, yam, sweet potato and enset are the source of food for a large number of populations. Cassava (manioc; *Manihot esculenta* Crantz*)* is staple food for about 600 million people worldwide and for more than 200 million people in Sub-Saharan Africa [31]. In

Africa, although it was cultivated on 64% of the global area in 2010, it accounted for only 53% of the total world production (Figure 1) [32]. This shows that the productivity of cassava is lower in Africa than in other parts of the world. Cassava is tolerant towards drought, and also performs better than other crops on soils with poor nutrients. Yam (*Dioscorea* sp) represents at least two species of the genus *Dioscorea*. In 2010, it was grown on about 4.8 million hectares of land worldwide, and of this 95% was in Africa [32]. The edible part of yam is similar to that of sweet potato [*Ipomoea batatas* (L.) Lam.], although they are not taxonomically related. Enset [*Ensete ventricosum* (Welw.) Cheeseman] is commonly known as 'false banana' for its close resemblance to the domesticated banana plant. Unlike banana where the fruit is consumed, in enset the pseudo-stem and the underground corm are the edible parts. Enset is the major food for over 10 million people in the densely populated regions of Ethiopia. It is considered as an extremely drought-tolerant crop that adapts to different soil types [19].

Figure 1. Share of Africa in the global crop area (**A**), and production (**B**) for selected orphan crops from 1985 to 2010. Adapted from FAOSTAT [32].



1.6. Fruits

Banana and plantain (*Musa* spp.) are among the major fruit crops grown in Africa. In the year 2010, about 13 million tons of banana and 27 million tons of plantain were produced in the continent [32]. According to Fungo [33], banana, especially the orange pulped type with high carotenoid and iron content, could reduce Iron Deficiency Anemia (IDA) by over 50% and also Vitamin A Deficiency (VAD) in East Africa, where both IDA and VAD affect a large number of people. Plantain is the staple food in central Africa, and it is mostly considered more as a vegetable than as a fruit since the fruit is used for cooking. In general, both banana and plantain are considered as a healthy food, and they are also rich in essential nutrients for humans.

2. Need for Improving African Crops

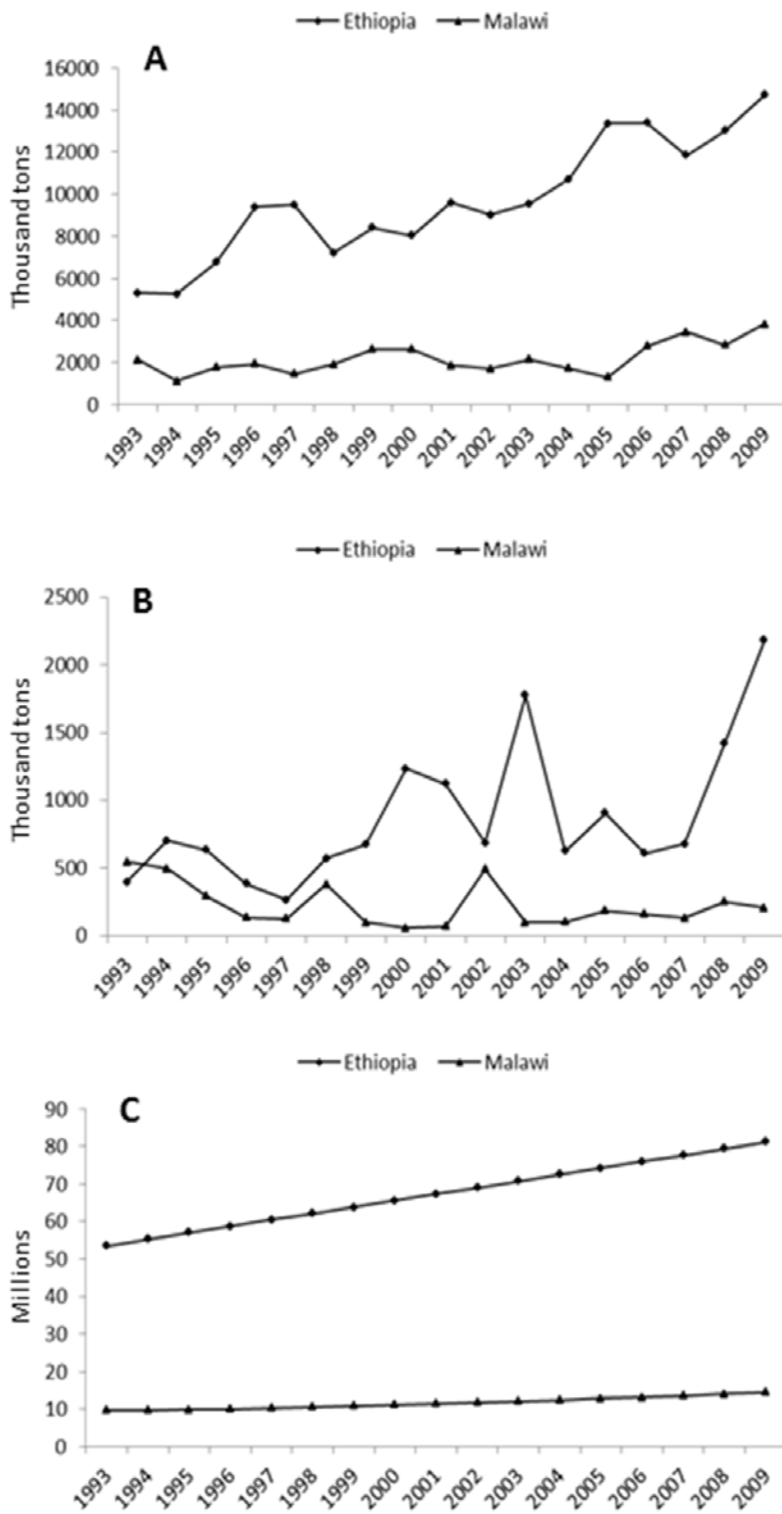
2.1. Africa is Largely Food Insecure

Food security is defined as the state in which people at all times have physical, social and economic access to sufficient food that meets their dietary needs for a healthy and active life [34]. Due to the high population increase in Africa, the demand for food is increasing over time. Figure 2 shows the total production and import of cereal crops from the early 1990s to late 2010 for Ethiopia and Malawi. Despite some years of crop failures due to drought, crop production was significantly increasing year to year (Figure 2A) [32]. However, the import of grains was also in an increasing trend, especially for Ethiopia (Figure 2B) [35]. This high demand for grain might be due to the huge population growth in the country. During the same period, the population of Ethiopia increased by 53%, *i.e.*, from 53 million in 1993 to 81 million in 2009 (Figure 2C) [36]. In order to achieve agricultural sustainability, the increase in food production should be at least proportional to the rate of population growth. It is, however, expected that with the current level of crop productivity, it might be difficult to feed the population in the developing world, especially in Africa, where the population is growing at an alarming rate. According to Tilman *et al.* [37], the demand for global food is rising rapidly with about 100%–110% increase in crop demand expected from 2005 to 2050. In general, there is big gap between increase in population and crop production.

2.2. Africa Missed Green Revolution

The major achievement of the Green Revolution in the 1960s and 70s was the development and introduction of semi-dwarf varieties of wheat and rice along with optimum levels of input. These broadly adapted semi-dwarf cultivars responded to fertilizer application and led to a tremendous increase in productivity. According to the International Food Policy Research Institute [38], the Green Revolution represented the successful adaptation and transfer of scientific revolution in agriculture. However, this agricultural revolution, which boosted crop production in Asia and Latin America, did not occur in Africa. This is mainly due to the fact that the Green Revolution was implemented on rice and wheat, but not on African crops such as sorghum and millets [39,40].

Figure 2. The total production and import of cereal crops and population growth in Ethiopia and Malawi from 1993 to 2009; (**A**) the total cereal production, which mainly constitutes tef, maize, wheat, and barley in Ethiopia and maize, paddy rice and wheat in Malawi (adapted from [32]); (**B**) the total cereal import for the two countries (adapted from [35]); (**C**) the total human population during the same period (adapted from [36]).



