Meeting Global Needs Via Genetics x Environment x Management

Meeting future food needs will carry some specific challenges.

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Summary: *Global food needs are projected to double by 2050 to feed a projected 9 billion people and the challenge presented to agriculture is whether this is feasible. These goals will be faced with an increasing variability in climate and more extremes in temperature and precipitation in all parts of the world, not to mention a decreasing land resource base in extent and quality. While there are many challenges to be met, focusing on the interactions of genetics x environment x management (G x E x M) offers the potential to feed the 9 billion. However, we must understand that a critical part of the management complex will be how we address nutrient management to ensure product quantity and quality and pest management to reduce the pressures on plants. We can meet this challenge; however, the paradigm of how we currently conduct research will not be rapid enough and we need to develop the transdisciplinary teams to represent each component of the G x E x M interaction.*

Feeding the projected 9 billion global inhabitants of 2050 is a topic of concern to agriculture because it is questionable if agricultural production can expand to meet this challenge. Projections of the required increase of global food production range from 60 to 110 percent above current levels. For the required increase to occur, assuming no change in population growth rate or food consumption and food waste management, the following production increases must take place by 2050 and beyond: cereals must increase by 940 million Mg to reach 3 billion Mg; meat production must increase by 196 million Mg to reach 455 million Mg; and oil crops must increase by 133 million Mg to reach 282 million Mg. Ray et al. (2013) argue that the current yearly increases of crop production for maize (Zea mays L.) at 1.6 %, rice (Oryea sativa L.) a 1.0 %, wheat (Triticum aestivum L.) at 0.9%, and soybeans [Glycine max (L.) Merr.] at 1.3% are insufficient to meet the projected demands of 2050, and thus, production of these crops must increase by 67% (maize), 42% (rice), 38% (wheat), and 55% (soybeans). A major component in this production increase is the nutritional quality of this produce to ensure food security in quantity and quality. The nutritional demands of 9 billion people must be the first aspect of how we view future production.

Another estimate of the needed increase for global maize during the time frame of 2000 to 2050 is more than 450 million Mg or nearly 30% (Hubert et al. 2010). A recent assessment of agricultural production by Sakschewski et al. (2014) argues that production increases can come from increasing land productivity or by increasing available land resources, and increasing available land resources is not an option. They suggest that productivity increase will be insufficient to meet global food demands and that technological advances will be needed to increase production. One of those technological advances is how we address nutrient and pest management in agricultural systems. Adding to the demand for increased production is the call to redirect agriculture toward a more sustainable path for food security (Godfrey et al. 2010) because of growing competition from nonagricultural sectors for land, water, and energy. These assessments illustrate the complexities of producing food and feed to satisfy global food demands of the future. Clearly, a challenge to the agricultural community exists, there are no simple solutions, and there is an urgent need for revolutionary (vs. evolutionary) innovations.

G x E x M

Here we explore the current state of agricultural production and where opportunities and challenges exist to increase yields. A suggested framework for approaching the challenges is built on an effort to understand the interactions among genetics, environment, and management, referred to as genetics x environment x management or simply: G x E x M.

Yield gap

A path to increased yields begins with a look at where current farmer yields are relative to potential yield. Potential yield has been defined as “the yield of a cultivar when grown in environments to which it is adapted; with nutrients and water not limiting; and with pests, diseases, weeds and other stresses effectively controlled” (Evans and Fischer, 1999). Potential yield (Y_p) is a measure of the capacity of a crop to convert solar radiation into dry matter with no stress during the growth cycle. Cassman et al. (2003) and Lobell et al. (2009) present a case for closing the yield gap, the difference between potential yield (Y_p) and farmer yield (Y_F), rather than seeking to increase Yp. A yield gap approach addresses all factors affecting crop yields and also when these factors affect yield during the growing season. Sinclair and Ruffy (2012) suggest that N and water limit crop yield more than plant genetics and thus N and water should be considered the primary factors limiting yield. This would argue for a renewed emphasis on nutrient management, especially nitrogen management to increase crop productivity (Spiertz, 2009). Fischer et al. (2014) suggest that closing the yield gap requires a more standardized method for yield comparisons and propose that yield gap be expressed as a percentage of the Y_F because increased production will come from greater Y_F rather than Y_p. Attainable yield was defined as the yield achieved by a producer under near optimum weather and management inputs. Hatfield (2010) and Egli and Hatfield (2014a, 2014b) looked at county level YF for Iowa, Kentucky, and Nebraska and found the frontier of the upper bound of Y_F achieved an optimal, which could be treated as Y_A for comparison with Y_F from any year. The results indicated that differences between Y_F and Y_A provide insights to the limitations of crop yield for any year. This is illustrated in Figure 1 with county level yield data for Iowa to show the difference between Ya and Yf and the variation of yield gap values each year. These data are typical of county-level yields and show yield gaps as a fraction of Ya have decreased since 1950 because yields have increased. Egli and Hatfield (2014) found that soil quality as defined by the National Crop Commodity Productivity Index (NCCPI) was positively related to soybean yields across Iowa and Kentucky; however, when irrigation was present this relationship was no longer valid as found in Nebraska county yields with extensive irrigation. Environmental conditions will have a major impact on our ability to close yield gaps, and increased attention on the factors limiting yield will provide insights into future increases of productivity.

Lobell et al. (2009) summarized a comparison of Y_F with Y_P data of maize, rice, and wheat. Using a combination of simulation models and experimental observations to estimate Yp they found that the yield gap for maize ranged from 44 to 84%, for wheat 11 to 60%, and for rice 16 to 70%. Their observations suggest that much can be achieved to meet production needs by closing the yield gap for these crops. For rain-fed crops, the average yield gap was close to 50% of the Y_p. They were not as optimistic for irrigated crops as observed yields, where Y_F was nearly 80% of Y_p. And they noted that increasing Y_F of irrigated crops is necessary for further yield gains (Lobell et al. 2009).

