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Redesigning crop varieties to win the race between climate change and food security

Kevin V. Pixley[1,*], Jill E. Cairns[2], Santiago Lopez-Ridaura[1], Chris O. Ojiewo[3], Maryam Abba Dawud[4], Inoussa Drabo[5], Taye Mindaye[6], Baloua Nebie[5], Godfrey Asea[7], Biswanath Das[3], Happy Daudi[8], Haile Desmae[5], Benoit Joseph Batieno[9], Ousmane Boukar[10], Clare T.M. Mukankusi[11], Stanley T. Nkalubo[7], Sarah J. Hearne[1], Kanwarpal S. Dhugga[1], Harish Gandhi[3], Sieglinde Snapp[1] and Ernesto Adair Zepeda-Villarreal[1]

[1]International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico
[2]International Maize and Wheat Improvement Center (CIMMYT), Harare, Zimbabwe
[3]International Maize and Wheat Improvement Center (CIMMYT), Nairobi, Kenya
[4]Lake Chad Research Institute (LCRI), Maidiguri, Nigeria
[5]International Maize and Wheat Improvement Center (CIMMYT), Dakar, Senegal
[6]Ethiopian Institute of Agricultural Research (EIAR), Addis Ababa, Ethiopia
[7]National Agricultural Research Organization (NARO), Kampala, Uganda
[8]Tanzania Agricultural Research Institute (TARI), Naliendele, Tanzania
[9]Institut de l'Environnement et de Recherches Agricoles (INERA), Ouagadougou, Burkina Faso
[10]International Institute of Tropicl Agriculture (IITA), Kano, Nigeria
[11]Alliance of Bioversity International and CIAT, Kampala, Uganda
***Correspondence: Kevin V. Pixley (k.pixley@cgiar.org)**
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ABSTRACT

Climate change poses daunting challenges to agricultural production and food security. Rising temperatures, shifting weather patterns, and more frequent extreme events have already demonstrated their effects on local, regional, and global agricultural systems. Crop varieties that withstand climate-related stresses and are suitable for cultivation in innovative cropping systems will be crucial to maximize risk avoidance, productivity, and profitability under climate-changed environments. We surveyed 588 expert stakeholders to predict current and novel traits that may be essential for future pearl millet, sorghum, maize, groundnut, cowpea, and common bean varieties, particularly in sub-Saharan Africa. We then review the current progress and prospects for breeding three prioritized future-essential traits for each of these crops. Experts predict that most current breeding priorities will remain important, but that rates of genetic gain must increase to keep pace with climate challenges and consumer demands. Importantly, the predicted future-essential traits include innovative breeding targets that must also be prioritized; for example, (1) optimized rhizosphere microbiome, with benefits for P, N, and water use efficiency, (2) optimized performance across or in specific cropping systems, (3) lower nighttime respiration, (4) improved stover quality, and (5) increased early vigor. We further discuss cutting-edge tools and approaches to discover, validate, and incorporate novel genetic diversity from exotic germplasm into breeding populations with unprecedented precision, accuracy, and speed. We conclude that the greatest challenge to developing crop varieties to win the race between climate change and food security might be our innovativeness in defining and boldness to breed for the traits of tomorrow.

Key words: climate change, food security, crop breeding, cropping systems, expert survey, sub-Saharan Africa

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INTRODUCTION

The world's climate is changing, and while some expected effects can be predicted (USGCRP, 2018; IPCC, 2022), future crops will grow in unprecedented environments, facing new challenges and offering new opportunities. Most recent estimates of the effects of climate change on crop yields are negative, e.g., –17% overall by 2050 (Nelson et al., 2014), median of –6% for major staple crops in West Africa (Carr et al., 2022), and median of –10% to –15% for maize in Africa (Zhai et al., 2021). Entomologists and pathologists warn that, although the effects of rising temperatures will vary, pest and pathogen generation times (life cycles) will likely shorten, their ranges will expand, and species with suitable hosts will prevail in less-favorable environments, all of which would have negative or unpredictable effects on crops (Bebber, 2015; Fones et al., 2020; Chaloner et al., 2021; Skendžić et al., 2021; Harvey et al., 2023). Molds and mycotoxins may also expand their ranges and become more problematic; for example, *Aspergillus flavus* thrives in high temperatures and aflatoxin (AFB1) production is stimulated by increased temperatures, drought stress, and CO_2 levels (Zingales et al., 2022). Finally, nutritional quality, particularly micronutrient and protein contents are expected to decline under increased CO_2 conditions (Soares et al., 2019), especially for C3 crops (Myers et al., 2014).

Sustainably achieving food and nutrition security for the growing global population under likely climate change scenarios is one of humanity's greatest challenges. There will be no single solution to this problem. A strategic approach begins with an assessment of the current scenario: our strengths, weaknesses, opportunities, and threats to achieve sustainable nutrition security for all.

Strengths

Vast collections of largely unexploited crop genetic diversity are easily accessible through national and international germplasm banks (Ramirez-Villegas et al., 2022), often with precise information about their site of origin, which allows accessing environmental and climate data defining their range of adaptation. Genetic resources are the fundamental building blocks or raw materials for all the food we eat, and dozens of examples have demonstrated the value of exotic genetic resources (crop wild relatives or landraces) in conferring pest or disease resistance, abiotic stress tolerance, quality, and other traits in crop improvement (Pimentel et al., 1997; Dempewolf et al., 2014; Kilian et al., 2021; Bohra et al., 2022). Genomic and pangenome data are available for major and minor crops (Sansaloni et al., 2020; Chapman et al., 2022), and molecular and biotechnology tools are widely available for discovery and breeding applications National Academies of Sciences, Engineering, and Medicine, 2016; Pixley et al. (2019).

Weaknesses

We cannot predict the effects of climate-changed environments on crop physiology or the complex genotypic and epigenomic characteristics (Kakoulidou et al., 2021) that will succeed in them. The complexity that characterizes crop and disciplinary science encourages specialization at the expense of transdisciplinary approaches that could elucidate innovative solutions to cope with changing climate. While germplasm banks contain large, untapped sources of alleles that can help in mitigating the effects of future climate, many wild crop species, especially in conflict areas, remain under-conserved and unavailable Vincent et al. (2019); Ramirez-Villegas et al. (2022). Finally, declining trends in public sector agricultural research investment (Beintema and Stads, 2017; Heisey and Fuglie, 2018) adversely affect the scientific community and its rate of progress on crop improvement.

Opportunities

Data science has and continues to advance, enabling the use and integration, including via machine learning and artificial intelligence, of big data from genomics, transcriptomics, phenomics, climate, soils, and other fields (Parmley et al., 2019; Siddiqui et al., 2021). Modern breeding methods, including genomic selection, speed breeding, doubled haploids, and genome editing promise faster development of new varieties that can quickly respond to emerging challenges (Atlin et al., 2017). Perhaps the most promising opportunity, however, is to design crop varieties for innovative cropping systems that maximize climate resilience, minimize climate risk, and benefit from climate-changed environments, e.g., by shifting cropping calendars, rotations, and relays (Swastika et al., 2004; Thanh Ha et al., 2004; Gathala et al., 2020), or exploiting genotype by environment and crop management interactions (Haug et al., 2020; Cooper and Messina, 2021; Zhai et al., 2021; Farooq et al., 2023). There may also be important opportunities to reap large returns on investments in research in low-income countries, where current yield gaps and predicted negative impacts of climate change are largest (especially in the tropics), and investment in agricultural research are currently smallest (Pixley et al., 2019; Yoshida and Iizumi, 2023).

Threats

The biggest threat is complacency and "business as usual." We are not on-track toward healthy nutrition security for all (World Resources Institute, 2019), nor for producing our food within safe planetary boundaries (Steffen et al., 2015). Recent crises have highlighted the vulnerability of food systems to external factors and have the potential to re-direct funding away from food and nutritional food security objectives (Mottaleb et al., 2022; Jr. Tabe-Ojong et al., 2023). Given the limited resources for agricultural research, the risk of unwisely prioritizing investments is huge, as is the risk of failing to seize the available opportunities.

The objectives of this paper are to: (1) survey experts from diverse disciplines for six major staple crops of Africa to elucidate (1a) likely agronomic changes in future cropping systems seeking sustainability, intensification, resilience and productivity under climate change, and (1b) associated desirable or essential crop traits, particularly those that are not currently prioritized in crop improvement programs, (2) review the current status and opportunities for improving (2a) future, prioritized traits and (2b) future traits that the authors consider potential "blind spots" among the surveyed experts, and (3) discuss novel approaches to harness genetic diversity to develop climate-resilient crops for combating climate change.

