

Breeding and Cereal Yield Progress

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ABSTRACT

This paper reviews recent progress in wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.) yields resulting from substantial breeding efforts in mostly favorable environments and examines its physiological basis. Breeding and improved agronomy lift potential yield (PY), namely yield with the best variety and management in the absence of manageable abiotic and biotic stresses, and PY increase is a key component of progress in farm yield (FY), the other component being closure of the PY to FY gap. Changes in PY and FY are reviewed for several key production regions, namely the United Kingdom and the Yaqui Valley of Mexico for wheat, Japan and Central Luzon in the Philippines for rice, and Iowa and briefly sub-Saharan Africa for maize. The PY growth rates have fallen and are currently generally no more than 1% per annum and usually much less. The trajectory of FY with time often closely parallels PY, but, especially in developing countries, there remain large yield gaps. In at least one instance (maize in Iowa) the gap between PY and FY appears to be closing rapidly. Current genetic progress is linked to increased biomass accumulation, and this will remain the way forward in the future given the limits to increased harvest index (HI). There is evidence that recent progress is related to increased photosynthesis (e.g., greater radiation use efficiency (RUE) at the canopy level and/or maximum photosynthetic rate P_{\max} at saturating irradiance at the leaf level) before and around anthesis. There is no theoretical reason why this trend cannot continue, especially given the vast genetic resources already found within each crop species. However, it will not be easily or cheaply accomplished, so prospects for higher rates of potential yield growth appear to be limited, notwithstanding new molecular tools and claims to the contrary. Closing the yield gap, therefore, becomes more important. Many factors are involved, but breeding can also help farmers achieve this through, for example, improved host plant resistance.

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Abbreviations: AY, attainable yield; CIMMYT, International Maize and Wheat Improvement Center; DM, dry matter; DS, dry season; FY, farm yield; GM, genetically modified; HGCA, Home Grown Cereals Authority; HI, harvest index; IRRI, International Rice Research Institute; LAI, leaf area index; NPT, new plant type; NPT2, new plant type, second generation; P_{\max} , light-saturated photosynthetic rate; PY, potential yield; PY_w , water-limited potential yield; RUE, radiation use efficiency; SLN, specific leaf nitrogen; TE, transpiration efficiency; T_{\min} ; minimum daily temperature; WS, wet season.

CEREALS, dominated by wheat, rice, and maize, provide approximately 50% of human food calories directly and considerably more indirectly via feed grains (Tweeten and Thompson, 2008). Over the last 20 yr, a period chosen to best estimate current rates of progress without influence of earlier periods, the linear rates of yield change for the world (Fig. 1) have been 25 kg ha⁻¹ yr⁻¹ (wheat), 38 kg ha⁻¹ yr⁻¹ (rice), and 80 kg ha⁻¹ yr⁻¹ (maize). With the exception of maize in some regions, there is no evidence for exponential growth in yield. In fact, relative rates of yield increase are declining and, expressed relative to predicted yield in 2007, are 0.9% yr⁻¹ for wheat, 0.9% yr⁻¹ for rice, and 1.6% yr⁻¹ for maize. Even if these relative rates could be maintained, various studies suggest they would not prevent real price rises for the three cereals, in the face of projected demand growth to 2050 (Tweeten and Thompson, 2008). Thus there is little doubt that the world needs to continue increasing cereal yields.

In this paper we focus on factors determining current rates of yield progress in several key situations (or case studies) and consider

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the physiological bases of this progress. We consider also the prospects for continued yield growth, in particular that resulting from plant breeding, which we believe is becoming a proportionally larger component of yield growth. Possible yield changes due to shifts in cropping regions or proportions irrigated, changes in cropping intensity, or climate change (apart from CO₂ increase itself) are not discussed, although these are also factors that need to be considered for a complete understanding of cereal yield changes. For example, wheat is likely to be gradually displaced from irrigated areas by higher value crops (fruits, vegetables, sugarcane, and forages). Finally, as we look at yield progress, it needs to be realized that CO₂ increase itself (current rate of change about 2 μmol mol⁻¹ yr⁻¹) will be currently adding about 0.3% annually to the yields of C₃ crops such as wheat and rice (Tubiello et al., 2007), assuming a relative responsiveness of yield to CO₂ change of 0.7, a number likely to decline with further CO₂ increase. The case studies presented here are, with the exception of maize in sub-Saharan Africa, favorable situations that have been the target of substantial agricultural research and development, in particular crop breeding, and should therefore illustrate what is achievable with such investments and what may lie ahead. The case studies are also chosen to represent major world agro-ecologies for the crops concerned.