The assumption that Y_F will continue to increase at the same rate as the past 50 years is challenged by other complicating factors. Brisson et al. (2010) analyzed trends of European wheat yields and showed that the lack of genetic improvements was not the

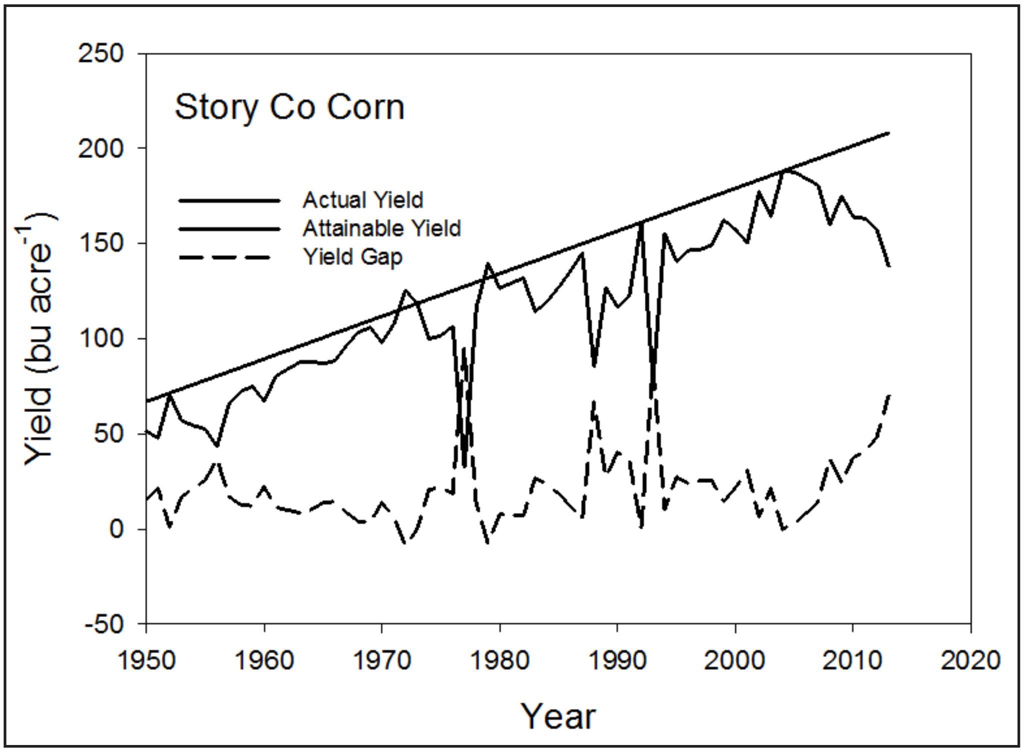

***Figure 1.** Attainaable yield, actual maize yields, and yield gaps from 1950 through 2012. (data from USDA-NASS).*

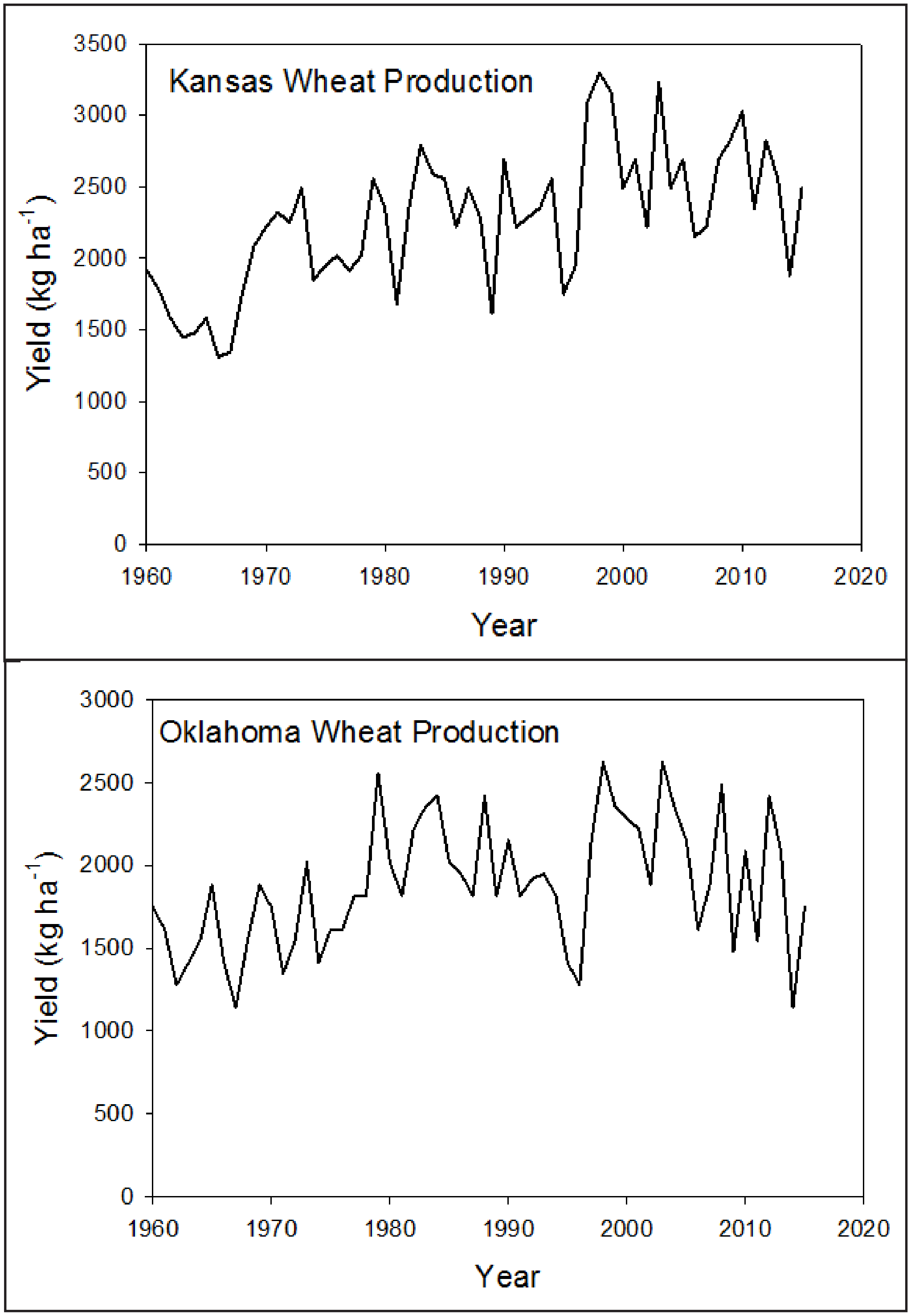

Figure 2. *Trends in Kansas and Oklahoma state level winter yields since 1960. (Data from USDA-NASS)*