	Very high	High	Intermediate	Low	Very low
Climate change: Rainfall scarcity	45	37	11	3	3
Climate change: Temperature and rainfall unpredictability- increased fluctuation and frequency of extreme events	42	39	11	4	3
Population growth: Increased demand for crop products	36	40	15	5	3
Emerging and re-emerging pests and diseases	33	36	16	8	5
Climate change: High temperature	28	40	21	7	4
Soil erosion\degradation (low soil fertility)	24	37	22	9	5
Increased market access: business awareness and entrepreneurship	21	38	22	10	5
Increased seed access: more seed companies trading	24	34	21	12	7
Availability of land: Population encroachment into agricultural land forces reduction in cultivated area	24	34	22	12	5
Diet change: Increased demand for nutrient dense varieties	21	35	26	11	5
Increased market access: transport and communication infrastructure	20	34	24	13	6
Increased demand for feed and industrial use	18	35	23	13	7
Increased demand for animal feed from stover	15	36	25	13	7
Transition into marginal lands: Due to expansion of alternative crops and population encroachment into agricultural land	14	35	27	15	6
Irrigation: Decreased water availability	16	33	20	15	11
Diet change: Increased global demand for aflatoxin free products	15	27	27	15	9
Shift to Off season production for both commercial and seed production	11	30	28	15	10
Irrigation: Increased water availability	13	23	21	20	16
Diet change: Increased demand for diversified sources of vegetable oil	10	23	26	19	13

Table 1. Factors likely to drive changes in crop agronomy or cropping systems for future climates across six crops, expressed as percentage of 588 survey respondents.
Numbers may not equal 100 due to the exclusion of "I don't know" responses.

DRIVERS OF CHANGE FOR CROP AGRONOMY AND CROPPING SYSTEMS MANAGEMENT AND LIKELIHOOD OF ADOPTION OF CROP MANAGEMENT INNOVATIONS UNDER FUTURE CLIMATES

The majority of survey respondents across all crops considered 13 drivers of crop and cropping systems change to be of high or very high importance. Climate change-related factors, such as increased likelihood of lesser rainfall, higher temperatures, and increased frequency of erratic or extreme climatic events, were perceived as the strongest drivers for changes in agronomy or cropping systems, followed by increased demand from a growing population, and the (re)emergence of pests and diseases (Table 1, supplemental Tables 2–7, and supplemental Figures 1–4). For the three cereal crops (pearl millet, sorghum, and maize), soil degradation through erosion or loss of fertility was considered an important driver by more than half of the respondents. In addition, for sorghum and maize, increased demand for stover for animal feed and grain for feed and industrial uses were identified as important drivers. For cowpea and beans, the increased demand for nutrient-dense crops was considered of high importance (supplemental Tables 8–43 and supplemental Figures 5–28 include crop specific survey results).

Regarding the likelihood of adoption of crop management innovations, the majority of respondents across crops considered likely or very likely that farmers will need to innovate around cropping systems diversification and intensification through, for example, optimized crop rotations, intercropping, relay, or double cropping, increased use of mechanization, and early sowing to extend the

	Very high	High	Intermediate	Low	Very low
Conservation agriculture: Crop rotation	21	39	26	8	3
Early sowing (season extension, optimizing crop rotation)	15	38	29	13	3
Intensification (intercropping, relay, and double cropping)	16	35	29	12	5
Mechanization	16	34	22	12	13
Higher planting densities	10	36	33	13	5
Greater use of pesticides (insecticides, fungicides, herbicides etc)	14	30	22	15	12
Greater use of chemical and organic fertilizers	10	28	32	19	9
More use of supplementary water (irrigation)	12	25	24	24	12
greater use of pesticides	10	26	32	18	11
Conservation agriculture: Reduced tillage	8	24	36	21	8
Precision agriculture: GPS directed machinery, implementing decision support systems based on remote sensing, etc.	8	14	25	21	22
Conservation agriculture: Permanent soil cover	4	15	34	28	14
More production for vegetative harvest; decreased focus on grain	4	11	25	31	24

Table 2. Likelihood of adoption of crop management innovations in sub-Saharan Africa under future climates, expressed as percentage of 588 survey respondents.
Numbers may not equal 100 due to the exclusion of "I don't know" responses.

cropping season and optimize crop rotations (Table 2). For the legume crops (groundnut, cowpea, and bean), increasing planting density was considered highly likely, while the use of hybrids was considered unlikely. An inverse pattern was found for cereals, whereby increased planting density was considered less likely than the increased use of hybrids. Notably for maize, greater use of hybrids was considered the most likely technological change. The adoption of sustainable agriculture techniques that maintain soil cover with crop residues and reduce tillage, adoption of precision agriculture machinery, and increased prioritization of fodder versus grain production were perceived to have a low likelihood of adoption by farmers across crops.

BREEDING FOR FUTURE CLIMATES

Current product profiles in pearl millet, sorghum, maize, groundnut, cowpea, and bean breeding programs in sub-Saharan Africa (SSA) primarily focus on increasing grain yield under abiotic and biotic stresses (see Table 3 and Concluding remarks). To sustainably reach food and nutritional security under changing climate may require realignments in breeding targets. We surveyed nearly 100 crop scientists for each of these six crops (see supplemental material: methods, figures, and tables) to elicit expert opinions about essential and desirable traits to enhance resilience and productivity of future crop varieties. About 90% of the survey respondents are based and work in Africa, half are plant breeders, 20% are women, and 16% work in CGIAR institutions. The small percent of female respondents, which was less marked for bean than all other crops, is slightly lower than previous estimates of women enrolled in higher education in science and technology fields in SSA (Tiedeu et al., 2019; Fisher et al., 2020). While this study focused on researchers working within a specific area of science and technology, it suggests a gender disparity in crop improvement teams in SSA.

Figure 1 summarizes the results of the survey, while extensive details across and per individual crop are available in supplemental materials. Highly impactful traits for future varieties can be grouped as very or not innovative, and as readily (feasible) or difficult to breed for. Below, we discuss two characteristics or traits for each crop, chosen to maximize both impact potential and innovativeness, because non-innovative traits are by our definition adequately addressed by current breeding programs. We also discuss for each crop one trait whose impact potential and innovativeness we believe may have been overlooked by the survey respondents (Table 4).

Pearl millet (*Pennisetum glaucum*)

Pearl millet is the sixth most extensively grown cereal crop in the world and has large area-expansion potential because of its excellent adaptation to drought and heat and exceptionally good nutritional value (Ghatak et al., 2021). Its production and

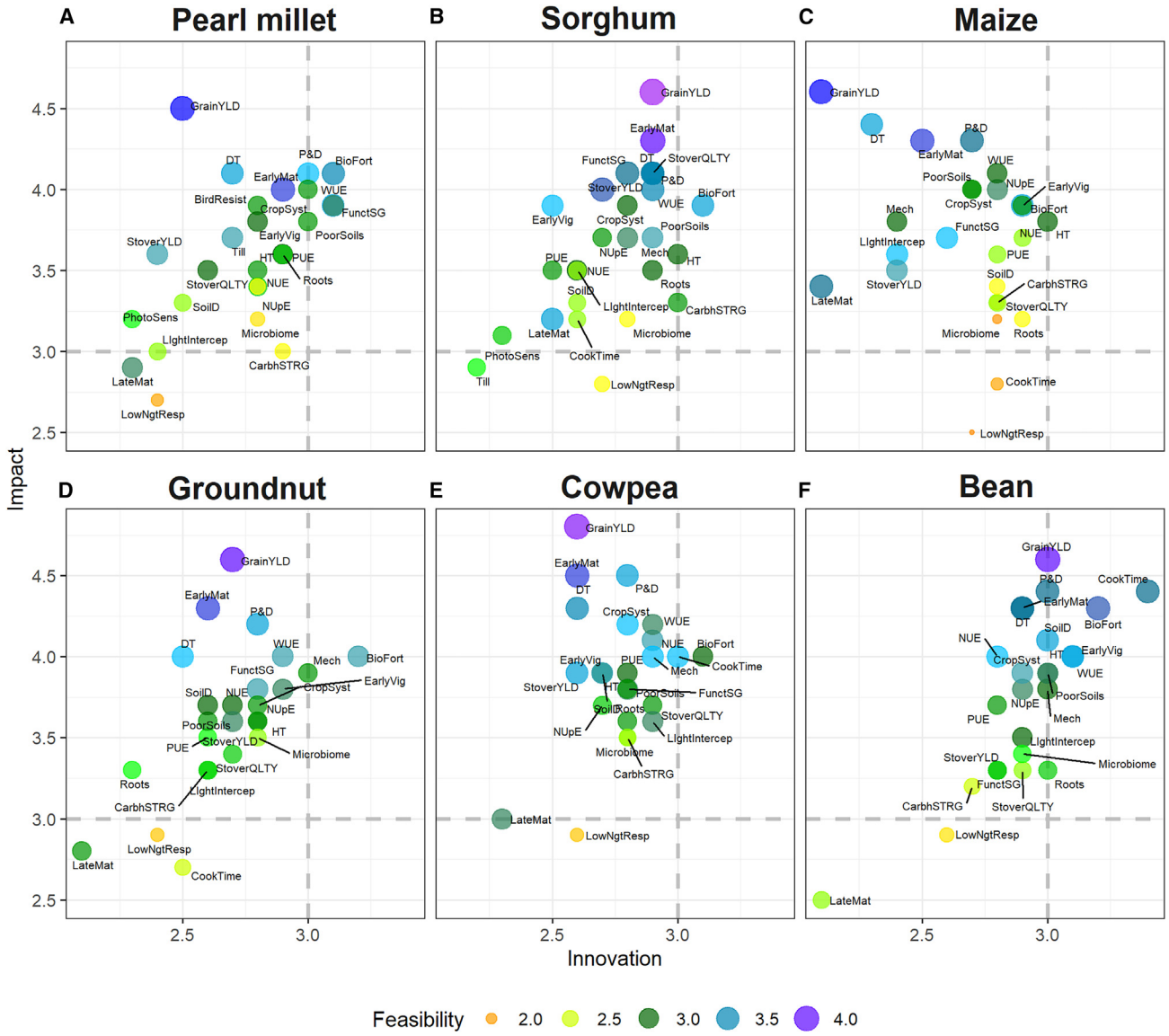

Figure 1. Perceived degree of innovation (X axis) and potential impact (Y axis) of characteristics or traits for breeding for future climates.