2.3. African Crops Fit the Agro-Ecology and Socio-Economic Conditions

As indicated above, most understudied or orphan crops perform better under adverse climatic and soil conditions than the exotic crops. In addition, orphan crops are compatible with the agro-ecology and socio-economic conditions of the continent. However, when these crops were replaced by other crops new to the locality, some problems were reported. The best example is from a study made in northwestern Ethiopia where the incidence of malaria increased when exotic crops, specifically maize, substituted large areas previously occupied by indigenous crops such as tef [41–43]. Tef is the staple food crop for about 50 million people in Ethiopia. Malaria is a major health problem in the world, particularly in Africa. In 2010, it caused an estimated 655,000 deaths mostly among Africans [44]. The pollen from maize facilitates optimum conditions for the anopheles mosquitoes, which carry *Plasmodium* parasites that cause malaria. Larvae of the mosquito had a survival rate of 93 percent when it fed on maize pollen, as opposed to a survival rate of only about 13 percent when it fed on other possible food sources. As a result, the cumulative incidence of malaria in high maize cultivation areas was 9.5 times higher than in areas with less maize [41]. This shows that the introduction of new crops to the local community might bring some adverse effects on the health of the population.

2.4. African Crops Are Poor in Productivity

African crops, despite their huge importance, have generally received little attention by the global scientific community. Due to a lack of genetic improvement, these crops produce inferior yields in terms of both quality and quantity. For instance, the seed yields of tef and millets are extremely low. The main cause for poor productivity of tef is its susceptibility to lodging [45]. Tef plants possess tall and tender stems, which are susceptible to lodging by wind and rain, and, therefore, lodging (the permanent displacement of the stem from the up-right position) inflicts significant loss in production. Some of the negative features associated with African rice (*Oryza glaberrima* Steud.), unlike Asian rice (*O. sativa* L.), are rapid shattering of the seeds, difficulty of milling the grain, and lower seed yield [9].

2.5. Efficient Tools and Inputs Are Not Applied in African Agriculture

Poor crop productivity in Africa is also due to the use of inefficient agricultural practices starting from land preparation, sowing, weeding, harvesting and finally to threshing. Post-harvest losses also account for over 10% yield losses in Africa [46]. In addition, sub-optimal use of inputs such as fertilizers, herbicides and pesticides are also responsible for the low productivity of crops in the continent [47,48].

2.6. Some African Crops Are Poor in Nutrition

Root and tuber crops such as cassava and enset produce high yields, however; the products are largely starchy materials that are deficient in other essential nutrients, particularly protein. Recent studies showed that children in Kenya and Nigeria who consumed cassava as a staple food were at greater risk of inadequate dietary protein [49], zinc, iron, and vitamin A [50] intake than those children who consume less cassava in their staple diet. Although these crops are staple food crops for a large number of Africans, supplementation with other nutrients, especially proteins and vitamins, is required.

2.7. Several African Crops Produce Toxic Substances

Some widely cultivated crops produce a variety of toxic substances that affect human health. The roots of cassava contain poisonous compounds called cyanogenic glycosides (CG), which liberate cyanide [18]. Konzo is a paralytic disease associated with consumption of insufficiently processed cassava. The pods and seeds of the hyacinth bean [*Lablab purpureus* (L.) Sweet] are poisonous due to high concentrations of cyanogenic glycosides, and they can only be eaten after prolonged boiling [2]. The seeds of the African yam bean [*Sphenostylis stenocarpa* (Hochst. ex A.Rich.) Harms] contain anti-nutritional factors such as cyanogenic glycosides and trypsin inhibitors. Cooking is required to reduce the toxins to safe levels, although prolonged cooking also decreases the level of nutrients in the seed [2]. The seeds of the grass pea contain a neuron-toxic substance called ODAP [β-*N*-Oxalyl-L-α, β-diaminopropanoic acid] [51]. ODAP is the cause of the disease known as neuro-lathyrism, a neuro-degenerative disease that causes paralysis of the lower body. Serious neuro-lathyrism epidemics have been reported during famines when grass pea was the only food source [52].

2.8. Prevalence of Large-Scale Biotic and Abiotic Stresses

Since most fertile lands are used to grow crops other than African indigenous crops, the productivity of the African native crops under the less fertile and moisture-deficit soils is extremely low. In addition, crop productivity is affected by a variety of abiotic and biotic stresses. Major abiotic stresses are drought, soil salinity and soil acidity. There is some evidence that, in recent decades, agricultural land has been lost to desertification, salinization, soil erosion and other consequences of unsustainable land use [40]. From the total global arable area, a third is affected by salinity and 40% by acidity [53]. Biotic factors such as diseases, insects and weeds also reduce crop production tremendously. Their adverse effects on crop productivity are more obvious in the tropical regions due to their presence in high density and diversity.

2.9. Climate Change Adversely Affects Crop Production

There is some evidence that the current changes in climate affect crop productivity in Africa. According to Müller *et al.* [54], climate change poses a significant threat to the present African production systems, infrastructures, and markets. The yield of rice declines by 10% for every 1 °C increase in temperature during the growing season [55]. The study by Funk *et al.* [56] using *in situ* station data and satellite observations indicated that the rainfall decreased by about 15% in the main growing-season in food-insecure countries in Eastern and Southern Africa. The authors predicted that due to the warming in the central Indian Ocean, the continental rainfall in Africa will decrease, and this will create a drought, which, as a consequence, will increase the number of undernourished people by 50% by 2030. Fauchereau *et al.* [57] indicated that due to the long-term variability and changes of rainfall in Southern Africa, droughts have become more intense and widespread. The probable changes in precipitation were also estimated for Southern and East Africa based on global climate models [58,59]. While a delay in the onset of the rainy season is the cause for the shortening of the rainy season in almost the entire region of Southern Africa [58], in East Africa, a wetter climate with more intense wet seasons and less severe droughts is expected [59]. The prediction in West Africa also indicates a decrease in rainfall and an increase in temperature in the Sahel coastline [60]. According to Sarr [60], the most drastic effect of climate change on agriculture will be from the late onset and early cessation of rainfall, and reduction of the length of the growing period.

3. Tools for Crop Improvement

Improvement of existing crop varieties and cultivation needs integrative research strategies. Crop improvement techniques are broadly grouped into; i) *conventional approaches* that include various types of selection methods, introgression (or hybridization), and mutation breeding; and ii) *biotechnological or molecular approaches* that include transgenic and non-transgenic methods such as marker-assisted selection (MAS) and TILLING (Targeting Induced Local Lesion IN Genomes). The major techniques implemented in crop improvement (Figure 3) are briefly described below.