cause of yield stagnation. Increased variability of climate during the growing season, creating heat stress during grain-filling and water stress during stem elongation and tillering, were noted as significant factors. They attributed some of the yield stagnation to policy and economic changes, which reduced the use of legumes in crop rotations and N fertilizer inputs. The impacts of climate change are already evident in the winter wheat yields for Kansas and Oklahoma where there has been a negative trend in statewide grain yields since 2000 (Figure 2). Analysis of farming in the tropics by Affholder et al. (2013) found that yield gaps between potential and non-limited water yields were not due to global radiation, temperature, rainfall, or soil water holding capacity, but rather due to poor soil fertility and weed infestation. This observation agrees with the Sinclair and Ruffy (2012) assessment of yield Limitations. Wang et al. (2014) noted that Y_F had already reached Y_p in the North China Plain and found that Y_p was declining due to decreasing solar radiation and increasing air temperature. They used the APSIM-maize model with local hybrid parameters under irrigation and non-limiting N supply to estimate Y_p. If we take the conclusions of Alexandratos and Bruinsma (2012) in which they estimated the yield (Mgha^{-1}) increase from 2005 needed to meet the 2050 demand, maize would have to increase by 28% to 6.06 Mgha^{-1}, wheat to 3.82 Mgha^{-1} (+38%), rice to 5.32 Mgha^{-1} (+31%) and soybeans to 3.15 Mgha^{-1} (+36%) to meet projected production requirements.

Before we can project the future needs, it is instructive to examine how much yields have increased and are projected to increase. Jaggard et al. (2010) stated that the increased atmospheric CO_2 concentrations will increase C_3 crop yields by 13%, and C_4 crops by a negligible amount with a reduction in water consumption offset by increased atmospheric demand due to increased temperature. They stated that plant breeders are likely to significantly increase crop yields because of increased atmospheric CO_2 concentrations, and we can assume that these yields will be realized if pests and disease remain controllable. For their analysis they assumed that only soil-borne pathogens would respond to a warmer climate and would be manageable, and that there would be no policy change that would affect the management of crops with chemicals. Given these assumptions, they felt that crop yield could potentially be increased 50% by 2050 and therefore adequate production goals would be feasible. Using simulation models for China, Erda et al. (2005) summarized that maize, wheat, and rice yields would decrease 37% by 2100 due to increased climate stress with no CO_2 increase, and only increase by 5 to 15% with a CO_2 increase. These projections for yield increase would be far from adequate to meet population demands. Zheng et al. (2012) found that the increasing mean temperature and occurrence of extreme temperatures will reduce wheat yields and subsequently conducted an experiment to evaluate patterns of frost and heat events across Australia. They simulated the flowering dates for three different maturity classes at different CO_2 and temperature scenarios for 2030 and 2050. These changes in climate (i.e., warmer winters) decreased the wheat growing season by up to 6 weeks. This shortened growth cycle decreased resource capture (growth-defining due to solar radiation capture and growth-limiting due to water and nutrient utilization), leading to a potential yield loss. Rezaei et al. (2015) proposed that warmer temperatures would advance phenological development, and increasing the rate would lead to a reduction of exposure to stress occurring later during the growing season. Lehmann et al. (2013) simulated different climate change scenarios with a range of management practices for winter wheat and maize in Switzerland, using a bio-economic model and the CropSys crop growth model. Their results showed climate change scenarios with reduced summer precipitation would increase the amount of irrigation required for economically viable yields. For winter wheat and maize, climate change reduced the optimal N fertilizer rate and there was greater uncertainty of profitability. For all climate scenarios, there was a decrease in grain yield for both crops between 20 and 40%, even under optimal management practices. During a recent study in Central Rift Valley of Ethiopia, Kassie et al. (2014) observed yield gaps of over 70% and that closure of the yield gaps would only be possible through improved crop and management practices. Water was the primary limitation in this environment to maize yield, and thus improved water management would be required to increase yields. There are no single or simple solutions to improving yields and no solid trajectories of crop yield by 2050, which leads to the conclusion that achieving yields necessary to feed future global populations will require innovative research and widespread deployment of agronomic practices.

One approach for evaluating yield gaps is to evaluate the fraction of attainable yield. When this is expressed as a frequency distribution, a typical response is that 20% of the yield gap occurs over 85% of the time (Figure 3), as illustrated for Story County in Iowa. This response is typical of maize and soybean production across the Midwest and wheat production in the Great Plains. If we are going to use yield gaps as a method of analyzing where improvements can be made, then the approach will offer insights into factors limiting yield and the magnitude and frequency of the yield gap we are trying to close. If we assume the theoretical upper limit of yield is a function of the amount of light available and effectively utilized by the crop, then the primary production (Pn) can be described as the amount of light absorbed by the crop canopy and the conversion efficiency of light to photosynthesis (light-use efficiency) expressed as:

$$P_n = S_t e_i e_c / k$$

where S_t is the annual integral of incident solar radiation (MJm^{-2}), e_1 is the efficiency that solar radiation is intercepted by the crop, ec is the efficiency at which intercepted solar radiation is converted to biomass, and k is the energy content of the biomass (MJg_{-1}). The conversion of Pn into grain yield is expressed as:

$$Y_C = nP_n$$

where Y_C represents the grain yield of a crop ($kgha^{-1}$) and is the harvest index (the efficiency at which biomass is partitioned into the harvested product, e.g. grain). Maximum values for e_1 are near 0.9, n values are near 0.6 and maximum value of ec for C_3 crops are 0.024 and for C_4 crops are 0.032 (Long et al., 2006). For C_3 crops, the highest short-term e_c values are near 0.035 and for C4 crops are near 0.043 (Beadle and Long, 1985; Piedade et al.; 1991; Beadle and Long, 1995). Relating light capture by the crop canopy with productivity can be traced back to Wilson (1967) with refinement by Monteith (1977). There has be extensive use of radiation use efficiency (ec; RUE) in the agronomic literature to describe the relationship between light capture by the crop canopy and productivity (Kiniry et al. 1989, Fletcher et al., 2013); Hatfield, 2014). Observations of maximum RUE are assumed to represent conditions when plant growth is not limited by water or nutrient stress. The concept of RUE is similar to water use efficiency (WUE) such that the maximum WUE describes the relationship between water use and plant productivity under non-limiting conditions. Linking WUE with RUE provides an opportunity for improved quantification of plant response to the environment.

