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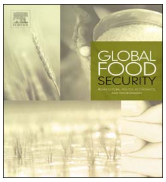

Review article

Rapid breeding and varietal replacement are critical to adaptation of cropping systems in the developing world to climate change

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ABSTRACT

Plant breeding is a key mechanism for adaptation of cropping systems to climate change. Much discussion of breeding for climate change focuses on genes with large effects on heat and drought tolerance, but phenology and stress tolerance are highly polygenic. Adaptation will therefore mainly result from continually adjusting allele frequencies at many loci through rapid-cycle breeding that delivers a steady stream of incrementally improved cultivars. This will require access to elite germplasm from other regions, shortened breeding cycles, and multi-location testing systems that adequately sample the target population of environments. The objective of breeding and seed systems serving smallholder farmers should be to ensure that they use varieties developed in the last 10 years. Rapid varietal turnover must be supported by active dissemination of new varieties, and active withdrawal of obsolete ones. Commercial seed systems in temperate regions achieve this through competitive seed markets, but in the developing world, most crops are not served by competitive commercial seed systems, and many varieties date from the end of the Green Revolution (the late 1970s, when the second generation of modern rice and wheat varieties had been widely adopted). These obsolete varieties were developed in a climate different than today's, placing farmers at risk. To reduce this risk, a strengthened breeding system is needed, with freer international exchange of elite varieties, short breeding cycles, high selection intensity, wide-scale phenotyping, and accurate selection supported by genomic technology. Governments need to incentivize varietal release and dissemination systems to continuously replace obsolete varieties.

1. Introduction: the challenge posed by climate change for crop production, and the problem of obsolete varieties

In food-insecure regions in Africa, climate change is expected to reduce yields through increased average temperatures (Cairns et al., 2013a; Knox et al., 2012; Challinor et al., 2016), and increased frequency of extreme weather events (Lesk et al. 2016). High temperatures during and after flowering reduce grain set in wheat (Stratonovitch and Semenov, 2015), and biomass accumulation and seed-set in rice (Peng et al., 2004). They accelerate development in maize and senescence in wheat, reducing yield potential (Challinor et al., 2016; Lobell et al., 2012; Asseng et al., 2015). Maize yield losses average approximately 1% for each growing degree day (GDD) above 30 C in sub-Saharan Africa (Lobell et al., 2011), and also result from extreme heat events (Lobell et al., 2013). Climate change also affects pest and disease prevalence (Dawson et al., 2015).

Concerns about such effects have prompted widespread efforts to identify major genes affecting drought, flooding, and heat tolerance. Some alleles with large effects on these traits have been identified ((e.g., in rice, Xu et al., 2006: Bernier et al., 2007; Ye et al., 2015), but they are relatively rare, and will likely provide only a small portion of the genetic variability needed for adaptation. Adaptation will be achieved by: matching phenology to growing season length through changes in cultivar day-length and temperature response (Kumudini et al., 2014), exemplified by the shift from photoperiod-sensitive landraces to photoperiod-insensitive semi-dwarf wheat and rice varieties during the Green Revolution, and changes in root architecture allowing better access to soil water (Lynch and Wojciechowski, 2015); transpiration response to high vapor pressure deficit (Messina et al., 2015); and cellular processes affecting heat and desiccation tolerance (Mickelbart et al., 2015). The genetic architecture of these traits tends to be highly polygenic. Even control of flowering time has been shown to be influenced by many genes with small effects (e.g. Buckler et al., 2009).

It is also unclear that widespread varietal adoption can be driven by

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major genes for stress tolerance. For example, incorporation of the highly effective Sub1 allele for submergence tolerance in rice has led to only limited adoption of Sub1 varieties except in areas where flash flooding is frequent and severe (IRRI, unpublished data). Farmers adopt new varieties based on many considerations, notably yield potential, end-use quality, and agronomic fit to their cropping system. Large-effect alleles for stress tolerance must be packaged in varieties that are profitable to produce and demanded by end-users (who, in developing countries, usually include the farmers themselves). Cropping system adaptation to climate change will therefore mainly result from breeding programs that deliver continuous optimization of quantitatively inherited trait complexes, requiring constant and rapid gene frequency change in elite populations, and seed systems that continuously deploy the improved cultivars extracted from these populations. The farmers who are best protected from climate change are those who have access to a steady stream of new cultivars bred in the current climate. Farmers in many temperate regions have this access, due to competitive seed sectors that encourage varietal turnover. In contrast, most farmers in climate-vulnerable areas of the developing world use improved cultivars selected thirty or more years ago, or landraces selected generations ago, in a different climate. To increase yields in these regions in the face of climate change, increased investment in accelerated breeding and varietal dissemination is urgently needed, as is access to elite germplasm from regions already experiencing the "future climate".