3.1. Domestication and Selection

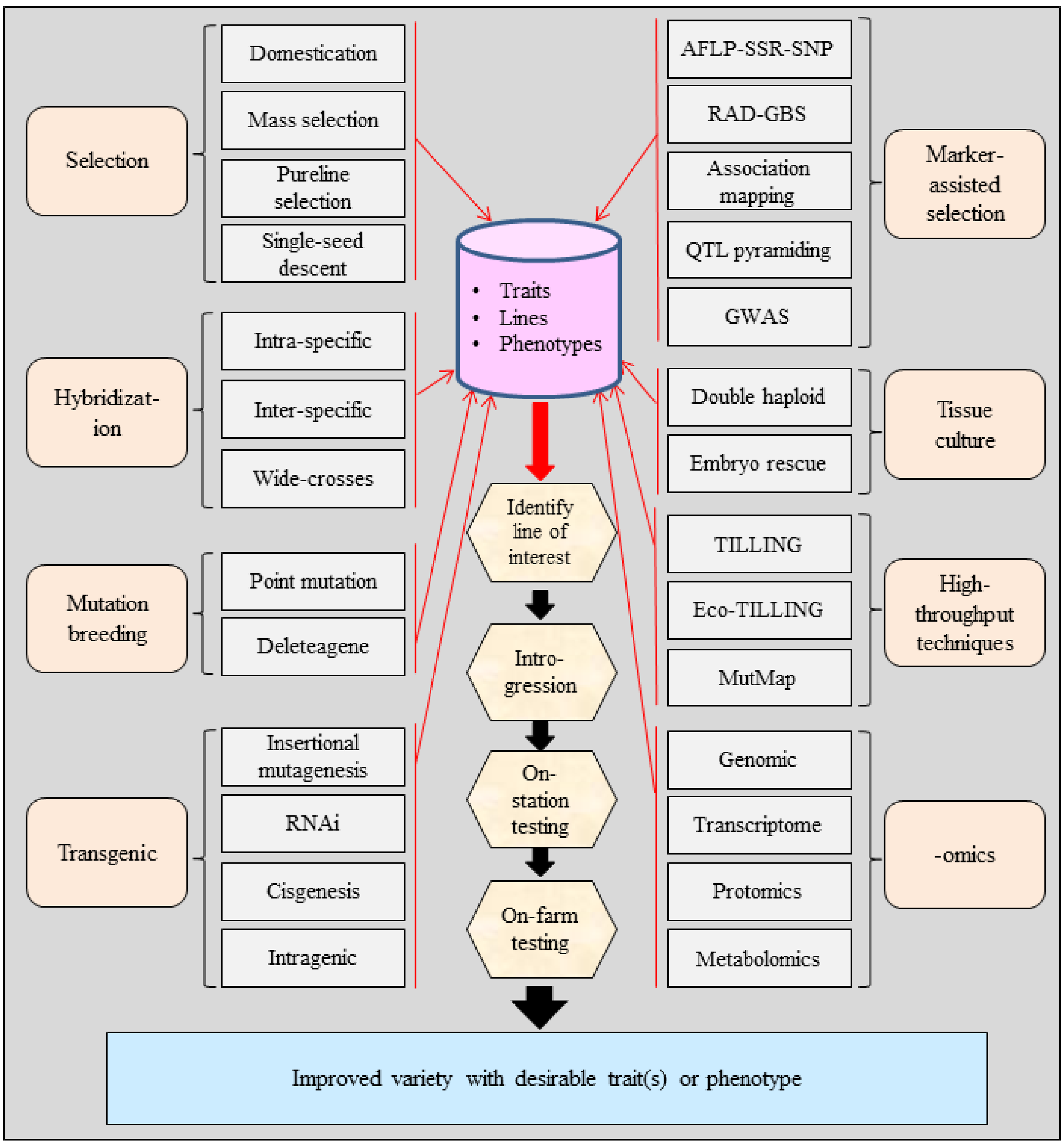
Crop domestication is the earliest improvement method in which humans selected for valuable traits such as non-shattering of grains, big grain or useable part size and loss of seed dormancy. The current important cereal crops including maize, rice and wheat were domesticated around 7000 to 10,000 years ago [61]. Advances made in understanding some domestication traits or genes were reported for these crops [61]. Methods applied in crop domestication and perceptions regarding the timing and spatial patterning of crop domestication have recently been reviewed by Gross and Olsen [62].

Selection is an ancient breeding method that is still implemented on a large-scale to improve crop plants. The technique relies mainly on the selection of plants according to their phenotype and performance. Diverse types of selection techniques have been developed for a variety of crops depending on the pollination behavior and other factors. For example, mass selection is applied to a certain level in self-fertilizing plants and is an effective method for improving landraces, especially for transferring highly heritable traits [63]. Mass selection refers to the technique whereby individual plants are selected based on their phenotypic performance, and bulk seeds from selection are used to produce the next generation.

3.2. Hybridization

Artificial hybridization or introgression refers to crossing closely related species in order to create genetic variation, which can be utilized for improving traits of choice. According to Baenzinger *et al*. [64] the success in hybridization depends mainly on the selection of parents. Hybridization can be broadly grouped into intra-specific (crossing within the species) or inter-specific (crossing between different species). Successes in intra-specific crosses resulted in semi-dwarf cultivars of wheat and rice, which boosted the productivity of both crops during and after the Green Revolution [65]. Intra-specific hybridization also increases phenotypic properties including important agronomic traits especially in cross-pollinated crops such as maize. This phenotypic superiority over the parents, which is exhibited only in the first generation of the cross, is known as heterosis or hybrid vigor. Although farmers need to buy F_1 seeds at every planting, the use of hybrid crop outweighs the use of open-pollinated crops. Genes responsible for these robust effects on yield or architecture of the plants are studied using diverse genomics tools [66].

Figure 3. Diverse types of tools implemented in crop improvement. *Rounded rectangle*: general grouping of improvement methods; *rectangle*: specialized or specific improvement technique; *can:* types of products obtained from preliminary screening or breeding; *rectangular pentagon:* further procedures to be followed before releasing new cultivar(s) to the farming community, which include introgression to locally adapted and/or high-yielding cultivars and multi-location testing at on-station and on-farm sites.



The crosses between individuals from either different species or different genera (also known as wide crosses) are useful in transferring valuable traits from wild species to crop plants. The major breakthrough from the inter-specific crossing was the development of an artificial cereal called Triticale. Triticale is a cross between wheat and rye, and it proved to be tolerant towards abiotic stresses such as soil acidity [67]. According to Sharma [68], successful wide hybrids with wheat were obtained when species with lower chromosome numbers were used as female parents.

3.3. Mutation Breeding

Mutation breeding relies on the implementation of either physical or chemical agents in order to create variability in the population of interest. While mutagens such as EMS (ethyl methane sulfonate) mainly create a point mutation in which a single nucleotide is altered, fast neutron removes pieces of DNA, which could be detected using a Deleteagene technique [69]. Mutations created by these mutagens were the base to develop and release more than 2000 crop varieties in the last seventy years [70]. Most mutation breeding programs aimed at altering traits such as plant height and disease resistance in well-adapted plant varieties of rice, barley and wheat.

3.4. Plant Cell and Tissue Culture

Plant tissue culture is the aseptic *in vitro* culture of cells, tissues, organs, and their components under defined physical and chemical conditions [71]. Developing an efficient regeneration system requires optimization for various types of explants and media components. Hormones and growth regulators play a key role in determining the conversion of somatic cells to embryogenic tissues [72]. The tissue culture techniques have been successfully implemented in diverse types of plants including cereals [73,74], legumes [75], vegetables [76,77], oil plants [78], fruits [79], trees [80], and forestry [81]. Tissue culture also enables to rescue and utilize desirable properties of endangered plant species [79,82]. Among diverse tissue culture techniques, the doubled haploids are becoming a popular method in crop improvement [83]. Uma and colleagues [79] developed an efficient regeneration method for wild banana, *Pisang Jajee* (AA), in which zygotic embryos were excised and cultured on 6-benzyl adenine (BA) and indole acetic acid (IAA) containing media followed by callus or plantlet formation. While fully matured embryos of wild banana regenerated directly into plantlets without producing callus, immature embryos required a medium supplemented with plant growth regulators (PGRs) for successful regeneration [79].

Successful embryo rescues were reported for diverse crop plants crossed with wild relatives. By applying the rescue technique developed for the inter-specific cross between cassava and *Manihot esculenta* ssp *flabellifolia*, almost 100% of the plantlets transplanted were established [84]. This shows that by applying appropriate tissue culture technique, cassava breeding could be enhanced. Although inter-specific crosses between chickpea (*Cicer arietinum* L.) and its wild relatives were not successful due to post-zygotic barriers, which result in abortion of the immature embryo, appropriate rescue time overcomes the problem. In this particular case, rescuing applied at the early globular stage of embryogenesis for chickpea × *C. bijugum* crosses and at the heart-shaped or torpedo stages for chickpea × *C. pinnatifidum* was found to be optimum [85]. The presence of strong reproductive barriers between sorghum (*Sorghum bicolor*) and its wild relative *S. macrospermum* negatively affects the formation of a zygote, but a viable hybrid was developed using embryo rescue [86].