The value of closing the yield gap for increased food production is evident. The challenge remains on how to close the yield gap because of interacting complex factors due to water availability, nutrient supply, and the genetic diversity (Hogy et al., 2013; El-Sharkawy, 2014). A synthesis document on the effects of climate change on agriculture recommends a balance of research on genetics and management practices to enable adaptation to the effects of climate change (Walthall et al. 2012). Observations of traditional crop varieties, outperforming new drought-resistant varieties because of differing soil management practices during recent severe drought in Iowa provide anecdotal evidence supporting this approach. For this review we present an analysis of the potential role of understanding the interaction of genetics x environment x management (G x E x M) in meeting the production needs for 2050 and beyond.

G x E x M

If the path to closing the yield gap is increasing Y_F via increasing the capacity of each unit of land to support higher yields (i.e., land productivity), then factors currently limiting yield and factors projected to limit yields warrant examination. Equation [1] demonstrates the value of greater radiation capture by the crop, increasing efficiency by which intercepted solar radiation is converted to biomass, and changing the energy content of the plant mass (Long). Long et al. (2006) expanded on the e_c term and suggested altering canopy architecture to improve the distribution of solar radiation interception to prevent leaves from being light-saturated, increasing photo-protection to increase the efficiency of photosynthesis of leaves, increasing the catalytic rates of Rubisco (ribulose bisphosphate carboxylase oxygenase), and increasing the capacity for Rubisco regeneration. They also stated that these changes do not appear feasible during the next 10 to 20 years, thus suggesting that efforts to achieve crop production increases must focus on other means. If we accept the conclusion of Duvick (2005) for maize, that yield increases of the past 50 years were due equally to breeding and improved management, then we have multiple opportunities to close the yield gap. To this end, we introduce the concept of the interaction of G x E x M as a foundation for moving forward to feed the future world. The rationale for a departure from the classic G x E interaction is to highlight the effects of climate variability on the environmental factor, and the opportunities for management to enhance performance of genetic resources under varying environmental conditions.

An example of this approach was undertaken by Martin et al. (2014) in which they evaluated these interactions for winter wheat from Denmark. They found that current annual grain yield improvements of 0.3 to 1.2 Mg ha^{-1} would be insufficient to keep pace with demand and improved management could potentially add to 1.8 Mg ha^{-1} to yield, and genetic improvements with a greater sensitivity to climate could add another 3.8 Mgha^{-1} of yield. This type of analysis combining climate scenarios with genetic and phenotypic improvements and management scenarios provides more realistic yield projections and identification of viable solutions. Simulation models can be effective in describing the genetic x environment interactions as demonstrated by Yin and Struik (2010) and Gu et al. (2014). This approach is the motivation for the international Agricultural Model Inter-comparison and Improvement Project (AgMIP), as described by Rosenzweig et al. (2013). AgMIP seeks to use the most advanced and robust crop simulation models to project future crop production and enhance development of adaptation strategies to cope with climate change. AgMIP is verifying that the current generation of crop simulation models inadequately account for soil-crop-atmosphere interaction responses to the wide variability of temperature and precipitation accompanying changing climate, as noted by Hatfield et al. (2011).

Solutions to yield reductions from non-optimal soil water, soil, and air temperatures, and N are most often addressed independently during research. The following sections examine these three limitations of crop production from the perspective of G x E x M and offer evidence that advocates for an integrated approach.

Soil water

The greatest challenge is non-optimal water supply and thus there is need for management strategies that conserve and provide adequate soil water to meet crop water demands for rain-fed agriculture. Hatfield et al. (2001) showed that improved soil management can increase WUE, and supplying more available water to the plant benefits production and ensures the Y_F is closer to Y_P for a given site.

The growing uncertainty of precipitation and rising air temperatures causing an increase in atmospheric demand are among the challenges posed by changing climate leading to crop drought stress. Genotypic variation of crop response to water stress offers insight into these interactions. For rice, Pantuwan et al. (2002) utilized a drought response index (DRI) calculated as the ratio of the $(Y_{act} – Y_{est})$/SE of Y_{est}, where Yact is the actual grain each for each individual genotype, Y_{est} is the estimated yield for each genotype, and SE of Y_{est} is the standard error of all entries. The Y_{est} was an estimate of the potential grain yield under non-limited conditions. They found drought stress before flowering delayed flowering and the delay was negatively associated with grain yield. Genotypes with delayed flowering continued to use soil water, had higher water deficits, and had larger yield reductions due to drought. The authors proposed that screening genotypes for drought resistance could be done with DRI or flowering response. Gu et al. (2014) combined simulation models with quantitative genetics to develop a genotype to phenotype approach for screen rice under drought stress, and this approach has the potential to provide new insights into the physiological factors limiting yield under stress. Kumar et al. (2012) proposed using a GGE biplot (genetics x genetics--environment interactions) to screen rice germplasm across multiple environments and identified stable genotypes across a wide range of environments. The GGE biplots quantify the genotype and genotype x environment interactions as two sources of genotypic evaluation (Yan et al., 2000) as potential tools for cultivar screening. Zhang et al. (2013) found that environments could be separated by year (Y) and location (L) and using a factor analytic model partitioned into G x Y, G x L, and G x Y x L interactions and applied this approach to canola (Brassica napus subsp. napus). They found phenology was an important factor for adaptation to specific environments. Abdolshahi et al. (2015) utilized selection criteria on 40 bread wheat varieties and observed heritability for secondary traits was significantly higher than for grain yield. Ten secondary traits include water use, relative ionic leakage, leaf length, root length, grain number, awn length, above-ground biomass, yield potential, days to flowering, and grain filling period, and could significantly discriminate high and low yield genotypes under drought stress conditions. Recent analysis by Razaei et al. (2015) observed shifts in winter phenology were able to offset the effects of increased temperatures, and earlier flowering reduces the likelihood of exposure to high temperatures at flowering. There is a need to implement the available tools and quantify genotypic responses to different environmental conditions to screen germplasm for G x E x M interactions. There are other indices besides phenology and yield that may be suitable for quantifying germplasm responses to water deficits. Carcova et al. (1998) used the crop water stress index (CWSI) with three maize hybrids and found that the CWSI changes were consistent across hybrids with no variation among hybrids. Earlier, Hatfield et al. (1987) found that cotton germplasm could be screened using canopy temperatures as a method of quantifying water conservation among lines. Bandyopadhyay et al. (2014) found water and N stresses in wheat could be quantified using remotely sensed spectral indices and proposed a normalized water stress index. The advantage of this method was that grain yield could be accurately predicted at the milk stage of wheat, providing a forecast of the potential drought effects (Bandyopadhyay et al., 2014). Further refinement of reflectance and thermal indices may advance our ability to screen germplasm for their response to water stresses.