YIELD DEFINITIONS

Along with farm yield (FY) (Fig. 1), attainable yield (AY) and potential yield (PY) are useful concepts (Loomis and Connor, 1992; van Ittersum and Rabbinge, 1997). Attainable yield has come to mean the yield a skillful farmer should reach when taking prudent account of economics and risk; it has complications because farmers vary, as do farm gate economics. The difference between FY and AY has been defined as the exploitable yield gap.

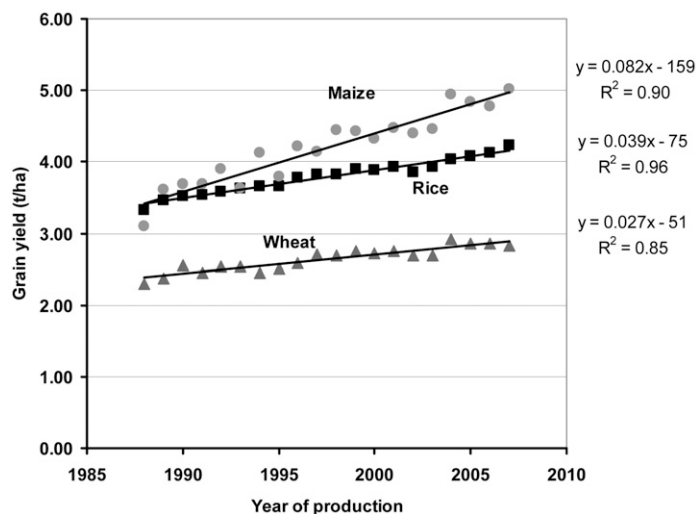


Fig. 1. World yields for wheat, rice, and maize vs. time, 1988 to 2007. Source: FAOSTAT. 2009. (Available at <http://faostat.fao.org/site/339/default.aspx> [verified 23 Dec. 2009]).

Our definition of PY builds on that of Evans (1993) and refers to the yield of an adapted cultivar when grown with the best management and without natural hazards such as hail, frost, or lodging, and without water, nutrient, or biotic stress limitations (water stress being eliminated by full irrigation or ample rainfall). “Yield” is used as a noun throughout, and for PY, it is the yield of the best cultivar available at a location, usually representative of a cropping region in terms of the natural resource base of the environment (photoperiod, solar radiation, temperature, vapor pressure regime, and soil type). The natural resource base cannot be readily changed by the manager, but the definition becomes blurred when including activities such as land leveling, tile drainage, or liming, which are long-term management investments that improve the natural resource base. PY is usually determined from carefully managed field experiments with the best cultivars, which in turn can be used to calibrate crop simulation models for PY prediction across time, space, and management options. Modeled PY must be based on the best available cultivar(s), meaning models should be regularly updated to match breeding progress in PY.

Usually PY progress is measured in side-by-side comparisons of historic sets of cultivars executed with modern agronomy and with protection from biotic stresses. As such, this measure includes that component of the progress that derives from positive cultivar × agronomy interactions. In fact this interplay of genetic improvement and agronomic improvement has been an important component of crop productivity progress and it cannot be attributed to breeding or agronomy alone (Evans, 1993; Fischer, 2009). Effective protection from biotic stresses is critical as breakdown in resistance to biotrophic pathogens in older varieties can otherwise lead to overestimated rates of PY progress. The abiotic environment may also change over the time span of varieties compared (e.g., climate or soil change, ozone increase, or CO₂ increase) in which case apparent breeding progress in gain yield could include adaptation to these changes. For rain-fed cropping it is also useful to define a water-limited potential yield (PY_W), where W refers to an amount of crop evapotranspiration that is notably less than potential evapotranspiration in the environment in which the crop is grown.

Because of constrained and variable farmer circumstances there is usually an FY to AY gap and, because of economics, always an AY to PY gap; here we express these gaps as a percent of FY, thus providing a number more relevant to any discussion of increasing supply to meet a growing global demand. It should be noted that plant breeding increases PY (and PY_W), but breeding can also help to close the yield gap between PY and FY.

WHEAT YIELD United Kingdom

The United Kingdom represents well-watered winter wheat around the world and is one of the more favorable

wheat growing environments: it is dominated by winter wheat planted in September to October and harvested in August the following year, thus occupying the land for 10 to 11 mo. The United Kingdom delivers one of the highest national farm wheat yields, averaging over 8 t ha⁻¹ (15% moisture) across 2 million ha (Fig. 2). Given the competitive private breeding sector, the substantial private and public sector crop management research, sophisticated farmers, and production that is not nowadays distorted greatly by price subsidies, this level of FY is probably close to AY. In the United Kingdom, fertilizer rates are high (the British Survey of Fertilizer Practice lists this as 190 kg N, 31 kg P₂O₅, and 39 kg K₂O per hectare in 2007), though the rate has been steady for the last 25 yr. Since 1989 yield has increased at a rate of 53 kg ha⁻¹ yr⁻¹ or 0.7% of the current yield level (Fig. 2). An excellent and extensive system of national trials is conducted by the Home Grown Cereals Authority (HGCA): with complete disease and pest control, these trials, which are dominated by the latest cultivars, averaged 10.4 t ha⁻¹ in 2004 to 2008. These HGCA protected trial yields can be considered a good measure of the current PY, since yield is little affected by water deficits (Sylvester-Bradley et al., 2005). The yield gap between FY and PY is currently 30% of average FY. This leaves little scope for gap closing through breeding, although greater host plant resistance could substitute for the biocides currently used to keep this gap small.