3.5. Marker-Assisted Selection

Marker-assisted selection (MAS) is the utilization of molecular markers located near genes, which can be traced, to breed for traits that are difficult to observe. Tester and Langridge [87] indicated the benefits of applying new technologies and molecular markers in crop improvement. These molecular markers are utilized to effectively assemble favorable alleles in phenotypic selection [88]. According to Collard and Mackill [89] the following factors should be considered before selecting the type of marker to apply: reliability, quantity and quality of DNA required; technical procedure for marker assay; level of polymorphism; and cost. The most common markers in use are SSRs (Simple Sequence Repeats, or microsatellites), SNPs (Single Nucleotide Polymorphisms) and INDELs (Insertions and Deletions). SSRs refer to a repeat of two to six nucleotides in the DNA sequences, and they are highly polymorphic and abundant in the genomes of organisms. SNP is a type of polymorphism, in which a considerable amount of differences in a single nucleotide is present among genotypes. INDELs refer to small sequences, which are either inserted in one genome or deleted from another genome. Commonly applied marker-assisted techniques are briefly described below.

AFLP (Amplified Fragment Length Polymorphisms): This is a genetic mapping method for detecting DNA polymorphism following restriction enzyme digestion of DNA and selective amplification of the resulting DNA fragments. The technique has been widely implemented in diverse crops especially in creating genetic maps for new species, determining relatedness among cultivars, establishing linkage groups in crosses, and studying genetic diversity and molecular phylogeny [90].

Association Mapping: This is a method of mapping quantitative trait loci (QTLs), and it involves the correlation of phenotypes to genotypes in unrelated individuals and is relatively more rapid and cost-effective than the traditional linkage mapping [43]. However, the major drawbacks of association mapping are the need for a large number of plants for screening, and the need for specific and accurate high-throughput phenotyping [91]. So far, the technique has been successfully implemented in identifying plant resistance to insects [91], wheat resistance to stripe rust [92], wheat resistance to *Fusarium* head blight [93], and dwarfing genes in sorghum [94].

QTL Pyramiding: This has also been implemented in several crops in order to come closer to the target trait. It enabled the breeders to dissect genes responsible for stripe rust of barley [95], crown rot of wheat [96], and blast resistance in rice [97]. In the latter case, the Jin 23B rice cultivar with extreme susceptibility to blast was introgressed to either one or more lines with blast resistance. According to the results, the level of resistance to blast improved by increasing the number of resistance genes, indicating the presence of a strong dosage effect on the resistance to blast [97].

GBS (Genotyping-by-sequencing): This is a recently discovered marker-related technique considered to be simple, extremely specific and highly reproducible in high diversity species [98]. Since the technique uses restriction enzymes to construct the library by using methylation-sensitive restriction enzymes, repetitive regions of genomes can be avoided and lower copy regions are targeted, which ultimately increases the efficiency [98].

RAD Tags: SSR and SNP markers could also be discovered in plants using a recently developed RAD (Restriction-site Associated DNA) tag method, which also involves high-throughput sequencing using the Illumina platform. The technique enabled the discovery of a large number of DNA markers in eggplant (*Solanum melongena* L.) in which about 10,000 SNPs, 1000 indels, and 2000 SSRs were obtained [99]. RAD tags were also used to identify three quantitative trait *loci* (QTL) for resistance to stem rust caused by *Puccinia graminis* subsp. *graminicola* in perennial ryegrass (*Lolium perenne* L.) from crosses between a susceptible and a resistant plant [100].

GWAS (Genome Wide Association Studies): This is a method of scanning the whole genome of the organism in order to analyze genetic differences, particularly SNPs, between genotypes of interest. The major benefit of GWAS is that it provides higher resolution mapping that is mostly at the gene level [48]. The technique was recently applied in Chinese maize inbred lines to identify candidate genes that affect plant height [101]. GWAS has also successfully identified multiple loci for aluminum resistance in wheat (*Triticum aestivum* L.) germplasm [102].

3.6. Candidate Gene Approach (CGA)

CGA is based on the hypothesis that genes with a known function in other species (*i.e.*, functional genes) or genes that are in close proximity to *loci* controlling the trait (positional genes) could control a similar function or trait in a target crop of interest [103]. Hence, research on understudied crops of Africa could benefit from this approach based on already known genes and knowledge in other well-studied crops.

3.7. High-Throughput Mutation Detection

TILLING (Targeting Induced Local lesions IN Genomes): This is a non-transgenic and a reverse genetics method, which uses traditional mutagenesis followed by high-throughput screening in order to identify single base pair changes in a target gene [104,105]. Some of the benefits of TILLING are: (i) It produces a spectrum of allelic mutations that are useful for genetic analysis; (ii) mutations difficult to know by forward genetics could be revealed since it can focus on a particular gene of interest; and (iii) it is a non-transgenic method, hence the product is readily accepted by all sectors of society. TILLING has been successfully implemented in maize [106], wheat [107,108], rice [109,110], barley [111,112], sorghum [113], and orphan crops such as tef [114].

Eco-TILLING: This is the modified form of TILLING, and in this case polymorphisms are detected in a natural population without the use of mutagenesis [115]. In general, TILLING and Eco-TILLING are useful in rapidly detectable point mutations in populations irrespective of genome size, reproductive system and generation time.

3.8. Genetic Engineering or Transgenics

Transgenic technology is proved to improve the productivity of crops. The technique enables molecular biologists to transfer a single or multiple gene(s) of interest to the plant of choice. As a result, plants, which are tolerant towards a multitude of environmental stresses or those with improved nutritional qualities, are obtained [116]. Due to the high adoption rate of the technology, the global area under transgenic crops has increased tremendously from just 1.7 million ha in 1996 to about 160 million ha in 2011 [35].

RNAi (RNA Interference): This technique is more and more widely applied in plant biotechnology, both as a useful tool for discovering or validating gene functions and as a quick way of engineering specific reductions in the expression of chosen genes [117]. The technique relies on the suppression of some biological activities in plants thereby resulting in plants with expected phenotypes [118]. Hence, RNAi has an enormous application in crop improvement. The application of RNAi in improving the nutritional value of plants, especially metabolomics, has recently been reviewed [119]. RNAi had also enabled the development of plants resistant to nematodes, herbivorous insects, parasitic weeds and fungi [120,121].

Marker-free Transgenics: Although transgenic technology has shown significant impact in increasing crop productivity, its expansion to other crops and geographical regions is restricted due to extensive regulatory procedures and negative public perception [87]. Some of the recent investigations on transgenics dealt with solving the major concerns affecting the acceptance by the public. Among the concerns, the presence of antibiotic- or herbicide-resistance markers and non-plant promoters are the major ones. Hence, it would be desirable to remove these markers or foreign genes in order to increase the acceptance of transgenic products. Mentewab and Stewart [122] enabled the substitution of antibiotic resistance markers with those without any adverse effects. Bhatnagar *et al.* [123] also recently developed a transgenic peanut without any selectable marker by using marker-free binary vectors harboring either the phytoene synthase gene from maize or the chitinase gene from rice inserted into the plant, and that can be identified by PCR. Advances in increasing the efficiency of gene targeting as demonstrated by Shukla *et al.* [124] and Townsend *et al.* [125] using zinc-finger proteins will also promote specific or targeted gene transfer and avoid unwanted or unnecessary pieces of DNA movement to the crop of interest.

Cisgenesis: This refers to a method recently developed by the group at Wageningen University, in which plant-specific promoters are used to drive the gene of interest instead of foreign promoters from bacteria or other organisms [126]. According to the inventors, materials developed through cisgenesis should be exempted from a stringent regulations set for genetically modified organisms [127].

Intragenesis: This is a technique, in which genetically modified plants are created that contain elements only from within the sexual compatibility group, as it excludes unknown or foreign DNA [128]. It is also claimed that as the technique mimics traditional plant breeding, that the products from intra-genics are as safe as those from traditional breeding [128,129].

TALEN (Transcription Activator-like Effector Nuclease): In this method, targeted expression of a gene of interest is made using sequence-specific nuclease [130]. The method was recently implemented in developing disease-resistant rice [131].

3.9. Application of Genome and Transcriptome Sequencing

Due to their high capacity sequencing, next generation sequencing (NGS) platforms such as 454, Illumina and Solid, provide large amounts of sequence information, which have direct application in other crop improvement techniques. Some improvement techniques, which rely on genome and transcriptome sequencing, are TILLING and Eco-TILLING, SSRs and SNPs, and markers linked to genes and QTLs [132].