Drought stress also affects grain quality and is of concern to achieving food security. Gous et al. (2013) found that in barley (Hordeum vulgare L.) a genotype with "stay green" characteristics had greater potential for maintaining starch biosynthesis and grain quality under severe water stress compared with the genotype without these characteristics. Saint Pierre et al. (2008) observed protein composition in winter wheat was affected by water and N management with no variation among wheat cultivars in their flour protein and protein composition to water or N stress. However, de Mezer et al. (2014) observed differences among barley cultivars in their physiological and molecular responses to water deficits and recovery. A comparison of maize hybrids by Aydinsakir et al. (2013) found that different irrigation levels significantly affected all yield components (e.g. anthesis-silking interval, plant height, ear diameter, ear length, kernel number, and 1,000 grain weight) except for ear number. For both genotypes, water deficit stress significantly increased glucose, fructose, and sucrose contents while decreasing protein content. The effect of water deficits on grain quality and the physiological reactions will provide insights into potential methods to alleviate the effects of water stress and should be a focus of future studies to be able to provide high quality grain for future generations.

Excess water also limits crop production, and often occurs in the mid-western United States, Southeast Asia and Europe when more intense rainfalls lead to excess soil moisture early during the growing season. Zaidi et al. (2004) screened maize genotypes and found the V2 (two leaves visible) and V7 (seven leaves visible) growth stages were the most susceptible to excess soil water. Excess moisture affected growth and biochemical processes, disrupted anthesis and silking, and resulted in poor kernel development and yield. The attributes of tolerant genotypes included good carbohydrate accumulation in stem tissues, moderate stomatal conductance, high root porosity, early brace root development, and less than 5d anthesis to silking interval (Zaidi et al, 2004). Earlier, Zaidi et al. (2003) concluded that tolerance to excess moisture conditions was primarily due to stress avoidance mechanisms due to anaerobic metabolic adjustments and morphological changes, e.g., brace root development.

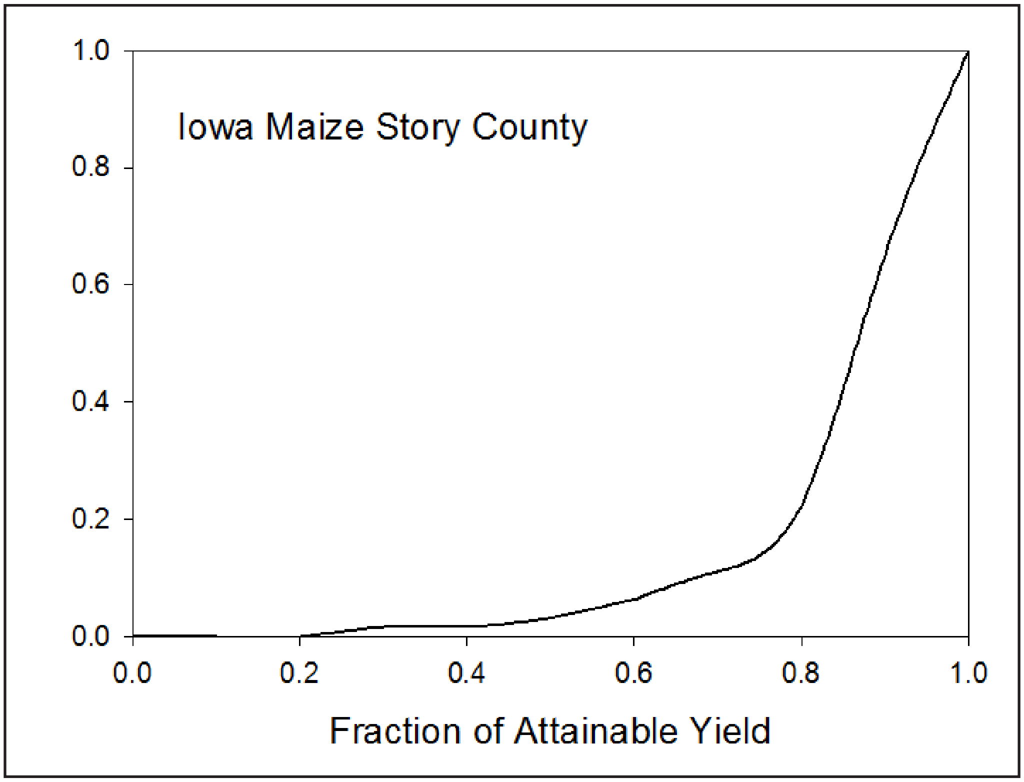

***Figure 3**. Frequency distribution of yield gaps for Story County, Iowa maize production since 1950.*

If we accept the premise of Sakschewski et al. (2014) that land productivity is a limiting factor, then yield improvements from occurrence of water shortage and excess water could be partially achieved by modifying soil water characteristics. Cairns et al. (2011) suggested that plant performance under drought is not simply defined as the ability to extract water, but attention must be given to soil physical environments to quantify the plant's ability to distribute roots throughout the soil profile. Passioura (2006) suggested increased crop productivity in water limited conditions could be achieved through crop breeding by capturing more water for transpiration, increasing WUE by exchanging water for CO2 more effectively, and converting more biomass into harvestable products. Management practices that reduce soil water evaporation losses and better couple crop development with water supply would prove to be beneficial to ensure adequate water supply throughout the growing season (Passioura, 2006). The findings from Egli and Hatfield (2014a, 2014b), demonstrating average county maize and soybean yields were directly related to a soil productivity index suggest agronomists pay attention to building soil quality based on water availability, which would include both soil water holding capacity and rooting depth, and improved soil structure to relieve anoxic condition by facilitating oxygen exchange under excess soil water and improved infiltration to increase effective precipitation, defined as the amount of rainfall entering the soil and available for crop water use. Improvements in WUE through soil management have been summarized by Hatfield et al. (2001) and suggest that soil management plays a key role in being able to supply adequate water to achieve maximum productivity.