This paper will argue that the key elements of cropping system adaptation to climate change are:

(i) Access to elite germplasm from other regions that currently experience conditions likely to occur in the target region as a result of climate change;
(ii) Rapid breeding cycles that provide farmers with a steady stream of new cultivars developed in and for the current climate;
(iii) Evaluation of potential new cultivars under the full range of climate conditions they are likely to encounter over their commercial life;
(iv) Seed systems that deliver new varieties to farmers quickly, and then just as quickly replace them, keeping pace with the changing climate.

These elements characterize highly commercialized systems in temperate regions, but are not in place in the developing world. Consequently, smallholder farmers in developing countries are at much greater risk from climate change than farmers in richer regions. Plant breeding and seed systems in the developing world must be rapidly upgraded to protect vulnerable farmers. Of course, improved plant breeding and varietal replacement systems are only part of the toolkit needed to deliver climate change adaptation. Especially in Africa, improvements in soil fertility management are urgently required. On a continent where the average inorganic N, P_2O_5, and K_2O fertilizer application rates on cropland were only 13.8, 5.9, and 2.2 kg ha^{-1}, respectively, in 2014 (FAO, 2015), or about one-sixth of the global average, yield losses for the foreseeable future due to climate change could be more than counterbalanced by bringing fertilizer use closer to the global mean. Smallholder farmers in the developing world need a host of supports to intensify production, including secure land tenure, improved market access, credit, and transportation infrastructure. However, this review will focus on the improved cultivar development and dissemination systems that are needed to quickly develop and deliver the shorter-duration, stress-tolerant, market-demanded, higher-yielding varieties demanded by small-holder farmers who are intensifying production in the face of a rapidly changing climate. In most countries severely affected by climate change, the systems for delivering these adaptation tools are inadequate.

2. Elements of climate-adaptive breeding and seed systems

2.1. Access to elite germplasm and performance data from other regions: the critical role of international public breeding programs

Most of the tools needed for adaptation are already in our hands. For most crop species, tolerance to the range of variability in predicted temperatures and precipitation over the next 100 years lies within the current genetic diversity (Burke et al., 2009; Braun et al., 2010). Little of this variability has been deployed as elite cultivars in the regions that are both most food insecure and most vulnerable to climate change. Elite cultivars from regions already experiencing the expected climate for the breeding target region, which are easier to use as direct parents in breeding than landraces, will often have to be acquired from beyond national borders (Galluzi et al., 2015). Unfortunately, the open culture of germplasm exchange existing until about 25 years ago has become restrictive (Galluzi et al., 2015; Heisey and Day Rubenstein, 2015). Until the 1990s, breeders exchanged varieties relatively freely. However, as plant breeding became highly commercialized, companies increasingly sought IP protection for products, culminating in the US practice of protecting cultivars with utility patents that prevent them from being used as parents by other breeders. At about the same time, many countries recognized their indigenous crop genetic resources as a unique patrimony, and restricted their international exchange. Any breeder who has recently attempted to obtain an elite variety from the national system of a different country knows that this has become very difficult. There is little "freedom to operate" for the public sector plant breeding programs that serve most smallholder farmers in developing countries.

What of the plant genetic resources collections of national agricultural systems and the international crop research institutes of the Consultative Group on International Agricultural Research (CGIAR)? CGIAR gene banks, as well as those of the USDA, still freely provide breeding programs with access to the great diversity in their collections (Heisey and Day Rubenstein, 2015; Galluzi et al., 2015). However, these collections consist mainly of unimproved landraces, which are important sources of alleles for stress tolerance and disease resistance but are usually narrowly adapted to their environment of origin, and are unsuitable for modern commercial agriculture because they lack the fertilizer responsiveness and yield potential farmers need now. Most breeding programs cannot afford to use unimproved gene bank accessions directly as parents in breeding for greater heat and drought tolerance, due to the yield penalty usually associated with them. Although inexpensive molecular marker systems are reducing the cost of localizing and exploiting genes for stress tolerance in unimproved materials, breeders still have great need of elite, commercially-acceptable materials from regions already experiencing the expected climate. Elite varieties from warmer, drier, or wetter regions are the critical building materials needed to construct varieties adapted to the future climate in their own target regions. Some public germplasm collections also acquire and maintain older elite improved varieties, but the vast majority of their improved holdings were developed over 30 years ago, in a different climate and under different agricultural conditions.

How, then, can breeders of the staple crops in the developing world acquire the elite germplasm needed to rapidly adapt to a changing climate? Multinational seed companies, which focus on highly commercialized crops like maize and soy, often have operations or alliances in different countries, and can move their elite proprietary germplasm among these countries. On the other hand, small national programs and regional seed companies usually lack the international connections needed to cope with a rapidly changing climate, and sharing of germplasm between national programs in different countries is limited and difficult. Of more direct use are the new elite materials continually being generated by CGIAR breeding programs, which focus strongly on developing commercial varieties with improved heat, flooding, and drought tolerance that are freely available to, and widely used by,