RNASeq: This was used to obtain the reference transcriptome for sugar beet (*Beta vulgaris* sp. *vulgaris*) and to investigate global transcriptional responses to vernalization and GA treatment [133]. The expression profiles due to vernalization and GA treatment suggest that RAV1-like AP2/B3 domain protein is involved in vernalization and efflux transporters in the GA response [133].

MutMap: This is a recently discovered method, which successfully identified the unique genomic position harboring mutations in semi-dwarfism in rice [134]. The technique was applied to an EMS (ethyl methane sulfonate) mutagenized population. MutMap is based on whole-genome re-sequencing of pooled DNA from a segregating population of plants that show a useful phenotype [134]. Selected mutant lines are first introgressed to the original non-mutagenized line and then self-pollinated in order to obtain F_2 progenies for SNPs discovery.

4. Agriculturally Important Traits

A partial list of valuable traits which contribute towards increasing crop productivity and those which enhance resistance against a variety of environmental stresses is indicated in Table 2.

4.1. Yield Components

The primary goals of many crop-breeding programs are to improve the productivity of crops, especially the edible and/or economically important parts. Since yield is affected by multiple traits, breeding programs focus mainly on improving individual traits known as yield components or yield-related traits such as panicle yield, number of tillers, seed weight, and others.

Table 2. Partial list of agriculturally important traits and method of isolation in major crops.

Traits		Gene or locus identified			Reference
General	Specific	Name	Crop	Cloning method	
Plant architecture	Semi-dwarfism	Sd-1	rice	Map-based	[135]
		Rht-1	wheat	Candidate gene	[136,137]
		D8	maize	Candidate gene	[136]
		D1	rice	Map-based	[138]
		D2	rice	Map-based	[139]
		D11	rice	Map-based	[140]
		D35	rice	Map-based	[141]
		Unnamed	rice	Mutmap	[134]
	Tillering	MOC1	rice	Map-based	[142]
		TAC1	rice	Map-based	[143]
		HTD1	rice	Map-based & Candidate Gene	[144]
	Culm strength	FC1	rice	T-DNA	[145]
	Lateral root	ZmHO-1	maize	T-DNA	[146,147]
	Fruit size	Fw2.2	tomato	Map-based	[148]

Table 2. *Cont.*

Traits		Gene or locus identified			Reference
General	**Specific**	**Name**	**Crop**	**Cloning method**	
Abiotic tolerance	Drought tolerance	Stg1	sorghum	Map-based	[149]
	Submergence tolerance	Sub1	rice	Map-based	[150]
	Aluminum tolerance	MATE	sorghum	Map-based	[151]
	Salt tolerance	SKC1	rice	Map-based	[152]
Biotic tolerance	Bacterial resistance	Xa21	rice	Map-based	[153]
	Fungal resistance	Pi9	rice	Map-based	[154]
Nutritional quality	Starch	Waxy	rice	Sequencing	[155]
Consumer preference	Eating & cooking quality	Several genes	rice	Sequencing	[156]
	Color of grain	R	wheat	Candidate gene	[157]
Multiple traits	Leaf angle & grain yield	DWARF4	rice	Tos17 Retrotransposon	[158]
	Shoot branching & grain yield	SPL14	rice	Map-based	[159]
	Branching pattern & grain yield	CKX2	rice	Map-based	[160]
	Grain size & seed yield	qSW5	rice	Map-based	[161]
	Grain filling & seed yield	GIF1	rice	Map-based	[162]
	Panicle & grain yield	DEP1	rice	Map-based	[163]
	Heading date & seed yield	Ghd7	rice	Map-based	[164]

4.2. Stress Tolerance

Due to the presence of extreme climatic and soil conditions, which adversely affect crop productivity, many breeding programs are geared towards developing crops, which are resistant to some of these environmental calamities. Breeding for effective use of water (EUW) is considered the best strategy towards mitigating the effects of moisture scarcity and to develop drought-tolerant crops [165]. Several tools have also been developed to create crops tolerance towards or resistance against a variety of weeds, diseases and insect pests.

4.3. Plant Architecture

Among traits that contributed to higher crop productivity in the last century, those, which alter the architecture of the plant, rank first. Architectural changes include alterations in branching pattern and reduction in plant height. Semi-dwarf wheat and rice varieties developed during the Green Revolution elevated the productivity of these crops tremendously. Plants with an erect leaf phenotype or narrow leaf angle were also efficient in capturing light, which also contributes towards increasing productivity.

4.4. Nutritional Quality

Traits, which improve the nutritional level of food crops, are also important, as edible parts of some staple crops such as cassava are deficient in protein, fat, and vitamins. In addition, traits related to consumer preference (e.g., cooking and eating quality, color of grain, *etc.*) are also useful to incorporate in the breeding program.

5. Institutions Involved in African Crops Research and Development

The list of some institutions involved in the research and development of African crops is given in Table 3. Brief descriptions are presented below for some of them.

5.1. National Agricultural Research Systems (NARS)

The Forum for Agricultural Research in Africa (FARA) website offers information about organizations, projects and experts in the agricultural research system in Africa [166]. The search tool gives options to obtain information on the thematic groups such as plant production, animal production, socioeconomics, farming systems, and others for each country's or regional organizations. Information about organizations and projects present in each African country is also available. According to the website, the total number of national institutes in the continent are 867, while countries with over 50 institutes are only South Africa (71), Uganda (57), Kenya (54), and Egypt (53) [167].

Table 3. Partial list of institutions involved in research and development of African crops. The list does not include national institutes. Information about national institutes involved in agricultural research and development is available on the Forum for Agricultural Research in Africa (FARA) website [166].

Major institute	Subsidiary institute/program	Role/involvement	Relevance to African crops	HQ or regional office	Reference
FARA	ASARECA	Strengthen NARS activity	Staple and non-staple crops	Entebbe, Uganda	[168]
	CORAF/	Research coordination	Staple and non-staple crops	Dakar, Senegal	[169]
	SADC/FANR	Research & Development	Not specified	Gaborone, Botswana	[170]
Other African institutes	AATF	Technology transfer	Cassava, banana & cowpea	Kenya	[171]
	Africa Harvest	Technology transfer	Banana & sorghum	Nairobi, Kenya	[172]
	ABNETA	Information provision	Not specified	Nairobi, Kenya	[173]
	AGRA	Capacity building	African crops	Nairobi, Kenya	[174]
	BeCA Hub	Research, training	Not specified	Nairobi, Kenya,	[175]
	BioInnovate Africa	bio-resource-based innovation systems	Millet, bean, cassava, sweet potato	Nairobi, Kenya	[176]
	CAADP	Research & development	Not specified	South Africa	[177]
CGIAR centers	Africa Rice Center	Research & development	African rice	Contonou, Benin	[178]
	Bioversity International	Research	Banana, plantain	Rome, Italy	[179]
	CIAT	Research	Beans, cassava	Cali, Colombia	[180]
	CIMMYT	Research	Wheat and maize	Mexico	[181]
	CIP	Research	Potato & sweet potato	Lima, Peru	[182]
	ICARDA	Research and training	lentil, barley and faba bean	Aleppo, Syria	[183]
	ICRISAT	Research	Pearl millet, Pigeonpea, chickpea, small millets	Patancheru, India	[184]
	GCP	Research & capacity building	Tropical legumes	Mexico	[185]
	IFPRI	Policy research	Not specified	Washington D.C.	[186]
	IITA	Research & capacity building	Cassava, yam, cowpea, banana, plantain	Ibadan, Nigeria	[187]