Temperature

High temperature exposure effects on crop productivity and yield were summarized for agronomic crops by Hatfield et al. (2011), and extensive literature documents specific effects on growth, pollination, and yield (Prasad et al., 2002). Rattalino Edreira et al. (2011) evaluated heat stress effects on temperate and tropical maize hybrids and found three sources of reduced productivity--decreased floret differentiation, pollination failure, and kernel abortion. They used normal temperatures and a daytime temperature between 33 and 40°C at ear level before and post-silking, and observed the effects of heating were greater for the anthesis stage with kernel abortion as the parameter most affected. Tropical hybrids were more resistant than temperate hybrids with respect to heat response. Li et al. (2013) conducted a similar study on durum wheat (*Triticum turgidum* L. ssp. durum) on nine different genotypes under drought and heat stress. They manipulated the planting date in northwestern Mexico to achieve the heat stress and managed the irrigation supply to induce drought stress. Heat and drought stress reduced grain yields across all genotypes and the G x E analysis showed E explained 90% of the variation in yield, 73% in the thousand kernel weight, and 60% in grain protein (Li et al. 2013). The G component was dominant for flour yellowness at 87% and they concluded that screening of durum wheat genotypes should account for both yield and quality parameters under abiotic stresses. In a screening study on grain sorghum [*Sorghum biocolor* (L.) Moench.], Djanaguiraman et al. (2014) found that exposure to 38/28°C for 10 d, compared with the normal temperature of 30/20°C at the boot stage, decreased quantum yield of PSII, electron transport rate and transcript levels of rubisco activase, glutathione peroxidase enzymes induced cell membrane damage, and decreased pollen viability, pollen germination and seed set. There was variation among genotypes in pollen response to high temperatures, with the tolerant genotypes exhibiting less oxidative damage in leaves and pollen grains than sensitive genotypes. These observations across multiple species suggest that exposure to high temperatures of short duration would affect the photosynthetic efficiency; however, the temperature effects may still not be as impactful as the drought effects on productivity.

High temperature effects on plants are particularly evident during the pollination stage of development. This sensitivity is increased when plants are water stressed. There have been some general observations of the impact of heat-induced spikelet sterility on another dehiscence, reduced pollen shedding, poor germination of pollen grains and decreased elongation of pollen tubes (Prasad et al., 2001, 2003, 2006a, 2006b, 2008; Das et al, 2014. Observations in crops (e.g., rice) have found that air temperatures greater than 35°C for more than 1 hour caused sterility (Jagadish et al. 2010) and exposure to temperatures greater than 35°C for more than 5 days caused spikelets to be completely sterile (Rang et al. 2011). Temperature effects on pollination have been observed, but the question often arises about the impact of day vs. night temperatures. Shah et al. (2011) found high night temperatures to be more damaging than high day temperatures. From an earlier study, Ziska and Bunce (1998) observed the ratio of respiration to photosynthesis increased with increasing temperatures. For maize, temperatures above 35°C are lethal to pollen viability (Dupuis and Dumas, 1990) and pollen viability (before silk reception) is a function of pollen moisture content, which is strongly dependent on vapor pressure deficit (Fonseca and Westgate 2005). Quantifying the impact of episodes of temperature extremes on pollen viability and the disruption of reproductive processes may become more important with the projection that extreme temperature events will increase under climate change (Tebaldi et al. 2006). Butler and Huybers (2013) suggested that maize in the United States may be more adapted to hot temperatures and yield declines from a 2°C warming would only be 6%; however, the variation in precipitation and extreme events were not considered during this analysis. Hatfield (2016) observed that exposure of maize hybrids to temperatures 4°C above normal temperatures reduced grain yield by 75% in the absence of water stress. There was no difference in vegetative growth when exposed to high temperatures except the phonological advancement was faster in the warmer temperatures. The effect on grain yield was due to a combination of disruption of pollination and exposure to high nighttime temperatures during grain-filling. Any of the disruptions due to temperature or water stress will limit the photosynthetic efficiency, ep, of plants throughout the growth cycle. Rezaei et al. (2015) demonstrated that shifting phenology of wheat offers a potential solution to exposure to high temperature and would be a viable avoidance mechanism. An opportunity exists to evaluate genetic response to temperature stress and how changing phenology can potentially affect photosynthetic efficiency.

An overlooked aspect of changing climate is the effect on soil temperature and exposure of roots to a warmer temperature regime. There have been no studies to document this impact; however, a study was conducted on the effect of warm water temperatures on rice by (Horai et al., 2014). During this study they increased water temperature by an average of 1.5°C for two different rice cultivars, an adapted cultivar, and a late-maturing cultivar, and found the warmer temperatures increased the flowering date by 2 to 5 days, with both cultivars showing the same response. The adapted cultivar showed a significant increase in dry matter production before heading, compared with the adapted cultivar; however, both showed a positive response of dry matter to warming. Leaf senescence increased in response to the warmer temperature for both cultivars and RUE decreased. Thus, they concluded that analysis of leaf senescence rates would be necessary to evaluate crop response to a warming climate (Horai et al., 2014; Hatfield, 2016).

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Water and temperature stress will not occur in isolation from each other and will tend to exacerbate the effects of either stress. These effects will impact both the vegetative and reproductive growth of plants. One example of the complexity of this response was reported by Sadras et al. (2013) in which they compared 29 pea (*Pisum sativum* L.) accessions using a combination of field experiments and simulated results. The differences among accessions are larger for the favorable environments compared with the stressed environments and they found a non-linearity between seed number per m^2 and crop growth rate, suggesting a decoupling between vegetative growth and reproduction that may constrain yield potential. These results, using multiple numbers of accessions, will be necessary to determine the factors that limit yield potential.

Nitrogen

Nitrogen is key determinant of plant productivity and fulfilling the future food needs of the world will require an adequate supply of N. The projected increase in N supply for the increased production and the amount of N to guarantee food security has been estimated to be 250 Mt $year^{-1}$ (Tilman et al., 2011). If we examine Eq [1] and the two efficiency terms e_i and e_c, then the essential role of N in the production of plant proteins and the expansion and functioning of photosynthetic area is necessary to allow plants to achieve their potential in growth and yield (Grindlay, 1997; Sinclair and Horie, 1989). The foundation for gauging the N response can be seen through RUE, which is a representation of the photosynthetic capacity of the leaves and canopies that are directly related to concentration of N per unit area of leaf (Monteith, 1977). Hatfield and Parkin (2015) observed that maintenance of green leaf area and delayed senescence was positively related to grain yield in maize. As these N concentrations fall below a critical threshold, RUE decreases (Massignam et al. 2009) and as N supply decreases, leaf area expansion decreases and senescence increases (Massignam et al. 2011). Three responses to a shortage of N for the vegetative period of growth are possible as defined by Lemaire et al. (2008): (i) reduce leaf area (light capture) and maintain leaf N content (photosynthetic capacity), creating a reduction in the radiation interception while maintaining RUE; (ii) maintain leaf area expansion and reduce leaf N content, which maintains the radiation interception but reduces RUE, or (iii) a combination of both responses.