(A–F) (A) Millet, **(B)** sorghum, **(C)** maize, **(D)** groundnut, **(E)** cowpea, and **(F)** bean. The size and color of bubbles represents the likely feasibility of incorporating individual traits into breeding pipelines. BioFort, biofortification/nutritional enhancement; BirdResist, bird resistance; CarbhSTRG, carbohydrate storage and remobilization; CookTime, reduced cooking time; CropSyst, changed cropping systems; DT, drought tolerance; EarlyMat, early maturity; EarlyVig, early vigor; FunctSG, functional stay-green; GrainYLD, grain yield; HT, heat tolerance; LateMat, later maturity (longer season); LightIntercep, light interception; LowNgtResp, lower respiration under high nighttime temperatures; Mech, mechanization; Microbiome, root microbiome; NUE, nitrogen use efficiency; NUpE, nitrogen uptake efficiency; P&D, emerging or re-emerging pests and diseases; PhotoSens, reduced photoperiod sensitivity; PoorSoils, poor soil quality including acidity; PUE, phosphorus use efficiency; Roots, root architecture; SoilD, resistance to soil-borne diseases; StoverQLTY, stover quality for feed; StoverYLD, stover yield; Till, tillering ability; WUE, water use efficiency.

use are largely limited to arid and semi-arid regions in SSA and India. With increasing temperatures and expected consequences of climate change, continued or increased breeding for climate-adaptive traits will be necessary (Serba et al., 2020). Pearl millet is known for its exceptional heat tolerance, and further improvement for this character is possible (Satyavathi et al., 2021), aided by recent elucidation of underlying regulatory and genomic factors (Yan et al., 2023). Our expert survey identified stay-green and nutrient biofortification as innovative and potentially impactful traits for future varieties, and we also discuss breeding for bird resistance because it is currently not within product profiles and was highlighted as a potentially highly impactful trait to breed for (Figure 1A and Table 4). Detailed survey results for pearl millet are summarized in supplemental Figures 5–8 and supplemental Tables 8–13.

Stay-green enables pearl millet genotypes to sustain photosynthetic activity during terminal drought, contributing to grain filling and yield (Ghatak et al., 2021). The effect of stay-green on water extraction by pearl millet after anthesis under drought stress is

Trait	Pearl millet	Sorghum	Maize	Groundnut	Cowpea	Bean
Drought-tolerance	–	+/–	+	+/–	+/–	+
Heat-tolerance	–	–	+/–	–	+/–	+/–
Poor soil quality including soil acidity	–	–	–	–	–	+
Root architectural traits	–	–	–	–	–	+/–
Lower respiration under higher night temperature	–	–	–	–	–	–
Improved carbohydrate storage and remobilization	–	–	–	–	–	–
Late maturity (longer season)	–	–	+/–	–	+/–	–
Early maturity	+/–	+/–	+/–	+/–	+/–	+
Functional stay green	–	+/–	–	–	+/–	–
Emerging pests and diseases	+	+	+	+	+	+
Increased water use efficiency	–	–	–	–	–	–
Increased nitrogen uptake efficiency	–	–	+/–	–	–	–
Increase nitrogen use efficiency	–	–	+/–	–	–	–
Increased phosphorus use efficiency	–	–	–	–	–	–
Early vigor	–	+/–	–	+	–	+/–
Resistance to soil borne diseases	+/–	+/–	–	–	+/–	+
Root microbiome	–	–	–	–	–	–
Intensified cropping systems	–	–	–	–	+/–	–
Mechanization of harvesting	–	–	–	–	+/–	+/–
Increased stover yield	+/–	+/–	–	+	+	–
Improved stover quality	–	–	–	–	–	–
Biofortification	+/–	+/–	+/–	+/–	–	+
Reduced cooking time	–	–	–	–	–	+/–
Increased grain yield	+	+	+	+	+	+
Increased light interception	–	–	–	–	–	–
Improved biomass partitioning	–	–	–	–	–	–

Table 3. Current target traits of CGIAR-NARS breeding pipelines in pearl millet, sorghum, maize, groundnut, cowpea, and common bean in sub-Saharan Africa.

Each crop has several breeding pipelines targeting different market segments. Blue cells with "+" indicate a trait is included in all breeding pipelines, green cells with "+/–" indicate the trait is included in certain breeding pipelines, and yellow cells with "–" indicate the trait is not used in selection within any breeding pipelines in sub-Saharan Africa, as known or assumed by the authors.

crucial for grain filling (Vadez et al., 2013). Molecular markers have been identified for stay-green in pearl millet (Debieu et al., 2018); for example, an InDel in a putative chlorophyll a/b binding protein gene was associated with stay-green and grain yield under drought conditions (Sehgal et al., 2015). Molecular markers associated with stay-green were mapped on chromosome 6, two of which were also associated with biomass yield under early drought (Debieu et al., 2018). Stay-green also contributes to fodder quality for animal feed (Kamal et al., 2019), making it a valuable trait for dual-purpose (food and feed) breeding, which was assessed as moderately impactful and innovative by survey respondents.

Compared with other cereals, pearl millet has high concentrations of antioxidants, amino acids, leucine, isoleucine, and lysine, and micronutrients, Fe and Zn, and provitamins A (Dube et al., 2021). Diet diversification, food fortification, and nutrition supplementation are used to address micronutrient deficiencies; however, these solutions are not affordable and accessible to all who need them. Biofortification of pearl millet can be a sustainable and

Crop	Characteristics prioritized by surveys and discussed	Characteristics prioritized by surveys but not discussed	Blind spot prioritized by authors and discussed
Pearl millet	stay green nutritional enhancement	water use efficiency emerging pests and diseases cropping systems	bird resistance
Sorghum	early maturity stay green	drought tolerance stover quality emerging pests and diseases	low soil phosphorus
Maize	cropping systems heat tolerance	drought tolerance early maturity emerging pests and diseases	microbiome
Groundnut	nutritional enhancement mechanization	early maturity emerging pests and diseases water use efficiency	dual purpose
Cowpea	early maturity emerging pests and diseases	drought tolerance cropping systems water use efficiency	root architecture
Bean	short cooking time nutritional enhancement	emerging pests and diseases drought tolerance early maturity	low soil fertility tolerance

Table 4. Characteristics or traits prioritized as impactful and innovative to breed for future climate-resilient varieties of six crops: prioritized by survey respondents and selected by authors for discussion; prioritized by survey respondents but not discussed due to space constraint; and characteristic or trait chosen and discussed by the authors but not prioritized by survey respondents, i.e., potential "blind spots" among respondents.

Note: grain yield was always prioritized by survey respondents as impactful, albeit not innovative for future varieties; it was not included for discussion to avoid repetitiveness and to focus on more innovative breeding opportunities.

cost-effective approach to alleviating micronutrient deficiencies and may have income-generating value for farmers. Genetic variability and molecular breeding strategies are available to enable breeding of Fe- and Zn-rich varieties (Govindaraj et al., 2016, 2022; Kumar et al., 2016; Singhal et al., 2021).

Although few studies have examined bird resistance in pearl millet, several for sorghum have reported high tannin grain, drooping and open panicles to have least bird damage (Mofokeng and Shargie, 2016). Sorghum cultivars expressing tannin binding proteins at immature grain stage, but not in ripened grain, would not significantly impact nutritional quality while reducing bird damage. A recent study revealed that *Tannin1*, which encodes a D40W protein that functions in the WD40/MYB/bHLH protein complex, controls bird feeding behavior in sorghum by affecting the accumulation of anthocyanins and tannin compounds in grain (Xie et al., 2019). Identifying and breeding for favorable alleles of an analog in pearl millet could make significant progress for bird tolerance. The extent to which bird damage can be controlled in pearl millet through genetic traits of the host plant is unclear; however, dense panicles with long bristles have been reported to suffer least bird damage (Akromah et al., 2008; Drabo et al., 2019). Unfortunately, varieties with these traits may be rejected by farmers who harvest and thresh the crop manually (Drabo et al., 2019), although the recent release of a bristled panicle millet in Nigeria suggests that some farmers are interested in growing them. Currently, non-genetic approaches, e.g., bird scaring or bird destruction, are the most effective, but with increased use of mechanization, as predicted by survey respondents (Table 2), and availability of novel breeding technologies such as genome editing, new opportunities to breed for traits that deter bird feeding may become feasible. The very likely increased use of hybrids will also facilitate mechanization of harvest. Finally, research on biochemical compounds and pathways may elucidate opportunities to breed or apply genome editing (e.g., to edit tannin genes) to confer resistance or non-preference by birds.