Table 3. *Cont.*

Major institute	**Subsidiary institute/program**	**Role/involvement**	**Relevance to African crops**	**HQ or regional office**	**Reference**
Other organizations	ABSPII	Promote agricultural biotechnology	Banana	Cornell Univ. Ithaca, USA	[188]
	CIRAD	Research & training	Banana, plantain, tree crops	Montpellier, France	[189]
	Crops for the Future	Training & policy issues	underutilized crops	Serdang, Malaysia	[190]
	CTA	Information & communication	Not specified	Wageningen, Netherlands	[191]
	ETH Zurich	Research & training	cassava	Zurich, Switzerland	[192]
	FAO	Development, Information systems	Not specified	Rome, Italy	[193]
	GFAR	Discussion forum	Not specified	Rome, Italy	[194]
	HarvestPlus	Research on biofortification	beans, cassava, maize, millet, rice, sweet potato	Washington DC, USA	[195]
	IFAD	Development	Not specified	Rome, Italy	[196]
	IPBO	Training and research	Banana, cassava, grass pea, sweet potato	Gent, Belgium	[197]
	IRD	Research & training	Not specified	Montpellier, France	[198]
	ISAAA AfriCenter	Development, & information provision	Banana	Nairobi, Kenya	[199]
	Joint FAO/IAEA Programme	Training, research & service provision	Not specified	Vienna, Austria	[200]
	Lab. Trop. Crop Improv.	Research and training	Banana and plantain	K.U. Leuven, Belgium	[201]
	PAEPARD	knowledge sharing	Not specified	Brussels, Belgium	[202]
	University of Bern	Research and training	Tef	Bern, Switzerland	[203]

5.2. Consultative Group on International Agricultural Research (CGIAR) Centers

The CGIAR is a global network of 15 international research centers with a strategy to tackle the major global problems in agricultural development. In their research and development programs, the CGIAR centers give particular emphasis to Africa. The recently revised CGIAR programs focus on improving: i) yields and profits of crops, fish, and livestock; (ii) sustainability and environmental integrity, and adaptation to and mitigation of climate change; (iii) productivity, profitability, sustainability, and resilience of entire farming systems; (iv) policies and markets; and v) nutrition and diets [204]. According to Renkow and Byerlee [205], the contributions of CGIAR to crop genetic improvement, pest management, natural resources management, and policy research gave strongly positive impacts relative to the investment, while crop genetic improvement research resulted in the most profound positive impacts.

5.3. African Institutions

5.3.1. Comprehensive Africa Agriculture Development Program (CAADP)

CAADP is the agricultural program of the New Partnership for Africa's Development (NEPAD) established in 2003 with the objective of eliminating hunger and reducing poverty through agricultural development. It works with four pillars, namely: land and water management; market access; food supply and hunger; and agricultural research [206]. The agreements made by African governments to increase their public investment in agriculture by a minimum of 10 per cent of their national budgets and to raise agricultural productivity by at least six per cent is also regulated by CAADP.

5.3.2. Forum for Agricultural Research in Africa (FARA)

The major goal of FARA is to sustainably reduce food insecurity and poverty and enhance environmental conditions by bringing together and forming coalitions of major stakeholders in agricultural research and development in Africa [167]. It also plays a key role in advocacy and coordination of agricultural research for development. African Sub-Regional Organizations that closely collaborate with FARA are ASARECA, CORAF/WECARD, SADC/FANR, and North Africa SRO [166]. These are briefly described below.

ASARECA (Association for Strengthening Agricultural Research in Eastern and Central Africa) focuses on enhancing sustainable productivity, value-addition and competitiveness in 11 countries in the region: Burundi, Democratic Republic of Congo, Eritrea, Ethiopia, Kenya, Madagascar, Rwanda, South Sudan, Sudan, Tanzania, and Uganda [168].

CORAF/WECARD (West and Central African Council for Agricultural Research and Development) focuses on improving the efficiency and effectiveness of small-scale producers and promote the agribusiness sector in 22 countries: Benin, Burkina Faso, Cameroon, Cape-Verde, Central African Republic, Chad, Congo, Côte d'Ivoire, the Democratic Republic of Congo, Gabon, The Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra-Leone and Togo [169].

SADC/FANR (Southern African Development Community/Food, Agriculture and Natural Resources) focuses on ensuring food availability, access, safety and nutritional value; disaster preparedness for food security; equitable and sustainable use of the environment and natural resources; and strengthening institutional framework and capacity building for 14 countries: Angola, Botswana, DRC, Lesotho, Malawi, Mauritius, Mozambique, Namibia, Seychelles, South Africa, Swaziland, Tanzania, Zambia and Zimbabwe [170].

North Africa SRO (Sub-regional Office) is a recently established one and is mandated for Algeria, Egypt, Libya, Mauritania, Morocco, Sudan and Tunisia [207].

5.3.3. AGRA (Alliance for a Green Revolution in Africa)

AGRA was established in 2006 by the Rockefeller Foundation and the Bill and Melinda Gates Foundation in order to increase the productivity, profitability, and sustainability of African farms [208]. Currently, AGRA focuses on seed system, soil health, access to market, and training.

5.3.4. BecA (Biosciences Eastern and Central Africa) Hub

BecA was established in 2005 to provide a common bioscience research platform, research-related services and capacity building for 17 countries in the region, namely: Burundi, Cameroon, Central Africa Republic, Congo Brazzaville, Democratic Republic of Congo, Equatorial Guinea, Eritrea, Ethiopia, Gabon, Kenya, Madagascar, Rwanda, Sao Tome and Principe, Somalia, Sudan, Tanzania, Uganda [175]. The Hub is based at the International Livestock Research Institute (ILRI) in Nairobi (Kenya), while the five nodes are located in Cameroon, Ethiopia, Tanzania, Uganda and Rwanda.

5.3.5. AATF (African Agricultural Technology Foundation)

AATF is a not-for-profit organization that facilitates and promotes public-private partnerships for the access and delivery of appropriate proprietary agricultural technologies for use by resource-poor smallholder farmers in Sub-Saharan Africa. The current AATF projects are *Striga* control, cowpea improvement, and Water Efficient Maize for Africa (WEMA) [171].

6. Successes in Improving African Crops: Case Examples

6.1. NERICA (New Rice for Africa): High Yielding and Stress Tolerant Rice

Improved cultivars of NERICA were developed in early 2000 by the Africa Rice Center (ex-WARDA: West Africa Rice Development Association) through crossing the high yielding Asian rice (*Oryza sativa* L.) with the locally adapted African rice (*O. glaberrima* Steud.). Some of the desirable properties of NERICA rice are high grain yield, high protein content, early-maturity, resistance to diseases and insects, and good taste. On-farm studies in Uganda indicated that a higher yield of NERICA was obtained by farmers who had rice-growing experience than by those who had no previous experience [209]. This suggests the need for improving the training and extension along the promotion of NERICA. A three-year study in Western Kenya using four NERICA and one local variety showed that NERICA 1 gave superior yield over the other varieties [210]. The adoption study with 600 rice farmers in Gambia indicated that significantly higher seed yield and income were obtained by NERICA adopters than by the non-adopters [211]. Another study involving 1500 farmers in Côte d'Ivoire showed that, although the potential adoption rate for NERICA was 27% in the year 2000, the actual adoption was only 4%, indicating a potential for high adoption through successful NERICA dissemination [212].

6.2. Quncho: A Popular Tef for Both Farmers and Consumers

Although tef is a staple food for about 50 million people in Ethiopia alone, it suffers from low productivity. Over 30 improved tef varieties were released to the farming community in the last several decades, however; the recently released *Quncho* variety received a nation-wide popularity. *Quncho* was developed from the cross between improved varieties *Magna* (DZ-01-196), a variety with consumer-preferred white grain color but with low productivity, and *Dukem* (DZ-01-974), a high yielding variety but with low market price due to the pale white grain color. Hence, a targeted cross was made between the two varieties with the objective of selecting lines combining the high yield of *Dukem* and the seed quality trait of *Magna*. *Quncho* was developed as a recombinant inbred line (RIL) through an F_2-derived single-seed descent method followed by a series of multi-environment yield tests in various major tef-growing regions of the country [213].