The system of HGCA trials also permits an accurate estimate of the relative rate of PY progress from breeding. Yields of cultivars released over the last 20 yr have increased linearly with time at a rate of 61 kg ha⁻¹ yr⁻¹ (or 0.6% of 2008 PY) with no sign of slowing. Although PY is plotted against the year of cultivar release (Fig. 2), it is reasonable to assume that the best cultivars moved quickly to occupy substantial portions of the area planted once released. Thus the relative rate of FY progress in the United Kingdom is similar to that from breeding over the last 20 yr (Fig. 2), and observers suggest that recent FY progress is dominated by genetic improvement (e.g., British Society of Plant Breeders, 2008); recent analysis of the HGCA wheat yields over the last 50 yr strongly supports the view that over 90% of progress since the 1982 is derived from breeding alone (i.e., independent of variety by agronomy interaction [I. Mackay, personal communication, 2009]).

A recent study of progress in U.K. winter wheats (1972–1995) under very well-managed conditions at Nottingham (with yields to 11.4 t ha⁻¹) showed, as have most wheat studies, that yield progress was associated closely with an increased number of grains per square meter. The increase is also associated with greater crop growth rate and radiation use efficiency (RUE) in the period leading up to flowering and with increased water soluble carbohydrates in the stem at flowering (Shearman et al., 2005). Although there are other less likely explanations, the increase in RUE

points strongly to greater P_{max} (light-saturated photosynthetic rate) in the more recent cultivars. United Kingdom scientists are confident of further genetic progress in PY, predicting it will reach 17.4 t ha⁻¹ by 2050, although FY, constrained by water and economic considerations, is predicted to average 13 t ha⁻¹ (Sylvester-Bradley et al., 2005; R. Sylvester-Bradley personal communication, 2009). This prediction relies on a reasonable assumption of RUE at 1.4 g dry matter (DM) MJ⁻¹ intercepted (total) solar radiation. It also includes novel but physiologically sound calculations of the dry matter that must be invested in stems to minimize lodging risk (Berry et al., 2007), thereby limiting harvest index (HI) to a value somewhat below the oft-quoted maximum estimate of 0.62 (Austin, 1982). It should be noted, however, that these predicted yields imply linear progress in PY and FY of 167 and 119 kg ha⁻¹ yr⁻¹, respectively—around 2.5 times the current rates.

Yaqui Valley, Mexico

The Yaqui Valley irrigation area in northwest Mexico (27° N lat) normally grows between 150,000 and 180,000 ha of irrigated spring wheat in each winter season (November–April) and is well representative of irrigated wheat in the developing world. Good records go back to the 1950s, when the wheat crop became the breeding target of the International Maize and Wheat Improvement Center's (CIMMYT) Wheat Program and its predecessor organization. Average farm yields increased dramatically in the first 30 yr, from 1.4 t ha⁻¹ in 1950 to almost 5 t ha⁻¹ in 1980 (>4% growth per annum; Fig. 3); semidwarf cultivars first appeared in 1962 and in less than 5 yr occupied the whole area, while N fertilizer application rose from zero to around 175 kg N ha⁻¹ in 1980 (Bell et al., 1995). Fischer (2008) argued that although the rate of progress has clearly slowed with time in the period

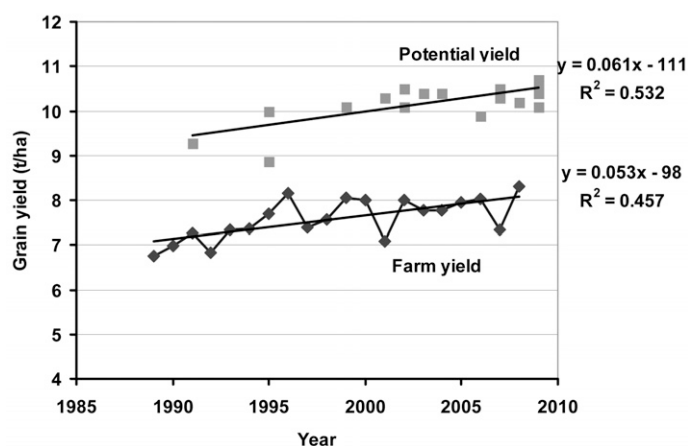


Fig. 2. Farm yield vs. time (lower line) and potential wheat yield (upper line) vs. year of release in the United Kingdom; yields at 15% moisture. Potential yields were obtained under fungicide protection and are averaged over the period 2004 to 2008. Sources: FAOSTAT, 2009. (Available at <http://faostat.fao.org/site/339/default.aspx> [verified 23 Dec. 2009]); HGCA Recommended Lists 2004–08.