Sorghum (*Sorghum bicolor*)

Sorghum is the second most widely grown crop in Africa with 28.1 M ha (69% of the global area) grown mainly across arid and semi-arid zones by smallholder farmers in a diversity of cropping systems. Most of the grain production is consumed at the household level, and the stover is increasingly used as livestock feed, especially during dry seasons where natural pasture is limited. Sorghum is a "climate smart" crop due to its water use efficiency and tolerance to high temperatures and rainfall variability. However, changing climate is predicted to increase temperatures, the numbers of dry days and heavy rainfall events, and cause yields to change by +10% to –40% by the end of the century (Akinseye et al., 2020; Mohammed and Misganaw, 2022; Alvar-Beltrán et al., 2023). The survey identified early maturity and stay-green among the most impactful traits for future sorghum production, and we selected low soil phosphorus as a potentially overlooked, high-value future trait (Figure 1B and Table 4). Detailed survey results for sorghum are summarized in supplemental Figures 9–12 and supplemental Tables 14–19

Previous reports indicating farmers' preference for early maturity and stay-green varieties in Ethiopia, Zimbabwe, Mali, and Nigeria (Belay and Wale, 2021; Melesse et al., 2021; Ahmad Yahaya et al., 2022; Traore et al., 2022) support the importance of these traits for adaptation to the changing environments. Early maturity may allow escape from terminal drought, reducing production risks.

Flowering time genes activate the transition from vegetative to reproductive growth (Faye et al., 2022); while stay-green genes delay leaf senescence and increase water and nitrogen use efficiency under post-flowering water stress (Abebe et al., 2021; Hou et al., 2021). Stay-green QTLs are co-located with genes associated with narrow root angle, which contributes to deep rooting and greater water extraction (Tebeje et al., 2020). In addition to its importance to drought stress adaptation, stay-green contributes to maintaining stover quality of dual-purpose (grain for food and stover for feed) varieties. Stover digestibility, which is severely reduced under drought (Somegowda et al., 2021) may be less affected for lines expressing stay-green. Molecular marker-assisted selection (MAS) has been reported for stay-green in elite lines (Nofou et al., 2017; Kamal et al., 2021).

Sorghum's yield gap in Africa can be reduced using improved varieties and appropriate fertilization, especially phosphorus and nitrogen. The survey did not identify P uptake and use as future impactful traits for sorghum improvement; however, low soil P availability is a major constraint for crop production in tropical regions (Hufnagel et al., 2014). P uptake in low-P soils is correlated with root architecture (length and surface area) and with grain yield. Breeding for increased P uptake will enhance crop resilience to climate change and increase yield in low-P soils. Significant genetic diversity and high heritabilities have been reported for P uptake and use efficiency among west and central African sorghums under low- and high-P conditions (Leiser et al., 2014). These traits are positively correlated and are controlled by few genes, including Al tolerance gene sbMATE (Bernardino et al., 2019) for which markers are available for MAS.

*Maize (*Zea mays*)*

Survey respondents, especially non-breeders, identified breeding for increased cropping system diversity as innovative with high potential for impact (Figure 1C). Breeders, however, identified heat tolerance as the most innovative trait, which all respondents believe has moderate impact potential although we believe it may be highly impactful in key maize-producing regions of SSA under climate change. Increasing cropping system diversity can increase productivity per unit area, reduce risk, suppress pests and diseases, and optimize resource capture while reducing erosion, soil carbon loss, and nutrient runoff from increased crop cover (Li et al., 2020; Burgess et al., 2022). We now discuss breeding for: (1) increased cropping system diversity, (2) co-occurrence of heat and drought, and as a potentially overlooked trait, (3) breeding to optimize the rhizosphere microbiome. Detailed survey results for maize are summarized in supplemental Figures 13–16 and supplemental Tables 20–25.

Despite the advantages of intercropping, maize breeding in SSA is primarily conducted under a mono-cropping system (Prasanna et al., 2022). While many farmers use intercropping when testing elite candidate hybrids from breeding programs (on-farm testing), this typically happens late in the product development process, when genetic variation and opportunity to select hybrids that perform optimally under intercrop systems is limited (Voss et al., 2021). Breeding varieties specifically for an intercrop-based system is complex because it requires the optimization of two or more crops simultaneously for complementarity in the same ecosystem (Moore et al., 2023). Genomic selection was recently shown to significantly increase the rate of genetic gain relative to phenotypic selection for grain yield alone when breeding for intercrop systems, regardless of the genetic correlation of intercrop with monocrop yield (Bančič et al., 2021).

Over the past 30 years, there has been a two-fold increase in the probability of the co-occurrence of heat and drought stress during maize-growing seasons (Heino et al., 2023). The co-occurrence of heat and drought stress reduces maize yields by 1.7% for every accumulated degree day above 30°C (Lobell et al., 2011). Research in southern Africa showed that screening for drought tolerance under moderate temperatures indirectly selected against heat tolerance, resulting in elite drought tolerant lines, widely used in commercial hybrids that are highly susceptible to combined drought and heat stress (Cairns et al., 2013). Therefore, the study highlighted the importance of selection for both heat and drought tolerance. Increased temperatures under climate change will result in many African countries experiencing temperatures unrepresented under current climates and increased germplasm exchange from countries identified as analogs of future climates will be essential (Burke et al., 2009).

Low and variable profitability of fertilizers in maize production is a key driver of sub-optimal fertilizer use and subsequently the maize yield gap in SSA (Bonilla-Cedrez et al., 2021). Although exploiting the root microbiome was identified as low in terms of feasibility and potential impact, and moderately high for innovativeness as a breeding target, it could play an important role in increasing fertilizer use efficiency (York et al., 2022; Michl et al., 2023). Maize genotypes vary in their ability to mediate soil organic matter mineralization, which can result in the mobilization of ammonium and subsequent nitrification providing nitrogen for plant uptake (Mwafulirwa et al., 2021). Biological nitrification inhibition (BNI) could play a significant role in nitrogen use efficiency in maize production (Petroli et al., 2023). Soil P content is a major driver of bacterial and fungal communities, with low soil P, which is pervasive in SSA, favoring microbial communities that suppress maize growth (Gomes et al., 2018). Measuring the rhizosphere microbial diversity is possible under field conditions (Peiffer et al., 2013), but quantifying rates of soil organic matter mineralization and nitrification is complex and generally conducted under controlled conditions (Mwafulirwa et al., 2021). Decades of selection in breeding programs for yield primarily under high-input conditions may have indirectly modified interactions between maize and its microbiome and altered the recruitment of specific N-cycling or low-P-tolerance functional groups within the rhizosphere. Landraces, including those held in germplasm banks, may provide an important source of novel alleles for improving the microbiome in the maize rhizosphere (Favela et al., 2021), while genomic selection may offer the needed tactic to incorporate such complex traits into breeding pipelines (Baggs et al., 2023).

Groundnut (peanut, *Arachis hypogaea*)

The future traits survey revealed grain yield, early maturity, emerging pest and disease resistance, drought tolerance, water use efficiency, and nutritional fortification, followed by mechanization, early vigor, stay-green, N use efficiency, soil borne diseases, and cropping systems as impactful traits for future groundnut varieties (Figure 1D). Several previous studies have also ranked grain yield, drought tolerance, early maturity, and disease resistance as essential for future groundnut varieties (Banla et al., 2018; Daudi et al., 2018; Sinare et al., 2021). While breeders and non-breeders

generally agreed on the most impactful future traits, they often disagreed on which traits are innovative breeding targets. All agreed that mechanization, nutritional enhancement, and cropping systems are innovative targets, while only breeders felt that early vigor, microbiome, and N use efficiency are innovative, and only non-breeders believe that water use efficiency, early maturity, and stay-green are innovative targets. We focus on three traits judged to have high potential impact and to be innovative targets for breeding: (1) nutritional enhancement, (2) mechanization, and (3) dual-purpose (grain and haulm production). Detailed survey results for groundnut are summarized in supplemental Figures 17–20 and supplemental Tables 26–31.

Groundnut is known for its high nutritional value and is a preferred ingredient for nutrient-dense foods to prevent malnutrition in children and pregnant and nursing women (Parmar et al., 2022). Nonetheless, substantial genetic variability exists to further improve the nutrient composition of groundnut, particularly oil content (Janila et al., 2016) and oleic-linoleic oil ratio (Deshmukh et al., 2020; Kamdar et al., 2021). Recent advances in analytical tools have enabled cost-effective and non-destructive phenotyping for oil and high oleic (HO) content using near-infrared reflectance spectroscopy (Misra et al., 2000; Pasupuleti and Nigam, 2013). In SSA, breeding HO groundnut is in its infancy despite documented health benefits (Bimro et al., 2020) and longer shelf-life through reduced oxidative rancidity (Deshmukh et al., 2020). Several QTL and marker-trait associations have been reported for oil and HO content (Sarvamangala et al., 2011; Pandey et al., 2014; Shasidhar et al., 2017; Liu et al., 2020; Guo et al., 2021), and MAS and marker-assisted backcrossing have been used to enhance oil quality for groundnut (Janila et al., 2016; Bera et al., 2018; Huang et al., 2019). Mutant *ahFAD2* alleles, conferring HO, have been successfully used for trait introgession (Huang et al., 2019). Nonetheless, HO groundnut varieties remain rare in SSA in contrast to other groundnut producing regions. Efforts to develop high Fe, Zn, pro-vitamin A, or protein groundnut varieties in SSA have been limited, but genetic variability exists for these traits within the primary gene pool (Janila et al., 2015; Chandrashekar et al., 2016; Kadirimangalam et al., 2022).