In order to speed up the supply of quality seeds of the *Quncho* to ultimate users, an intensified seed multiplication scheme was followed by involving research centers, seed enterprises, farmers, and private seed growers. Through the use of on-farm seed production, efforts were made towards exploitation of the indigenous knowledge in tef seed production and maintenance [214]. An effective innovative approach was adopted in the demonstration, popularization and dissemination of the *Quncho* tef technology. The major features of this approach were; (i) dissemination of technology as a package; (ii) use of large farmers' fields for on-farm demonstrations and scaling-up of the technology; (iii) coordinated multi-stakeholders' partnership extension approach; (iv) distribution of improved seed on 'revolving seed loan' basis; (v) provision of regular training on the technologies for farmers, development agents and extension personnel; (vi) regular follow-up and supervision of the scaling-up activities by a team of researchers and extension agents; and (vii) provision of inputs and marketing options through farmers' cooperatives and cooperatives' unions. Due to the implementation of the above extension system, over 31,000 tef-producing farmers' households with an area of more than 10,000 ha directly participated in the scaling-up activities of *Quncho*. This activity was carried out by the collaborating research centers and the National Crop Technology Scaling-up Program and enabled the distribution of about 306 tons of seeds, and the average yield obtained by the farmers ranged from 2.0 to 2.3 t ha^{-1}.

The Tef Improvement Project (TIP): This is based at the Institute of Plant Sciences in University of Bern, Switzerland, with the goal of boosting the productivity of tef by tackling major production constraints. Priority is given to developing semi-dwarf and lodging tolerant tef cultivar(s). Tef has a tall and tender stem that is susceptible to damage by wind and rain. As a consequence, the yield from the crop is severely reduced in terms of total yield and quality of both the grain and straw. The project applies the following strategies: (i) implementing TILLING on a population of about 6000 mutagenized families in order to identify mutations important for the traits of interest; (ii) phenotypic screening of the mutagenized population for traits such as drought tolerance; (iii) sequencing and analyzing the genome and transcriptome of tef; and iv) collaborating with the Ethiopian agricultural research system in the area of new variety development and training. Several semi-dwarf and lodging tolerant candidate lines obtained from the mutagenized population have been introgressed to high yielding tef cultivars and are currently being evaluated in the field in Ethiopia. The project also focuses on developing drought-tolerant tef lines, in which two drought-tolerant candidate lines are under field-testing in Ethiopia. Although products from TIP have not yet reached farmers, the performance of several lines at the on-station testing is encouraging.

7. Suggestions for Future Research and Development

It is difficult to provide the same recommendation for the whole of Africa, as the continent is divergent in the types of crops, cropping systems and agro-ecology. Hence, we forward some general suggestions, which we think are applicable to at least the majority of regions.

7.1. Invest in Agricultural Research and Development

About a decade ago, African countries agreed to allocate at least 10% of their national budgetary resources to agriculture and rural development policy implementation. However, among 24 countries, only six countries achieved the target by 2005 [215]. African governments also need to implement policies, which support agricultural development. These include conducive policies on land, marketing, and credits, which favor productivity. Commitment to invest in African research also comes from the private sector. Syngenta has recently announced to invest a total of $500 million over 10 years to transform African agriculture with shared knowledge, tools, technologies and services by focusing on seven countries, namely: Ethiopia, Ghana, Ivory Coast, Kenya, Mozambique, Nigeria and Tanzania [216].

7.2. Germplasm Collection and Utilization

The germplasms of many understudied crops have not been properly collected and utilized by researchers. Hence, collections of these germplasms need to be done from diverse agro-ecologies. In order to harness the genetic diversity among the landraces, the germplasm also need to be available to researchers from both developed and developing countries.

7.3. Identify the Right Breeding Tools

Among diverse types of tools developed for major crops of the world, those, which are efficient, cost-effective and easily applicable to the present conditions and institutions of each country should be selected and implemented. Some of the major tools currently applied in crop improvement (as shown in Figure 2) have already been discussed in earlier sections.

7.4. Define Ideotypes for Each Crop and Environment

Ideotype breeding refers to theoretically defining the most efficient plant type for a particular crop and environment, and then breed towards this goal. The ideotype approach has been used in global rice breeding programs where ‘super’ hybrid cultivars with high yield potential were developed [217].

In this case, emphasis was given to obtain rice plants with large panicle size, reduced tillering capacity, and improved lodging resistance. Ideotype breeding was mostly done to determine the morphology or architecture of the plant, which include the height of the stem, branching pattern and the angle and size of leaf. Sarlikioti *et al.* [218] indicated that a new tomato ideotype with more spacious canopy architecture due to long internodes and long and narrow leaves led to a 10% increase in crop photosynthesis.

Berry *et al.* [219] indicated that the best ideotype of wheat plant would be one with the yield potential of 8 t ha^{-1}. Key parameters required to develop this type of wheat are shorter plant height, wider root plate, and appropriate stem strength especially at the bottom internode [219]. Breeding tools such as marker-assisted selection were efficient to create the ideotype of choice. For instance, a rice line with submergence tolerance and best cooking quality (also called ideotype 1, ID1) was developed using this method [220]. In addition to being tolerant to waterlogging and having jasmine-like cooking quality, ID1 lines exhibited a low-amylose content, a fragrance and a high alkali spreading value. According to Mi and colleagues [221], in order to efficiently utilize nitrogen, maize plants need to have the following three root ideotypes: (i) deeper roots with high activity that are able to uptake nitrate before it moves downward into deep soil; (ii) vigorous lateral root growth in order to increase N availability in the soil; and (iii) strong response of lateral root growth to localized nitrogen supply so as to utilize unevenly distributed nitrate, especially under limited N conditions.

7.5. Focus on Both Boosting Crop Productivity and Improving Ecosystem

Food security is becoming the major concern especially due to the high level of population growth. According to Parry and Hawkesford [222], integrated and sustainable crop production approaches should be urgently implemented in order to achieve the projected doubling of food production by 2050. Misselhorn *et al.* [223] also suggested strong interaction between diverse actors and sectors ranging from primary producers to retailers and consumers, and the use of frontier technologies in order to obtain global food security. Hence, due to the diversity in the agricultural conditions, the goals of breeding programs and the tools applied also vary.

Narrowing the yield gap is crucial to provide food for every citizen of the world. Based on the study in Yaqui Valley in Mexico, Ahrens *et al.* [224] indicated that the yield gap in wheat could be minimized by improving nitrogen use efficiency (NUE). According to them, split applications of N fertilizer significantly increased seed yield and profit, and reduced N pollution. Based on earlier studies, Lobell *et al.* [225] estimated the yield potential for several cereal crops in irrigated and rain-fed systems. Although up to 80% of the yield potential was achieved for irrigated wheat, rice, and maize, a maximum of only 50% of the yield potential was obtained for rain-fed conditions, indicating that large increases in crop production is expected from the latter system [225]. Studies on the yield potential and gap for several understudied crops such as cassava and tef showed that crop productivity could be increased several-fold for these orphan crops using improved genotype and/or management (Table 4). Since studies also indicated that agricultural production increased in Africa through optimum use of input such as fertilizers, herbicides and pesticides [47,48], this sector should also be given priority.

Table 4. Potential yield and yield gap for some understudied crops in Africa. The average farmers' yields for millet and tef were based on: millet in Mali [23], tef in Ethiopia [25].

Crop	Average farmers' yield	Yield potential (kg ha^{-1})	Yield gap	Improved system	Location/ country	References
Banana	6,080	27,400	21,320	Genotypes and management	West Africa	[226]
Cassava	6,800	19,680	12,880	Management, genotypes & fertilizer	Kenya	[227]
	10,300	23,333	13,033	Management, genotypes & fertilizer	Uganda	[227]
	9,150	14,000	4,850	Genotypes and management	West Africa	[226]
Millet	720	2,430	1,710	Genotypes and management	West Africa	[226]
Pearl millet	1,610	4,200	2,590	Genotype (dwarf type)	Samanko, Mali	[228]
	1,610	4,500	2,890	Genotype (early maturing)	Cinzana, Mali	[228]
Tef	1,200	4,599	3,399	Genotype (Dukem cultivar)	Debre Zeit, Ethiopia	[229]

7.6. Select the Right Type of Strategy

The main reason for poor productivity of African crops is related to little investment in research and development of these crops. African crops were not represented in the famous Green Revolution, which doubled or tripled productivity of major crops. According to Ejeta [39], in order to achieve a Green Revolution in Africa, locally appropriate technologies need to be developed in addition to human and institutional capacity building as well as forming conducive policies. Due to the large diversity in agricultural systems and crops cultivated in Africa, some institutions or individuals suggest "rainbow evolutions" that differ in nature and extent among the many systems from a single "Green Revolution" type that occurred in Asia [230]. According to Horlings and Marsden [231], the real green revolution will be realized in Africa by implementing an ecological modernization process, which includes social, cultural, spatial and political aspects. In this approach, also known as "agri-food eco-economy", the collaboration of many stakeholders including farmers, consumers and those in the marketing is important [231].