1950 to the present, with significant curvilinearity in yield vs. time, current yield progress is best represented by the linear slope of yield vs. time over the last 30 yr (Fig. 3; 49 kg ha⁻¹ yr⁻¹ or about 0.8% per annum of the current average yield of 6 t ha⁻¹). However, it has been pointed out that secular weather changes in the Yaqui Valley, namely warming (Bell and Fischer, 1994) and later cooling (Lobell et al., 2005), can confound the interpretation of yield change over time. Allowing for the recent steady decline in minimum daily temperature (T_{\min} , 0.07°C per year over 1979–2008, $R^2 = 0.38$) and an apparent FY responsiveness to T_{\min} , calculated using the first difference method to be 377 kg ha⁻¹ °C⁻¹ ($R^2 = 0.43$), suggests therefore that technological progress was less than the FY numbers indicate in Fig. 3 but still positive at 23 kg ha⁻¹ yr⁻¹ or 0.4% per annum.

Potential yield progress in the Yaqui Valley has been measured many times in sets of historic and new cultivars grown side by side at the centrally-located Centro de Investigaciones Agrícolas del Noroeste (CIANO) research station, using optimal agronomy and frequent fungicide applications for complete disease control; yield is regressed against year of release in Fig. 3, and rapid adoption of the best cultivars can be assumed. Clearly an important factor driving up FY since 1950 has been the initial rapid increase in PY (>1% per annum) of the cultivars released and quickly adopted (Fischer and Wall, 1976; Bell et al., 1995). However, PY progress has slowed in the last 30 yr to around 23 kg ha⁻¹ yr⁻¹ or 0.3% per annum (Fig. 3). Thus it would seem that the relative rates of progress in FY and PY are about the same. Currently FY and PY are at 6 and 9 t ha⁻¹, respectively, and the gap between them is fairly steady at about 50% of FY. Much has been

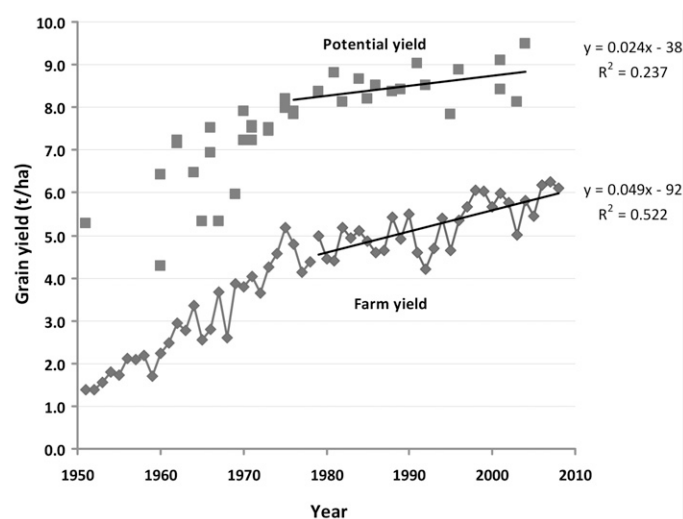


Fig. 3. Yield of wheat vs. time in the Yaqui Valley, Mexico, and potential yield (upper line) of bread and durum wheat varieties versus year of release; yields at 12% moisture. Potential yields were determined in experiments over the period 1990 to 2005 with fungicide protection and standardized against a common check, ‘Siete Cerros 66’, with an average protected potential yield of 7.0 t ha⁻¹. Regressions refer to the last 30 yr data only. Source: K.D. Sayre, personal communication, 2009.

learned about variation between yields in farmers’ fields using ground surveys and, more recently, satellite imagery. About one third of this yield gap is readily exploitable with better agronomy (earlier sowing and improved water and weed management) (Lobell and Ortiz-Monasterio, 2008; Lobell et al., 2005; Ortiz-Monasterio and Lobell, 2007).