Groundnut harvesting and pod stripping are labor intensive and expensive and are often complicated by dry soil at harvest. For smallholder farmers, especially the women who are the main producers, labor is becoming more expensive and scarcer. Mechanization of the groundnut production process is one of the key factors that can improve efficiency and profit margins. Stay-green is a trait that would facilitate mechanized harvesting through the maintenance of peg and stem strength, thus minimizing pod losses during harvest. Stay-green may also protect the crop from yield loss (e.g., peg detachment, and termite and insect damage) when the harvest is delayed due to labor shortages or competing priorities. Stay-green also contributes to drought tolerance (Williams et al., 2022) and improved fodder quality. The underlying physiological mechanisms leading to stay-green expression, QTL identification, and gene discovery have been important research areas for various crops including sorghum (Borrell et al., 2014), wheat and barley (Williams et al., 2022), and groundnut (Vadez and Ratnakumar, 2016). Introgression of QTL for stay-green has resulted in sorghum varieties with improved drought tolerance and yield (Vadez et al., 2011; Sintayehu et al., 2018). Simultaneous selection for stay-green and grain yield has been recommended to ensure that delayed senescence is not caused by low sink demand (Borrell et al., 2014). In addition to contributing tolerance to terminal drought stress, stay-green contributes to groundnut haulm quantity and quality, disease tolerance (Danful et al., 2019), and grain quality. Drone-based sensors can measure physiologic and agronomic characteristics useful for breeding stay-green varieties with high yield (Sarkar et al., 2022).

Because the price of groundnut's haulm can equal or exceed that of its grain, breeding for dual-purpose (grain and fodder) varieties with stay-green, nutritious haulm would be valuable. Dual use groundnut was not highlighted as a critical future trait, particularly by non-breeders, but evidence suggests that fodder quality should be included in selection criteria for future groundnut varieties (Samireddypalle et al., 2017). Already groundnut haulms are exported as livestock feed from Sudan to the Middle East, and changing climate is likely to increase pressure on cropping systems to produce feed for livestock as rangeland areas are reduced (Godde et al., 2021). Substantial genetic variation exists, and fodder quality is already being mainstreamed as a release criterion for groundnut varieties for some market segments. With the existing genetic diversity for nutritional quality traits, stay-green traits, and haulm quality traits, and the advances in phenotyping and genomic tools, it is feasible for breeding programs to develop nutrient-rich, stay-green, and dual-purpose groundnut varieties that are climate resilient and meet farmer and market demands.

Cowpea (*Vigna unguiculata*)

The survey of experts identified early maturity and resistance to emerging pests and diseases as the most impactful traits for adaptation and to diminish the risks of cowpea crop failure under changing climate (Figure 1E). Breeding for optimal root architecture would address two of the characteristics prioritized as future-impactful, drought tolerance and water use efficiency. Breeding for root architecture would also be highly innovative, likely because of the challenges for phenotyping and hence currently low feasibility for breeding. For these reasons, we discuss root architecture as a potentially overlooked trait, after discussing breeding for early maturity and resistance to emerging or re-emerging pests and diseases. Detailed survey results for cowpea are summarized in supplemental Figures 21–24 and supplemental Tables 32–37.

In the Sahel and Sudan Savanna, early maturing cowpea varieties provide food during critical hunger periods when food supplies from the previous cropping season run out. Early maturity allows cowpea to escape terminal drought and thrive in arid and semi-arid environments. Adaptation to short growing seasons sacrifices yield potential in favor of stable and reliable yield during most cropping seasons (Thierfelder et al., 2016; Acevedo et al., 2020). Genetic variation for earliness exists (Ribeiro et al., 2014; Owusu et al., 2018b) and earliness is an important objective in most cowpea breeding programs in SSA (Padi, 2007; Santos et al., 2020). In addition to escaping unfavorably high temperatures during flowering and podding stages, early maturity is valuable for avoidance of pests and diseases (Halder and Srinivasan, 2011; Owusu et al., 2018a; Mulwa et al., 2023).

Emerging pests and diseases pose threats to crop production, and currently minor pests may become major pests under changed climate (Sadda et al., 2021). As examples, evolving aphid biotypes have overcome resistance in improved cowpea varieties (Abdou et al., 2013) and leaf thrips (*Hydatothrips adolfifriderici* Karny), formerly occurring sporadically, now pose a serious threat and cause devastating effects through regular outbreaks in some areas in Nigeria (Moritz et al., 2013). Multiple races of *Striga gesnerioides* have recently been reported in West African countries where previously only one race was present (Ohlson and Timko, 2020; Sawadogo et al., 2021). After resurgence of scab disease in Uganda in 2010, widespread presence with moderate to severe disease symptom levels was found in all the 17 cowpea growing districts surveyed in 2015 (Afutu et al., 2017).

Few respondents to the survey opined that root architecture is likely to provide high impact in future; however, we believe that this trait deserves greater attention in breeding cowpea for adaptation to climate change. Root architecture is important for plant acquisition of nitrogen and water (Lynch and Brown, 2001; Lynch, 2013), and of phosphorus, which is highly immobile and commonly limiting. Considerable genetic diversity exists for root traits that enhance growth in nutrient-poor and dry environments (Krasilnikoff et al., 2023). Root traits contributing to efficient root architecture and improved productivity under stressful (low soil fertility and drought) and optimal environments have been identified in cowpea (Adu et al., 2019). Significant genotypic variation and high heritability were observed for phenotypes including primary root length (he ritability = 0.77), basal root number (0.72), and taproot branching density (0.67) (Mohammed et al., 2022). With the development of high-throughput methods for phenotyping root architecture, e.g., robotic imaging tools and analysis pipelines to visualize, quantify, and analyze diverse root traits (Galkovskyi et al., 2012), genetic diversity for root architecture could be exploited in cowpea breeding.

Common bean (*Phaseolus vulgaris*)

The common bean expert survey identified resistance to emerging pests and diseases, short cooking time (CKT), drought tolerance, early maturity, and nutritional biofortification as impactful future traits, while CKT, nutritional biofortification, early vigor, and water use efficiency were considered the most innovative traits for breeding (Figure 1F). We discuss CKT and nutritional enhancement, and include tolerance to poor soil fertility as a potentially overlooked characteristic for bean (and likely for all six crops in this review). Detailed survey results for common bean are summarized in supplemental Figures 25–28 and supplemental Tables 38–43.

Beans are a major staple food in many parts of Africa; however, long CKT is a disincentive to consumption since it demands large amounts of water, fuel, and time (Shellie-Dessert and Hosfield, 1990). Women constitute more than 60% of bean producers across Africa (Nchanji, 2021) and benefit from improved common bean varieties with shorter CKT (Nakazi et al., 2017). Over 85% of the rural and urban poor use wood or charcoal as fuel to cook beans, which has environmental impact due to deforestation. Research on ''cookability'' in common bean began in the 1960s, and CKT and rate of water absorption were later shown to be unique traits, with a low phenotypic correlation between them and relatively small genotype by environment interaction for both traits (Jackson and Varriano-Marston, 1981; Shellie and Hosfield, 1991). Wide genotypic variability associated with CKT exists in both Andean and Mesoamerican bean accessions (Ribeiro et al., 2014, 2021; Cichy et al., 2015). Variation in CKT has been associated with seed qualities including color, size, and seed coat thickness (Reyes-Moreno and Paredes-López, 1993; Klasener et al., 2019; Bassett et al., 2021). In breeding for reduced CKT, care must be taken to maintain protein content and quality. Studies indicate that few QTLs contribute to CKT in beans, and high narrow-sense heritability of CKT in beans (h^2 = 0.74) has been reported (Jacinto-Hernandez et al., 2003; Cichy et al., 2015). Using an African bean panel of 358 genotypes, it was recently reported that genomic selection with optimal contribution selection can accelerate breeding of high yielding, biofortified, and rapid cooking common bean cultivars (Saradadevi et al., 2021).