Management of N will become a major limitation for plant productivity because of the need to increase N use efficiency (NUE). Two avenues need to be more fully explored by agronomists to achieve greater NUE: (i) utilizing enhanced efficiency fertilizers to increase the availability of N later in the growing season (Hatfield and Parkin 2014); and (ii) understanding the potential of increased soil biological fertility in which the activity of the microbial system recycles nutrients in the soil profile and makes them available to the plant (Abbott and Murphy, 2007; Lazcano et al. 2013, Rogers and Burns, 1994). In both of these cases, there are indications that these N management practices increase the duration of green leaf area and the photosynthetic efficiency of the canopies. This response is similar to the observations by Gous et al. (2013) on the maintenance of green leaf area in sorghum offering an advantage to grain yield. Hatfield and Parkin (2014) demonstrated that both a chlorophyll summation index and a senescence index based on remote sensing were related to grain yield because of the greater duration of green leaf area in the grain-filling period induced by the enhanced efficiency fertilizer. The yield parameter affected by this change was the weight per 100 kernels, suggesting that increased photosynthetic area and duration would increase the capacity of the maize plant to fill the grain. Improved management of N along with all nutrients will be necessary to capture the yield potential of all crops and increase vegetative and grain quality. Teixeira et al. (2014) observed an interaction between water and N stresses on maize, which affected the ability of the plant to achieve optimum use of the natural resources. This evaluation of NUE and WUE under water or N stresses provides a framework for evaluating genotypic responses. Nitrogen requirements of worldwide crops to achieve nutritional security are estimated to be in excess of 150 million MT by 2050.

Other challenges

If we utilize the G x E x M approach as our foundation for meeting future food needs, we have the opportunity to examine the potential of each component. One of the largest components will be the environment, which includes the soil and atmosphere. However, the weather variations within and among growing seasons and among locations is expected to increase, leading to more variation of crop growing conditions. Ray et al. (2015) concluded that climate variation led to global yield variation in maize, rice, wheat, and soybeans. The magnitude of this variation was nearly 40%. Climate variation in temperature and precipitation were considered the primary climate factors affecting crop yield. Since drought is a major limitation to crop yield, supplying irrigation water is a viable option for some locations; however, attention to improving water availability for the crop by increasing the potential storage of soil water in the soil profile and decreasing the evaporation component of evapotranspiration also offer promise (Hatfield et al. 2001).

Degradation. One of the first challenges in meeting global food demands will be maintenance of a high-quality soil resource and its ability to provide adequate water and nutrients, and sufficient rooting depth for the plant to obtain these resources (Sakschewski et al. 2014). Lal (1993) proposed that soil degradation (chemical, physical, and biological) is extensive throughout the world and especially so in the tropics and subtropics. Because water availability is critical to the crop, the changes in soil structure and saturated hydraulic conductivity related to cropping systems, i.e., tillage and residue removal, led to a degradation of soil structure in the profile causing maize yield reductions as large as 50% (Wang et al., 1985). This decrease in yields could be partially explained by shallow root growth and limitations of water availability to the growing plant. Impacts of poor soil structure on plant growth and yield can be significant and thus continued degradation of the soil resource will have a major impact on the ability of the plant to produce grain, fiber, or forage. Degradation of the soil resource will also exaggerate the effects of a variable climate and limit the ability of the genetic resource to achieve its potential.

Water use by crops is dependent on the available water resource in the soil and under rain-fed conditions. Wessels et al. (2007) found that degraded soils have reduced precipitation use efficiency for rangeland soils. De Vita et al. (2007) observed increased durum wheat yields under no-till during years with limited rainfall during conventional vs. no-tillage systems comparisons for southern Italy. No-till systems had an advantage over conventional tillage because of reduced soil water evaporation coupled with the enhanced soil water availability induced by better water holding capacity (Hulugalle and Entwistle, 1997). Greater attention is warranted to the relationship between soil organic matter and water holding capacity as described by Hudson (1994), along with soil management practices required to increase soil organic matter and root exploration into the soil profile. Unger et al. (1991) found conservation practices that maintained crop residue on the soil surface had a positive impact on water conservation and translated into increased water availability for the crop in semi-arid regions, leading to greater yield potential. Manipulation of the soil and adoption of conservation practices can have a positive impact on WUE; therefore, adopting these practices can provide one avenue for crop yield enhancement to meet future food needs (Hatfield et al., 2001). The amount of yield increase will vary depending on the atmospheric conditions during the growing season; however, a more stable soil water supply fosters less variation of crop yield.

Genetic improvement

Genetic improvement of crops has proven to advance yields over the past 50 years and as Duvick (2005) pointed out, yield increases in maize can be attributed equally between genetic improvement and management improvements. Yield trends in crops have shown a positive advance and yet Grassini et al. (2013) found these increases vary among rice, wheat, and maize. They conducted a thorough analysis of rice yield in China, India, Indonesia, Republic of Korea, Vietnam, California and the south central United States; for wheat in Australia, China, France, India, the Netherlands, and the United Kingdom and for maize in Brazil, Central Africa, China, India, Italy, the eastern U.S. Corn Belt, the western rain-fed U.S. Corn belt, and the western U.S. irrigated Corn Belt, using several different statistical models fit the annual grain yields. They found that there was evidence of a yield plateau in different countries (e.g. rice in eastern Asia and wheat in northwest Europe), whereas in others there was a linear trend in grain yields. They suggested that attention be directed to yield trajectories for more effective strategic planning about future production estimates. The assumption that yield improvement trends will be maintained at the current rates may not be true. George (2014) points out that in spite of advances in germplasm and agronomic advances there, more attention is warranted to enhancing agronomic practices to increase actual yield if yields in developing countries are expected to increase. Mueller et al. (2012) suggested that closing the yield gap is possible through a combination of intensive nutrient and water management; however, these authors acknowledged the presence of a changing climate and did not consider the potential disruptions to crop production due to changing climate as a barrier to achieving potential yields.