Of great relevance here is the physiology of the more recent PY increase shown in Fig. 3. Using six key semi-dwarf bread wheat cultivars spanning 1962 to 1988 and grown with full foliar disease protection, Sayre et al. (1997) showed that PY progress of 0.8% per annum over the period was associated with several traits (Table 1), including increased grains per square meter ($r^2 = 0.71$, $p < 0.01$) and increased HI ($r^2 = 0.66$, $p < 0.05$) as seen in earlier studies of tall and short wheats (e.g., Fischer and Wall, 1976). Physiological measurements over 3 yr (1993–1995) revealed that the yield progress was also associated with stomatal conductance ($r^2 = 0.88$, $p < 0.01$), which increased by 63% over the release period, and with P_{\max} ($r^2 = 0.72$, $p < 0.01$), which increased 23% over the same time interval (Fischer et al., 1998); these correlations were found both before anthesis as well as after. A parallel unpublished study of seven semidwarf durum cultivars released between 1967 and 1989 found similar associations among yield, grains per square meter, and physiological activities (Table 1). In both studies, there was no correlation between grain yield and plant height or days to flower. Attempts to relate grain number and yield to crop growth rate and RUE in the three week period just before flowering (as in Shearman et al., 2005) found significant correlations in only one out of the 3 yr (Fischer et al., 1998), though RUE estimates had large errors.

The above results strongly suggest that progress for PY is related to increased stomatal conductance and provide some support for an accompanying increase in P_{\max} ; some earlier spring wheat studies showed clearly increased P_{\max} (e.g., Shimshi and Ephrat, 1975; Watanabe et al., 1994). It is interesting that in both bread wheat and durum wheat the morphological changes in the flag leaf seen with this breeding progress at CIMMYT (e.g., smaller, more erect, higher N per unit area, and higher chlorophyll concentration) were not unlike those reported for winter wheat progress in the United Kingdom (Shearman et al., 2005). CIMMYT has reported some success in the use of stomatal conductance as an early generation selection criterion for PY (Condon et al., 2007). Although this trait can be remotely sensed quickly and cheaply, it appears that there has been insufficient support to properly validate this selection strategy.

RICE YIELD

Japan

Japan has a long and rich history of research in rice breeding, agronomy, and physiology, and well represents higher latitude japonica rice grown under the summer monsoon.

Japan had its “green revolution” in rice in the 1950s to 1970s, resulting in rapid yield growth from new cultivars, fertilizer, and improved crop management through mechanization (Horie et al., 2005). National yield increased by about 50% in this period and reached about 6 t ha⁻¹ in 1975 (all rice yields are for rough or paddy rice, although the Japanese literature often quotes brown rice yields). It should be noted that winning yields in farmer contests peaked at over 12 t ha⁻¹ in the 1950s and 1960s, more than double the national yield, highlighting what can be achieved with certain specific management techniques and presumably fortuitous weather conditions (Horie et al., 2005). Since then yield has grown only slowly (Fig. 4), now approaching 6.5 t ha⁻¹, and rice area has actually declined around 1.5% annually to reach 1.7 million ha today. Area decline reflects less favorable policies for rice and may be part of the reason for the slow yield growth of only 0.4% per annum relative to present FY (Fig. 4). Another reason for slow growth in yields is increased attention paid to better rice quality, which requires reduced N fertilization levels and absorbs much of the breeding effort (T. Horie, personal communication, 2009).

An increase in rice PY in Japan appeared to occur in the early 1990s. The cultivar ‘Takanari’, released in 1990, has been widely assessed in central and southern Honsu, giving an average yield of 10.5 t ha⁻¹, 36% more than ‘Nipponbare’, a landmark cultivar released in 1963 (San-oh et al., 2004; Horie et al., 2005; Takai et al., 2006; Katsura et al., 2007; Taylaran et al., 2009; H. Yoshida, personal communication, 2009); the yield advance was seen even when crop protection was clearly specified (e.g., Takai et al., 2006; Katsura et al., 2007). Both varieties are conventional cultivars (inbreds), yet Takanari yielded as well as one of the best current Chinese hybrids (Katsura et al., 2007). Needless to say, Takanari is not a good quality food rice, and more recently breeders have produced other very high yielding feed-type rices such as ‘Hokuriku 193’ in 2007 (Goto et al., 2009) and ‘Momiroman’ in 2008 (Yoshinaga et al., 2009), as well as a reasonable food quality variety, ‘Akita 63’, which has recorded an average yield of 11.1 t ha⁻¹ over 3 yr (Mae et al., 2006). Between Nipponbare and Takanare, PY increased at around 100 kg ha⁻¹ yr⁻¹ as shown in Fig. 4; this is close to 1.0%. It is not possible, however, to get an accurate measure of the more recent PY progress, but it seems reasonable that progress has continued and that the current potential is at least 11 t ha⁻¹, giving a yield gap of 70%. We suggest that this large gap and the apparent stagnation of Japanese yields is the consequence of the overriding emphasis on producing excellent food quality rice for the limited home market. All the new high-yielding varieties respond to higher N levels, but they have high N utilization efficiency (e.g., Katsura et al., 2007), and new agronomic techniques can lift N recovery efficiency substantially (Horie et al., 2005). It is not

Table 1. Correlation between physiological traits and grain yield in CIMMYT bread wheat and durum wheat semi-dwarf cultivars. Source: bread wheat: Fischer et al., 1998; durum wheat: R.A. Fischer, unpublished data, 1997.