In many African homes, beans are an accessible source of Fe and Zn, which are essential to the health and well-being of women and children, and of protein which is essential for the entire household. In a bio-efficacy trial among college-age women in Rwanda, high Fe beans improved Fe status and enhanced cognitive ability, brain function, and work efficiency (Murray-Kolb et al., 2017). The opportunity exists to improve the health of women and children through increased consumption of rapid-cooking beans with high and bioavailable Fe and Zn content. Genetic variation exists for nutritional composition of cooked bean, including Zn, P, K, Ca, and Fe in the Andean Diversity Panel (Katuuramu et al., 2018) and in varieties released by Pan Africa Bean Research Alliance (PABRA) programs (Amongi et al., 2018; Mukankusi et al., 2019). Future breeding efforts may focus on improving the bioavailability of Fe and Zn by incorporating mechanisms such as non- or slow-darkening grain, or low phytate mutants (Beebe, 2020). However, a homeostatic mechanism that regulates Fe and Zn uptake has been found to impede biofortification progress and breeders may need to cross between gene pools to achieve higher levels of Fe and Zn uptake; using sister species that have evolved in Fe-poor environments and are more receptive to Fe uptake could also be a viable strategy (Beebe, 2020).

Common beans exhibit considerable genetic variability for specific single or multiple edaphic stress tolerances including low N, low P, and soil acidity with associated Al and/or Mn toxicities (Lunze et al., 2012). Research on root phenotypes and their role in enhanced soil exploration and P acquisition has been ongoing for a long time, leading to better understanding of these traits (Lynch, 2011). Several traits such as greater root branching and longer root hairs (Lynch, 2011), percentage of N derived from atmosphere (Rao et al., 2016), BNI (Subbarao et al., 2015), receptor kinases, transmembrane transporters, and transcription factors (Kamfwa et al., 2017) have been employed to select for tolerance to specific mineral deficiencies. However, developing varieties that are adapted to multiple soil mineral deficiencies occurring in combination with abiotic stresses such as drought, heat, and waterlogging common under farmers' conditions has made little progress. Definition of target population of environments has mainly focused on climatic factors with less emphasis on soil characteristics and deficiencies, which could guide variety testing for low soil fertility tolerance. Gaps in breeding for multiple edaphic stress tolerance include inadequate mapping of soil deficiencies, poor understanding of the genetic basis of tolerance

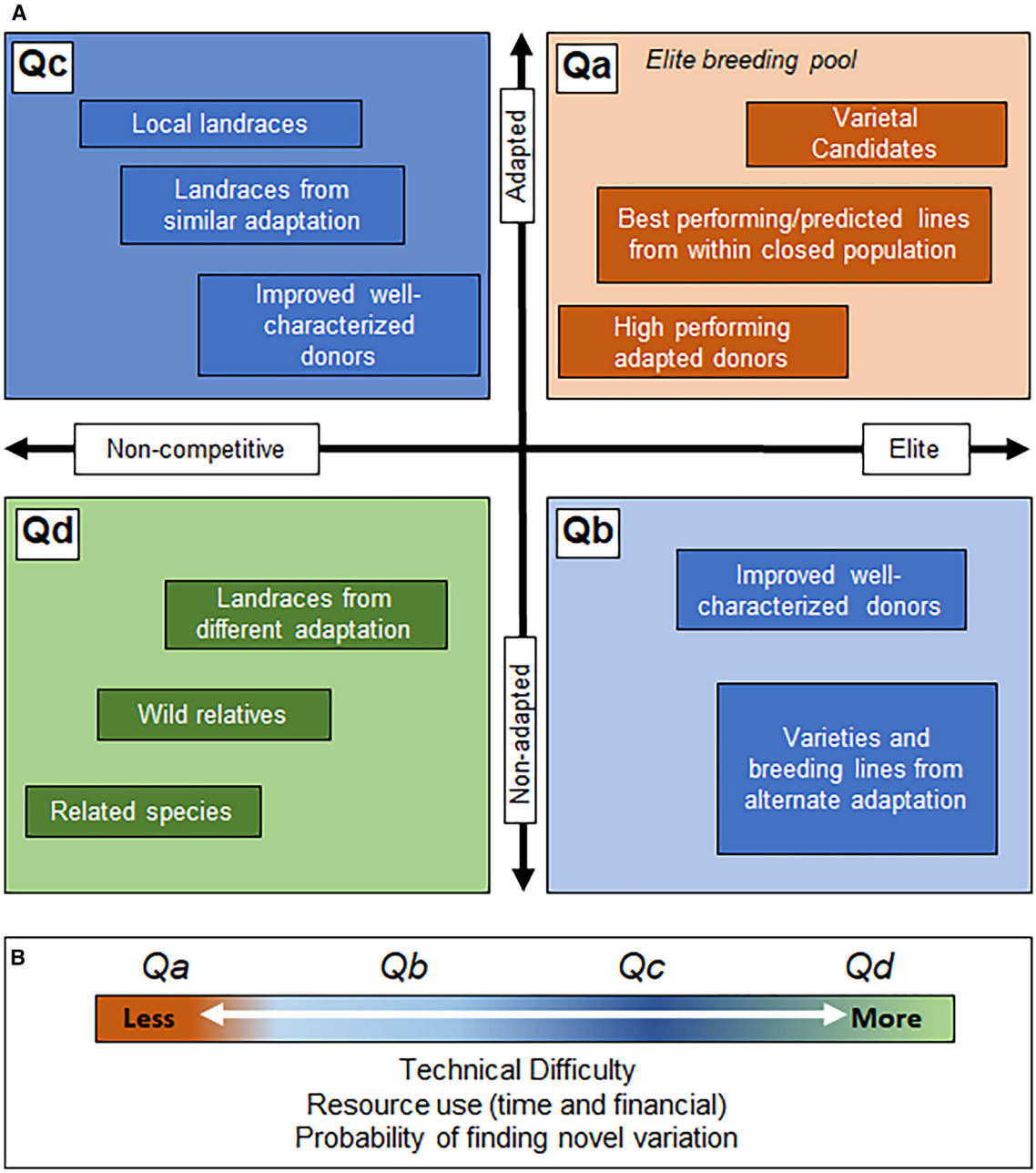

Figure 2. Source germplasm types for trait discovery to serve a core breeding pipeline.
(A) Four trait discovery and deployment quadrants, Qa, Qb, Qc, and Qd, separate potential trait donor germplasm sources along two axes, one focused on the adaptation of the potential source germplasm to the target population of environments that the core breeding pipeline is serving, and the other axis indicating the competitiveness of the germplasm compared with elite performance.
(B) The relative technical difficulty, cost, and probability of finding and deploying novel variation from each of the quadrants.

to multiple soil mineral deficiencies, difficulties in developing suitable screening protocols, and limited cooperation between breeders and soil scientists.

Innovative methods for mining genetic diversity

The extensive expert surveys reported herein propose traits with high potential value for future crop varieties, some of which are innovative in the sense that they are not currently prioritized by breeding programs. Initiating breeding work for such desirable or essential future traits relies on the availability of genetic diversity and the ability to accurately phenotype the trait or linked secondary trait(s). When useful diversity is not available within the elite, adapted breeding germplasm pool, trait discovery in exotic germplasm is necessary, and breeding teams must balance the benefits from incorporating the desired genetic variation with the linkage drag effects from less-desired variation from the same donor. Therefore, breeding programs seeking trait variation not found in the immediate elite breeding pool (Figure 2A, quadrant Qa), generally initially explore elite germplasm from outside the

adaptation target zone (Figure 2A, quadrant Qb). This approach avoids the most deleterious impacts of linkage drag and minimizes the difficulty, cost, and time of developing new, competitive, and adapted germplasm (Figure 2B). Despite these advantages, the challenge faced when exploring elite unadapted (Qb) germplasm as potential sources of "new" traits is their relatively limited variation (Figure 2B). This limitation drives many teams to consider adapted landraces (Qc) and non-adapted landraces and wild relatives (Qd) as sources of genetic variation novel to the elite pools. Despite challenges of using landrace and wild relatives as trait donors, there are numerous examples of successful trait identification and deployment in modern breeding from these sources (Kilian et al., 2021). Common challenges of using exotic germplasm include sorting through many thousands of potential sources, little relevant information to aid germplasm selections, difficulties applying elite-breeding-based phenotyping assays to often heterogeneous and very diverse materials, and the inevitable linkage drag observed when breeding from these germplasm sources.

Over the last 15 years, genomics has begun to open the black box of genetic diversity through the evolution and application of cheap, fast, and precise DNA sequencing technology. Unprecedented scales of crop genetic resource genomic characterization, such as those conducted in the 3000 genomes work in rice (Wang et al., 2018) and for maize and wheat at CIMMYT (Sansaloni et al., 2020), leveraged sequencing technology advances to understand genetic resources. This genomic framework, while powerful, required relevant phenotypic data to conduct primary discovery activities through genome-wide association study (GWAS) and genomic prediction approaches (Crossa et al., 2016; Romero Navarro et al., 2017; Singh et al., 2018). Exploration of the use of other variables, specifically germplasm collection site enviro-climatic variables such as precipitation, temperature, soil pH, etc., has facilitated a step-change in our ability to quickly identify (1) novel genetic variants of potential value for pre-breeding and (2) the germplasm bank accessions most enriched in the desired genetic variants (Forester et al., 2016; Mosca et al., 2016; Yu et al., 2016; Romero Navarro et al., 2017; De La Torre et al., 2019; Gates et al., 2019; Lasky et al., 2023).