7.7. Develop Crops That Adapt to Changing Climate

Since abiotic stresses such as drought, salinity and heat as well as the changing of climate substantially affect the productivity of crops and food security, future research should also focus on developing resistance or tolerance against these environmental calamities. Ahuja *et al.* [232] enumerated some physiological and molecular mechanisms involved in plant stress adaptation especially on how genes, proteins and metabolites change after individual and multiple environmental stresses. In order to identify adaptation priorities, Lobell *et al.* [233] analyzed climate risks for crops in 12 food-insecure regions in Asia and Africa. According to them, due to extreme predictions for negative impact of climate change, priorities for adaptation should be given to sorghum (*Sorghum bicolor* L. Moench) in the Sahel region, and maize in Southern Africa [233].

7.8. Invest in Innovation Agriculture

Stakeholders involved in African agricultural research and development need to invest in agricultural innovation, as it contributes towards improving the production, marketing or distribution system. A study in Cameroon on plantain banana (*Musa paradisiaca* L.) indicated that both institutional and organizational innovations play key roles in increasing crop productivity and income in rural areas, and also in the production of human and social capital and the protection of forest resources [234].

Among agricultural innovations made in Africa, the Push-Pull system [235], which was developed by the International Centre of Insect Physiology and Ecology (ICIPE) in Kenya, is remarkable. The system is effective in protecting maize from dangerous stem borer and a parasitic weed called *Striga*. In this system, maize is intercropped with *Desmodium* whereas Napier grass is planted around the field. While *Desmodium* produces a smell that drives away stem borer adults and also a chemical that prevents *Striga* from attaching to maize roots, the Napier grass attracts stem borer adults towards it. The adult insects lay their eggs on the Napier grass and when the eggs hatch, the grass produces a sticky substance that kills the larvae or young stem borers. The system is also useful in reducing the amount of pesticide application [236]. The uptake and dissemination of the 'Push-Pull' technology was studied in Western Kenya using randomly selected 112 farmer teachers and 560 follower farmers who had adopted the technology [237]. In addition to improving the productivity of maize through controlling insect pests and parasitic weed, the Push-Pull technology also provides forage for the livestock, releases essential plant nutrients to the soil and reduces soil erosion [238]. In order to further investigate the adoption of the Push-Pull technology, a four-year on-farm study was made in 14 districts of Western Kenya involving twenty randomly selected farmers who had adopted the technology from each district [239]. According to the interviewed farmers, the 'Push-Pull' technology is outstanding in reducing stem borers and *Striga* infestation and in increasing soil fertility and maize grain yield. African agricultural researchers could also learn from innovations implemented in developing and successfully disseminating technologies of NERICA rice and *Quncho* tef (both technologies are described above).

7.9. Focus on Sustainable Agriculture

African countries also need to focus on achieving sustainability in their agricultural research and development. A recent study showed that 40 projects from 20 African countries benefited over 10 million farmers and their families [240]. According to Pretty *et al.* [240], the outputs from sustainable intensification are two-fold: multiplicative (boosting yield per unit area) and additive (diversification through introducing new crops or other food items).

7.10. Create Robust Extension System

Success in agricultural development is not achieved without the adoption of improved technologies by a vast number of farmers. This calls for the establishment of a strong extension system, which links the research community to the farming community. The transfer of new technologies to farmers is facilitated if the studies are made towards solving the major constraints and also by involving farmers from an early stage of technology development as it enhances the ultimate acceptance of the technology. Since farmer-to-farmer extension is more efficient in expanding the new technologies than the formal system, involving farmers in seed production and distribution is important as it has been witnessed in the dissemination of *Quncho* technology (also indicated above) [214].

7.11. Establish Partnership with Relevant Stakeholders

Establishing a genuine partnership with national, regional and international institutions is important for the success of any intended project. Nowadays, public-private partnership (PPP) is considered as an effective system to bring together the public and the private sectors towards enhancing agricultural sustainability in the developing world. Ferroni and Castle [241] presented several promising PPPs in which the Syngenta Foundation for Sustainable Agriculture has been actively involved over the last decade. These partnership projects in Africa include a lodging tolerant and semi-dwarf tef [242], rust-resistant wheat, and biofortification of sweet potato. Spielman *et al.* [243] also investigated 75 PPP projects carried out by the International Agricultural Research Centers considering three criteria: (i) the contribution towards reducing the cost of research; (ii) added value to research by facilitating innovation; and (iii) impact of research on smallholders and other marginalized groups in developing country agriculture.

8. Conclusions

African crops provide food and income for resource-poor farmers and consumers. They also grow under extreme environmental conditions, many of which are poorly suited to major crops of the world. A number of these indigenous crops are extensively grown in Africa. For instance, all global production of bambara groundnut, fonio and yam comes from Africa [32]. Africa also devotes large areas of land to the cultivation of cassava, millet, plantain and taro. Dio *et al.* [244] predicted a rapid growth in staple food production in Africa with an expected impact in lowering food prices by 20%–40% for consumers and 10%–20% for producers, which also contributes to a significant increase in farm income and an about 6.5% or higher increase in annual agricultural growth.

However, the proportion of area devoted to the crops and production volume in Africa are not comparable to those in other parts of the world. For example, in 2010, Africa accounted for 64% of the global cassava area but only for 53% of the global production (Figure 1) [32]. This might be due to the use of unimproved planting materials and poor management. The major bottlenecks affecting the productivity of African crops are genetic traits such as low yield (e.g., in tef, millet), poor nutritional status in some aspects (cassava, enset), and production of toxic substances (cassava, grass pea). Environmental factors such as drought, soil acidity and salinity, pests, diseases and weeds also contribute to large losses in quality and quantity of the yield.

Crop production could be increased by either expanding the arable area or by intensification, *i.e.*, using improved seeds, fertilizer, fungicides, herbicides, irrigation, and the likes. According to the Food and Agriculture Organization (FAO), agricultural intensification represents about 80% of future increases in crop production in developing countries [245]. Based on this goal, crop breeders and scientists are focusing on achieving improved cultivars that produce higher yields and at the same time tolerate the sub-optimal soil and climatic conditions prevailing in the target areas.

Since the Green Revolution did not occur in Africa, the continent did not benefit from the positive effects of this agricultural revolution that boosted the productivity of food crops in other parts of the world. However, due to the lack of genetic improvement, orphan crops produce inferior yields in terms of both quality and quantity. Modern improvement techniques are not yet employed in African crops. Breeders of these crops are mostly dependent on conventional techniques such as selection and hybridization. Only limited numbers of breeders implement modern techniques such as marker-assisted breeding, transgenics, and other non-transgenic genomics tools. Yield potential studies on these understudied crops of Africa have indicated that the productivity of these crops could be increased several fold by using improved genotypes and/or management practices [226–229].

Hence, an agricultural revolution is required to increase food production for under-researched crops in order to feed the ever-increasing population of Africa. The next Green Revolution for Africa needs to also include these locally adapted crops that are mostly known as orphan or understudied crops. Although these crops are largely unimproved, the implementation of modern improvement techniques on these crops has many advantages. There is an increasing interest both from private and public institutions in developed countries to support African agriculture. Hence, African institutions need to devise strategies and approaches, which also focus on establishing partnerships that have to be implemented to tackle the challenges, especially in the face of climate change.

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