	Bread wheat	Durum wheat
Number of varieties	8	7
Release period	1962–88	1967–1989
Independent variable	Association with grain yield (<i>r</i>)	
Year of release	0.97**	0.66*
Total dry weight	0.07	0.79**
Harvest index	0.66*	0.88**
Grains per square meter	0.71**	0.98**
Kernel weight	-0.01	-0.4
Days to anthesis	0.03	-0.23
Stomatal conductance	0.88**	0.79**
P _{max}	0.72**	0.52
δC ¹³	0.50*	0.61*
Canopy temperature depression	0.58*	na

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

known whether even higher yields could be obtained with contest-winning management, since contests have been discontinued, but there is some evidence to support this (e.g., San-oh et al., 2004).

The physiology of the high PY cultivar, Takanari, relative to its lower yielding predecessors has been studied in detail at Kyoto. It had the highest filled spikelet number per square meter and the highest crop growth rate during the late reproductive period (just before heading). These were associated with a higher RUE (2.11 g MJ⁻¹ total intercepted solar radiation) and higher nonstructural carbohydrate content at heading (Takai et al., 2006). The parallel between this result and that of Shearman et al. (2005) with winter wheats in the United Kingdom is clear. Katsura et al. (2007) continued studies in Kyoto and confirmed these results when

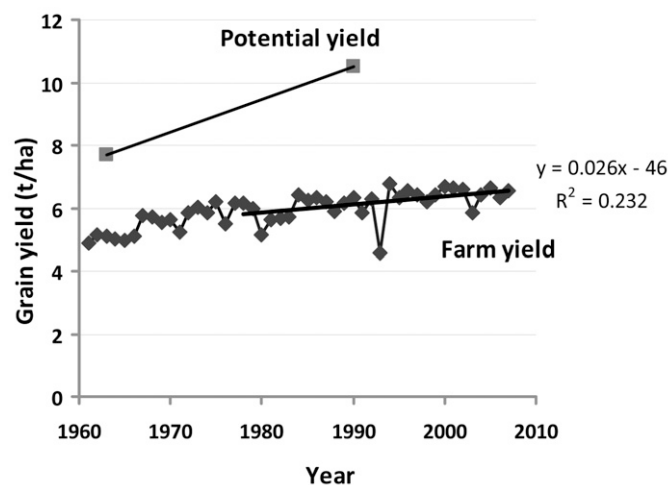


Fig. 4. Japan’s rice yield vs. time and potential yield for varieties Nipponbare and Takanari; yields for rough rice at 14% moisture. Sources: FAOSTAT. 2009. (Available at <http://faostat.fao.org/site/339/default.aspx> [verified 23 Dec. 2009]); for potential yield see text.

comparing Takanari with Nipponbare, again recording a very high RUE in the preheading stage with Takanari (1.96 g MJ⁻¹); they also reported a tendency for Takanari to take up more soil nitrogen, although specific leaf nitrogen (SLN) was not superior. The same authors confirmed that the increased crop growth rate of Takanari was due to greater daytime canopy photosynthesis and not due to any genetic differences in respiratory parameters (Katsura et al., 2009). At the same time Ohsumi et al. (2007) confirmed a higher P_{max} in Takanari compared with other high yielding cultivars and showed it to be associated with higher stomatal conductance rather than higher SLN, although ontogenetic variation in P_{max} was related to SLN. Ohsumi and colleagues concluded that simultaneous improvement in stomatal conductance and in SLN are essential for breeding cultivars with higher P_{max} (and yield). Physiological data on the newer high-yielding varieties does not appear to be available.

Central Luzon, the Philippines

Central Luzon is a major rice growing plain in the Philippines, with the International Rice Research Institute (IRRI) located just to the south and the Philippine Rice Research Institute (PhilRice), the national research center, located in its northeast corner. This region has been the target of intensive rice breeding efforts for at least 50 yr, grows about 1.2 million ha of rice, and is representative of tropical irrigated *indica* rice growing environments. About two thirds of this rice area is planted to the wet season (WS) crop and the balance to dry season (DS) rice under irrigation. Farm yields have been surveyed from time to time by IRRI since 1966. At that time only traditional cultivars were grown, fertilizer use was negligible, and cropping intensity only 110% for an average yield of 2.5 t ha⁻¹. Farm yield for survey farms over the last 30 yr period when only modern cultivars were grown is shown in Fig. 5 (Estudillo and Otsuka, 2001; P. Moya, personal communication,