Environmental GWAS (EnvGWAS) and environment-based prediction use climate variables alone or in combinations as response variables replacing phenotype(s) used in classical GWAS. This "allele mining" paradigm offers a new scale of experimentation because isolation of environmental variables from georeferenced germplasm collections is many orders of magnitude cheaper than phenotyping the same material. EnvGWAS therefore avails all germplasm bank accessions with genomic data and georeference data for their collection site. These large and diverse germplasm panels offer powerful resources to explore adaptation to features strongly represented in the environmental data, such as tolerance to drought, high temperature, flooding, and low soil pH. Where historic and endemic disease and pest distributions are well documented, these can also be used for EnvGWAS analyses (Bellis et al., 2020). This paradigm does not extend well when the features of interest are poorly represented in environmental data, for example poor data on disease distribution, poor spatial resolution of variables such as salinity, or limited ranges for a feature of interest, e.g., freezing temperatures among maize collections.

Furthermore, using genomic data per se, comparison of landrace with modern cultivars can help identify genomic regions where diversity in elite materials is narrow or fixed compared with landraces. While this assessment and comparison of diversity does not provide an understanding of direct benefit or cost of using exotic diversity, it provides a structured approach to sample and test exotic diversity in regions of the genome where breeding bottlenecks have arisen (Sansaloni et al., 2020).

Gene editing to develop climate-resilient crops

Forward breeding, which has been and will continue to be a mainstay of crop improvement, requires crossing of genotypes with complementary traits followed by selection of desirable recombinants in the target environments, often taking more than a decade to develop an improved cultivar. In contrast, introduction of high-value traits such as herbicide tolerance and insect resistance using biotechnology has contributed substantially to food production over the last two and a half decades (Klümper and Qaim, 2014). The impact of these products has been limited by onerous regulatory approval processes, and opposition to transgenic plants in many countries. CRISPR-Cas, which was introduced as a tool for genome editing a decade ago, enables altering of genes directly in crop plants without permanently introducing foreign genetic material (Wang and Doudna, 2023). Myriad examples of modifying genes using this technology to improve crop plants have already been reported (Nascimento et al., 2023).

Success of gene editing in any crop plant is contingent on the transformation and editing efficiencies. In rice and maize, for example, almost any gene can be edited, whereas in difficult-to-transform crop plants, including pearl millet, none or very few examples are known (Nascimento et al., 2023). Two common scenarios in gene editing with CRISPR-Cas are: (1) repair of the Cas-catalyzed double-stranded DNA break by non-homologous end joining (NHEJ), which deletes or introduces nucleotides, often leading to frameshift mutations, and (2) template-directed repair, referred to as homology-directed repair (HDR), which allows introduction of targeted changes. HDR is used for precise replacement or deletion of specific nucleotides and insertion or replacement of large DNA segments (Anzalone et al., 2020; Wang and Doudna, 2023). Other methods that can produce results like HDR include base editing and prime editing, which provide value where HDR is difficult to perform, for example, in non-dividing cells. In plants, although all the various CRISPR-Cas-mediated methods of gene editing have been reported, NHEJ and HDR suffice to introduce any type of the aforementioned changes (Anzalone et al., 2020). The CRISPR-Cas system has been demonstrated to introduce random mutations (NHEJ), change or replace specific nucleotides (HDR), and replace or insert DNA segments (HDR) in commercial crops (Svitashev et al., 2015; Shi et al., 2017).

Mutant libraries could be useful for the discovery and validation of genetic diversity for use in breeding. The CRISPR-Cas system was used to generate a library of mutations of the coding genes in rice, which is a useful resource for gene discovery, similar to TILLING and transposon-tagged populations (Slade et al., 2005; McCarty and Meeley, 2009; Liu et al., 2023). For example, mutations in genes for plant architecture and stalk strength were isolated from a mu-tagged maize population (Gallavotti et al.,

2004; Ching et al., 2006; McCarty and Meeley, 2009). Similarly, a TILLING population of wheat was screened to isolate mutants of all three homeoalleles of the powdery mildew resistance locus (Slade et al., 2005; Acevedo-Garcia et al., 2017).

CRISPR-Cas can be a useful tool in validating the effect of selected gene candidates from field or laboratory screening, or which may be predicted by other methods, for example, EnvGWAS and bioinformatic analyses, as long as a knockout provides the requisite information. However, HDR would be required if the objective is to measure the effect of a functional candidate gene or genetic region on plant performance in the target environment. CRISPR-Cas technology allows the insertion of large pieces of DNA spanning several to many kilobases into the genome (Anzalone et al., 2020). The resources required to accomplish this would be extensive, though, first to perform HDR, the frequency of which is an order to two orders of magnitude lower than that of NHEJ, and to subsequently test the individual coding sequences in the candidate interval. Gene editing where HDR is required would preferably be reserved, in practice, for the narrowed genetic intervals that have been proven with high confidence to confer yield or performance advantage in a target environment. Furthermore, the selected genetic interval would ideally contain only a few genes to allow rapid identification of the causal gene. Yet, there is no dearth of desirable traits where an inactive gene results in a favorable phenotype, or where the specific polymorphisms are known to improve the performance of a plant. Gene editing, thus, can certainly contribute to crop improvement.

To study the effect of multiple genes on a trait, instead of combining individual, edited genes by crossing and selection, a multiplex approach to edit the multiple target genes simultaneously in the same line would be more efficient. Mutant maize populations for various combinations of 48 growth-related genes were generated via multiplexing (Lorenzo et al., 2023). Several loci in wild tomato were altered to increase fruit size and quality characteristics (Zhang et al., 2020). These types of studies are useful in advancing knowledge but, for expedited product development, if a combination of three or more genes results in a measurable effect on the desired trait, it would be preferable to create it afresh in each target cultivar instead of crossing and selection.

A major advantage of editing a gene to improve a trait is that it can be performed directly in a commercial cultivar or elite line, eliminating traditional pre-breeding steps of backcrossing and selection for the parental genetic background and genetic drag that inevitably accompanies these steps (Dhugga, 2022; Li et al., 2022; Pixley et al., 2022; Biswal et al., 2023). Furthermore, it reduces the time to develop an improved cultivar by nearly two-thirds relative to forward breeding (Dhugga, 2022). In the many countries that have approved guidelines to consider gene-edited crops as non-transgenic, improved crop varieties incur no costs for deregulation, and the costs and procedures for registration are similar to the candidates developed by traditional methods.

Pre-breeding approaches

Our expert survey identified several traits for pearl millet, sorghum, maize, groundnut, bean, and cowpea that will be impactful in mitigating and adapting to climate change. There has been limited work for several of these traits, particularly in some of these six crop species. Therefore, there is an immediate need to intensify research to better understand the inheritance and genetics toward developing population improvement strategies and breeding tools.

New machine learning algorithms facilitate the identification of candidate genes (Sun et al., 2020). Growing understanding of structural variations in genomic regions, and comparative genomics in related species, enabled by the availability of pan-genomes, have further enhanced our ability to discover, validate, and implement such knowledge in breeding programs (Ruperao et al., 2021; Petereit et al., 2022; Yan et al., 2023). Gene editing also provides tremendous opportunities for simple or oligogenic traits with known causative gene information to rapidly deliver improved germplasm where regulatory frameworks permit (Pixley et al., 2022; Rock et al., 2023). For traits with simple or oligogenic inheritance, these technological advances allow fast and cost-effective genetic mapping of traits, and rapid forward and backcross breeding using speed breeding techniques (Ghosh et al., 2018; Wanga et al., 2021) and MAS (Bankole et al., 2017; Baloch et al., 2023).

For complex traits, the impact of genomic selection in accelerating genetic gain in crop breeding has been facilitated by cheaper costs of mid-density genotyping, the availability of computing power, new and novel algorithms, and rapid recycling of elite material through doubled-haploid and speed-breeding methods (Jeon et al., 2023). Genomic selection will be appropriate for improving many of the traits identified in surveys.

Over the last decade, there have been several successful uses of high-throughput phenotyping tools, such as drone- and satellite-based images to rapidly screen thousands of breeding plots with higher accuracy. There are several options already available to deploy in breeding programs and active areas of research. These technologies combined with machine learning algorithms have significantly improved our ability to measure traits reliably and consistently and allowed us to measure component traits, which were previously unthinkable due to labor costs or other constraints (Gill et al., 2022). Such technologies can be used to dissect genetics and reliably measure component traits at higher scale, accuracy, and precision in breeding programs.

Despite tremendous technological advancements for breeding crop varieties, their use is often limited by genotype-by-environment or genetic background effects, and availability of digital platforms to integrate genetic information in decision making. Most of the investments are in model species, in developed countries (Marks et al., 2023), and targeting commercial traits, crops, and cropping systems (Pixley et al., 2019, 2022). This disproportional investment in crops and geographies is concerning and challenges efforts to upscale the use of technologies equitably to benefit farmers and societies where agriculture is most vulnerable to changing climate.

BREEDING FOR FUTURE CROPPING SYSTEMS

The demand exerted by a rising middle class and growing population will continue to put pressure on agriculture to intensify.

Nutritionally dense food and feed are expected to be in demand, which will require breeding attention to novel traits as predicted by survey respondents (Figure 1). On the other hand, our survey did not explore additional, post-farm societal demands such as innovative plant protein products to reduce meat consumption, or environmental services, e.g., net carbon sequestration, biodiversity conservation, and others (Kuyah et al., 2023). All of these growing demands require transdisciplinary efforts, where plant breeders work closely with diverse experts.