Neumann et al. (2010) conducted a global scale analysis using frontier yields, yield gaps and efficiencies for maize, wheat, and rice production. They defined the frontier yields as the highest observed yield for a combination of conditions and used the definitions of van Ittersum et al. (2003) to quantify the variables for their frontier analysis. van Ittersum characterized these variables as growth-defining (potential crop yield under a given physical environment where conditions cannot be managed), growth-limiting (water and nutrient limitations preventing the crop from achieving potential yield), and growth- reducing (pests, diseases or pollutants and require some agronomic management to reduce these yield impacts). Actual crop yield represents the interaction among these three factors (van Ittersum et al. 2003). Neumann et al. (2010) defined the process of closing the yield gap as intensification and would require a country-specific process to close the yield gap because the yield constraints are not uniform across countries: e.g., in developing countries the lack of capital investment, access to technology, and infrastructure may be the liming factors, whereas in developed countries, improved genetics and management may be viable options.

Feeding 9 billion people presents a major challenge because of a combination of factors. Increased production is not possible without new lands and increased yield and cropping intensity (Gregory and George, 2011). Smith et al. (2010) estimated that per capita land area will decrease and actually declined from 0.415 ha in 1961 to 0.214 ha during 2007, and they estimated average cereal yield will need to increase by 25% from the 3.23 Mg ha^{-1} of 2005-2007 to 4.34 Mgha^{-1} during 2030. To meet future production requirements, Gregory and George (2011) summarized that only 20% would come from new land and 80% from intensification (increased yields and greater cropping intensity). These conclusions would suggest that increased emphasis on improved management for nutrients and pests would increase the capacity for food production. West et al. (2010) argue that clearing land for agricultural production will lead to increased carbon losses, and for the tropics, the efforts must be directed toward increasing crop yields rather than clearing more land. Increasing productivity will require increased management and improved agronomic techniques. Unfortunately, since the land resource will become a premium, this option will remain as the most viable solution.

Challenges

There are numerous constraints to crop yield, and the constraints must be overcome to produce the quantity of crops necessary for the projected population of 2050. However, there are additional aspects of the production puzzle that need further discussion. One is the quality of grain or produce to achieve nutritional security and supply the calories to sustain the population. To achieve this goal will require an emphasis on nutrient management, forms, and timing of nutrients to ensure adequate nutrient availability for optimum crop production. To achieve this goal will require we fully embrace the linkage of ecology with agriculture to ensure we achieve both production and environmental goals at the same time. An emerging challenge for agronomists is the need to evaluate the quality of the grain with as much vigor as the evaluation of grain yield. There have been limited studies on grain quality and its relationship to G x E x M. Another component of feeding the world is food waste, which in turn translates to wasted resources as discussed by Kummu et al. (2012). They found that one quarter of the food supply produced is lost within the food supply chain and that this lost production accounts for 24% of the freshwater resources, 23% of the total cropland area, and 23% of the global fertilizer use. They put forth the argument that reducing food losses and waste would increase food security and increase the efficiency of the resource use during food production (Kummu et al. 2012). Another challenge will be to critically examine the water footprint of agriculture as suggested by Sun et al. (2013). They suggest that the water footprint of a crop could be controlled through enhanced management of all crop production inputs, ultimately leading to increased WUE. These examples present a sample of the broad challenges to agriculture needing attention. The impact of insects, diseases, and weeds on production are part of the E and M components of this puzzle, and addressing these interactions as part of G x E X M is warranted.

"Aspects of agriculture may appear to offer the conclusion that we face the impossible."

Meeting future food needs will carry some specific challenges as yield in many areas of crops are showing a plateau (Grassini et al., 2013), yield gaps are often extremely large (Lobell et al., 2009, Rijk et al. 2013, van Ittersum et al., 2013, van Wart et al., 2013; Fischer et al., 2014) and the projected yield increase varies widely, from 30 to 60% (Ray et al., 2013. Solutions to these challenges include:

- Focus on soil improvement for both water supply characteristics and nutrient cycling to remove growth limiting factors (van Ittersum et al. 2003) as growth-defining factors (temperature and precipitation) will become more variable and more extreme (Tebaldi et al., 2006), and availability of water and nutrients will become more critical to achieve high yields (Liu et al., 2013). We need to reverse the trend of soil degradation and focus our attention on soil improvement to close the yield gap because the land base is decreasing and attention sh oul be focuse on yield improvement (Gregory et al, 2002; Gregory and George, 2011).
- Increase the emphasis on improved nutrient management strategies and practices that increase nutrient use efficiency and reduce potential environmental impact (Spiertz, 2009). He suggested that a multi-scale approach form the plant level, crop level, farm level, watershed and landscape level, and eco-region level be undertake to enhance nutrient use efficiency. The development of the 4-R concept is a first step; however, the value of this concept in increasing production needs to be demonstrated to producers.
- Incorporate multi-disciplinary science into efforts to improve yields by building transdisciplinary teams of agronomists, geneticists, plant pathologists, entomologists, weed scientists and human nutritionists to evaluate the response of different genotypes to stress and management practices for yield and grain quality, to ensure all aspects of G x E x M are addressed in a comprehensive manner.
- Develop and implement more robust tools for assessing leaf photosynthetic efficiency and canopy interception of light to be able to screen increasing numbers of germ-plasm across multiple environments and management systems. Capture of solar radiation is essential to improving yields; however, food security can only be achieved when solar radiation is converted into a harvestable, high-value product.
- Focus on why crops are not achieving their potential via a comprehensive analysis, realizing that dominant factors may be different for each growing region or locality. The traditional view of universal yield limitations must yield to a more site-specific focus (Fischer et al., 2014).
- Adopt new technologies, (e.g., precision agriculture, enhanced efficiency fertilizers, alternative crops), to infuse innovation into cropping systems.
- Utilize crop simulation models in a robust fashion to enable a more comprehensive analysis of potential alternative scenarios under future climates and management options (Yin and Struik, 2010, Rosenzweig et al.,2013, Gu et al, 2014), and build a community of modelers (crop and climate) and experimentalists to improve the models and provide feedback on genetic and management responses.
- Incorporate the producer into applied research to determine what practices are feasible from their perspective and solicit their feedback on technologies and approaches.
- Characterize plant responses to different stresses and also develop rapid screening methods to allow more comprehensive comparisons across a larger number of genotypes (Abdolshahi et al., 2015; de Mezer et al., 2014, Djanaguiraman et al., 2014).

It may seem like a daunting task to provide for future generations. The current literature on many different aspects of agriculture may appear to offer the conclusion that we face the impossible. We would offer that approaching the problem from a more integrated G x E x M approach can potentially achieve the goal of feeding 9 billion by 2050.

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