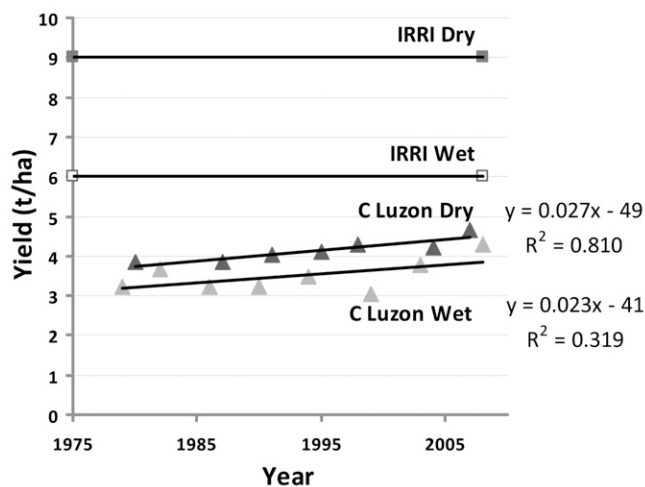


Fig. 5. Farm rice yield vs. time of harvest in Central Luzon in the wet and dry seasons, and potential yield at IRRI; yields for rough rice at 14% moisture. Source: see text.

2009). Farm yield progress is slow but steady at 0.6% per annum from both wet- and dry-season rice. The surveys showed fertilizer use rising from around 70 kg ha⁻¹ (elemental N+P+K) in the early 1980s to 150 kg ha⁻¹ now, while rice cropping intensity has remained steady at 150%.

Current estimates of PY of 6 and 9 t ha⁻¹ for WS and DS, respectively, are derived from yields of inbred varieties in current very well managed irrigated trials at IRRI in the absence of significant diseases, pests, and weeds (e.g., Yang et al., 2007); Peng et al. (1999) declared a DS PY of 10 t ha⁻¹ but yields appear to have declined since then (see Table 2). Despite the rice climate in Central Luzon being slightly more favorable than at IRRI (S. Peng, personal communication, 2009), the WS yield gap is therefore 60% of FY, and the gap is even larger in the DS (100%). These gaps do not reflect significant current use of older disease-susceptible cultivars, because cultivar turnover is rapid in the region. More recent wet-season surveys closer to IRRI (Laguna Province) suggest that the average yield of the top one third of farmers is approaching 6 t ha⁻¹. However, the average of all farmers is considerably lower at 4.4 t ha⁻¹ in Laguna, with a 0.4% annual increase over the last 30 yr, and 4.0 t ha⁻¹ with no trend in Nueva Ejica Province (close to PhilRice). These data suggest yield gaps of 36% and 50%, respectively, or somewhat less than the 60% observed by the Central Luzon WS survey.

Changes in PY are difficult to assess in the current trials at IRRI, because older cultivars such as 'IR8', the first tropical semidwarf cultivar released in 1966, cannot now be easily protected from pests and diseases or may not be well adapted to recent unfavorable changes in the natural resource base, including the climate (Peng et al., 1999, 2000). The latter possibility is suggested by the fact that even when, with protection and in the DS there is no obvious disease or pest damage, IR8 yields no more than 8 t ha⁻¹ or 1 to 2 t ha⁻¹ below its yields in the late 1960s (S. Peng, personal communication, 2009). Progress in the PY of inbreds since the release of 'IR72' in 1988 seems also to have been very slow (see Table 2). Therefore, in accord with Peng et al. (2000), Fig. 5 shows no progress in PY, even if maintaining PY in the face of a deteriorating physical environment would clearly constitute genetic progress. It should be noted that breeders have made good progress on other fronts such as disease and insect resistance, earliness, and grain quality.

Since the early 1990s IRRI breeders have made a concerted effort to boost rice PY by design, breeding first for the new plant type (NPT) ideotype and more recently for a second generation of NPT products (NTP2). NTP2 cultivars perform better than the original NPTs, but barely better than the best cultivars of the same vintage coming from the conventional inbred breeding program (Yang et al., 2007; Table 2). This is a disappointing outcome for physiological plant breeding, especially since the development of IR8 itself came from ideotype breeding (Jennings, 1964). However, NPT thinking has spilled over into China

where it appears to be an important factor in the design of the very high yielding hybrids now in current use (Peng et al., 2008). Yields in the irrigated eastern China lowlands, under a climate similar to the warm cloudy Philippines WS, are now surpassing 12 t ha⁻¹. Some of this technology has flowed back to IRRI from China, and the best Philippine F₁ tropical hybrids are now yielding 11 to 14% more than the best inbreds in the DS at IRRI, though they show little advantage in the WS (Yang et al., 2007; Table 2). A more recent study of hybrids and inbreds carefully matched for phenology found 18% (DS) and 14% (WS) yield advantages for the hybrids (Bueno and Lafarge, 2009).