Intensified cropping systems will take a range of forms, from monocultures to double and triple cropping systems, to relay and intercrop arrangements. Cropping calendars will shift with changing climate, and cropping options will adapt based on management innovations, access to appropriate inputs (including varieties with novel traits), and market forces. Mechanization, for example, is expected to increase over time and space, supporting and demanding the use of different varieties to tolerate new stresses, e.g., sowing in wetter soils or higher plant population density, and opportunities such as dual-purpose, or bird-resistant, or avoiding varieties. Increased use of hybrids is predicted by our survey to be of primary importance in cereal crops, which will require plant architecture that is compatible with close spacing (Richards et al., 2019), and increased levels of drought, disease, and pest tolerance expected in such intensive planting systems (Ando et al., 2007).

Novel cropping systems will offer new stress-coping and productivity- or profit-maximizing options requiring system-optimizing management practices and crop varieties. Complementary architectural and growth traits are already utilized in intercrop systems such as cereal–legume associations and legume–legume systems (Kuyah et al., 2021). For example, farmer participatory research has shown that farmers in Rwanda select for ideotypes of beans that perform well when intercropped with maize (Isaacs et al., 2016). Architectural traits can be selected to facilitate complementarity, such as slow growth aboveground, with a retarded rate of branching in one crop, combined with selecting for rapid growth in a complementary crop that is also selected for shade tolerance. Maize and pigeonpea are a widely grown example of such complementarity of plant phenotypes, which could be enhanced through deliberate selection (Snapp et al., 2019). Belowground competition could be minimized by developing crops with steep root angles to reduce root overlap at the surface (Bonser et al., 1996; Lynch et al., 2022).

As highlighted by respondents in this study, heat- and drought-tolerant varieties will be very important to the success of future cropping systems. Drought avoidance has been widely relied upon historically and, as confirmed by our survey, will continue to be important through selection for early maturing and rapid growth types (Snowdon et al., 2021). In addition, a wide range of plant physiological characteristics can enhance adaptation to water deficiency and heat stress; these will need to be selected as stand-alone traits and in combination (see maize section, above). Crops with exceptional heat and drought tolerance attributes, notably pearl millet, are expected to achieve further progress in climate change adaptation traits, and some of these traits will be extendable to related cereal crops through studies of genomic synteny and application of modern breeding technologies. Breeding for these traits will provide varieties for novel cropping systems and to allow continued cultivation of crops in their traditional agro-ecologies as climate change alters the weather associated with them.

The ability of crops to tolerate nutrient-deficient soils is expected to be of future importance and is highly complementary to drought tolerance. This includes both belowground and aboveground traits, as nutrient acquisition, allocation, and efficiency of use are all involved (Liu et al., 2022). The plasticity of roots and related factors that lead to large genotype by environment interaction effects have historically complicated and slowed progress in breeding for tolerance to low nutrient status, but the advent of molecular and statistical tools could lead to breakthroughs in this field. Progress in improving nutrient acquisition and use efficiency will provide crop types that are expected to improve the performance of conservation, sustainable, and restorative agricultural systems.

Future scenarios that may vary widely are those driven by globalization, altering land use, farming systems, and market demand. These could include greater integration of crop and livestock systems, which will increase the demand for crop types that are dual use for fodder and food (Thornton and Herrero, 2014). Forage quality and quantity of stover are very important in such systems (Melesse et al., 2021). This is an area where respondents predict rapid progress can be made. A much longer-term project would be to breed for perennial and semi-perennial grain crops, the prototypes of which have shown to provide a wide range of environmental services such as reduced loss of nitrogen to the environment (Culman et al., 2013), although others caution that perennial crops may be highly vulnerable to pests and diseases. More specifically, enhanced soil carbon gain has been proposed in a dual-use crop type through selection for enhanced suberin and related biochemical properties in roots of cereal and pulse crops (Eckardt et al., 2023). BNI is another example of an environmentally friendly service that can enhance crop performance in an intensive cropping system, well suited to cereal crop genetic improvement (Subbarao et al., 2021).

CONCLUDING REMARKS

Climate change will affect agriculture in every corner of the world. Our survey respondents echoed predictions that temperatures will increase, rainfall distribution will be less predictable, and pest and disease ranges will change (Table 1). Not all changes will be negative. Warmer temperatures will accelerate crop development, enabling use of longer-duration and higher-yielding varieties, or novel or intensified cropping systems (Table 2). Optimal options for relay cropping may change in regions where this practice is already common, such as Indonesia, Vietnam, and India (Swastika et al., 2004; Thanh Ha et al., 2004; Jat et al., 2020), and new opportunities may arise in areas where only one crop was previously possible, for example, in parts of West Africa predicted to become hotter and wetter (Zhai et al., 2021).

Changing cropping systems will expose crops to new environments that may require or benefit from characteristics that are not valuable in today's varieties. Relay cropping may force crops out from their optimal monocrop or current relay crop season, exposing them to wetter or drier than optimal soils at planting,

sunnier or cloudier conditions during vegetative growth, hotter or cooler temperatures during grain fill, fewer or different insect pests, etc. Short turn-around time between crops may incentivize redesigning of crop varieties, for example to facilitate mechanization of harvest or planting, and to prioritize rapid emergence, early vigor, quick dry-down, and early and enhanced accumulation of nutritional components in grain (e.g., protein, Fe, Zn, and provitamins A) (Figure 1 and Table 4). Dual-purpose varieties, suitable for grain and fodder production, may be increasingly valued for averting the risk of crop failure during seasons when grain production is poor or fails. For crops that will be intercropped, traits related to growth architecture (e.g., erect leaves, branch angle, plant height) and growth habit (e.g., early vigor, spreading habit, determinate vs. indeterminate) will play important roles. Breeding crop varieties for intercropping or relay crop systems may require selection at early stages in breeding programs to consider general and specific mixing ability (GMA and SMA), assessing the suitability for use in multiple or specific systems (Moore et al., 2022, 2023).

The expert survey prioritized very few future-essential traits that are not already targeted in current breeding programs (Table 3 and supplemental information). These were mainly water use efficiency in pearl millet, groundnut, and cowpea, adaptation to cropping systems for pearl millet and maize, and suitability for mechanization in groundnut. This finding is consistent with recent surveys in 19 low- and middle-income countries that concluded that changing climate has resulted in greater urgency and intensified breeding work on traits that already had high priority (Galluzzi et al., 2020). While smarter and faster breeding for currently important traits is essential, we suggest blind spots and potentially large, missed opportunities from relying entirely on this approach. We describe recent advances in diverse fields of science that make or could soon make it feasible to breed for: (1) optimized rhizosphere microbiome, with impacts on P, N, and water use efficiency, (2) optimized performance across or in specific cropping systems, (3) decreased nighttime respiration, (4) improved stover quality, (5) increased early vigor, and (6) improved heat tolerance. Each of these traits would be valuable in most or all crops' adaptation and resilience to climate change.

Survey respondents perceived a low likelihood of adoption of sustainable agriculture approaches including reduced tillage, increased soil cover, increased vegetative yield, and increased use of precision machinery in agriculture to maximize efficiency of fertilizer and other inputs (Table 2). This is a surprising result given worldwide soil health concerns, conservation agriculture being on the rise, and marked competition in uses for crop residues. A strong case can be made for designing crops with traits that are key to successful conservation farming, such as vigorous early growth for improved performance under mulch. The views documented here highlight a perception challenge, suggesting that many experts view conservation farming practices and precision agriculture narrowly, limited to approaches that require a high degree of mechanization, which may contribute to skepticism about adoption potential.

Breeding varieties that are redesigned for agriculture under changed climate will require innovative phenotyping approaches and transdisciplinary teams with expertise in agronomy, soil science, microbiology, biochemistry, physiology, genomics, data science, and more. These teams must be bold enough to tackle traits found only in exotic germplasm (see Figure 2) and for which selection methods must be developed, validated, and optimized. As described herein, recent and emerging methods for gene discovery, allele mining, and plant breeding offer unprecedented opportunities for precision, accuracy, and speed in developing new varieties. By consequence, the greatest challenge to developing crop varieties that win the race between climate change and food security might be our innovativeness and boldness in defining the future traits we breed for today.

SUPPLEMENTAL INFORMATION

Supplemental information is available at *Molecular Plant Online*.

AUTHOR CONTRIBUTIONS

K.V.P., project concept and lead author. J.E.C., S.L.-R., and C.O.O., coordinated the sections: M.A.D. and I.D., pearl millet; T.M. and B.N., sorghum; J.E.C. and G.A., maize; B.D., H. Daudi, and H. Desmae, groundnut; B.J.B. and O.B., cowpea; C.T.M.M. and S.T.N., bean; S.J.H., allele mining, including the figure; K.S.D., genome editing; H.G., pre-breeding; S.S., breeding for cropping systems; S.L.R. and E.A.Z.-V., survey analysis, and figures and tables. All authors contributed to manuscript planning, and reviewed and approved the final manuscript.

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