Retrospective physiology on recent PY progress in tropical rice is also hampered by concerns over the validity of side-by-side comparisons of historic sets of cultivars. There is some evidence that increased HI was important from 1966 to 1980 as cultivars became shorter and earlier, but since 1980 total biomass and a slightly longer duration seem to be associated with the highest yielding inbreds (Peng et al., 2000). Changes in filled spikelets per square meter and seed weight were not consistent, and the decline in yield of IR8 seems to be related to falling HI and lower filled spikelet percentage (Peng et al., 1999). Yang et al. (2007) recently compared the best of the inbreds derived conventionally and from NPT2s with IRRI hybrids (Table 2). Hybrids were superior in the DS by virtue of both greater biomass and greater HI, more spikelets per square meter, and heavier seeds but have a lower proportion of filled spikelets. Bueno and Lafarge (2009) also found higher biomass and HI with the hybrids. Little data on leaf-level physiology has been reported lately, although the earlier study of conventional inbreds found no difference among cultivars released between 1966 and 1995 for crop growth rates in the critical panicle initiation-to-flowering stage, while Peng et al. (1999) reported lower P_{max} in a hybrid compared to IR72. Later Peng et al. (2008) note that the best hybrid “super” rices in China appear to have higher biomass and P_{max} around heading, higher specific leaf weight, and higher leaf chlorophyll than older hybrid check cultivars, which they outyielded by 10 to 20%. In addition, the final three leaves of super rice hybrids are very erect, like the NPT rices, but, unlike modern wheats, the leaves are long and reach well above the panicle. Zhang et al. (2009) recently confirmed the superior yield of the hybrid “super” rices in eastern China but could not explain this via increased RUE.

MAIZE YIELDS

Iowa State, United States

The state of Iowa grows 5.3 million ha of maize under very favorable rain-fed conditions in the heart of the U.S. Corn Belt. This region represents the majority of temperate maize environments globally. The Corn Belt, and Iowa in particular, is a major battleground for the large maize breeding and biotechnology transnational companies, Monsanto, Pioneer-DuPont, and Syngenta, who have

invested heavily in maize improvement, especially over the past 20 yr. Global expenditures on maize improvement, widespread testing, and refining farm-level agronomy for the new hybrids by these three companies alone are currently estimated to exceed \$3 million per day. Maize yield growth in the United States has been strong and steady, while in Iowa it is nothing short of spectacular (Fig. 6). The Iowa average yield is currently 10.5 t ha⁻¹, with a linear slope of 214 kg ha⁻¹ yr⁻¹ or 2.0% per annum of the current yield; progress has also accelerated since 1990. What is behind this impressive growth, and how much is due to breeding?

The changes from 1961 through 1990 were largely due to increases in fertilizer use, chemical weed control, and higher plant densities, coupled with the use of hybrids that could respond to fertilizers and tolerate crowding (Cardwell, 1982). Nitrogen use, a key factor driving yield increases in the 1960s, has stabilized since the late 1970s at around 140 to 160 kg N ha⁻¹, meaning fertilizer use efficiency has increased notably since then (Fig. 7). Irrigated land in Iowa has only increased from 0.5% of the area in 1997 to 0.7% in 2007 and has not been a factor in productivity increases. Precision farming, where input levels are varied in response to within-field fertility variation, may have led to small improvements in yield (Cassman, 1999), and more uniform spacing between plants because of improved machinery has also contributed to a minor rise in yields. One key factor recently contributing to the rapid increase in yields in Iowa has been earlier planting. Maize crops in Iowa today are planted on average 12 d earlier than in 1979, thus allowing the crop to capture more radiation and to fill grain under a more favorable temperature regime. Kucharik (2008) estimates that early planting may account for half of the annual increase in grain yields in Iowa in the last 30 yr; this has been facilitated by zero tillage, improved seed fungicide dressing, hybrids with herbicide resistance and greater early cold tolerance, and

Table 2. Grain yield (14% moisture), biomass, harvest index, and duration of recent inbred, hybrid, and second generation new plant type (NPT2) rice cultivars, compared to IR72 released in 1988. Trials were grown at IRRI and averaged for 2003 and 2004 (from Yang et al., 2007).

	IR72	Inbreds (n = 3,4)	Hybrids (n = 5)	NPT2 (n = 5)
<u>Dry season</u>				
Grain yield†	8.29b	8.73b	9.55a	8.38b
Biomass, g m ⁻²	1726	1722	1792	1691
Harvest index	0.45	0.46	0.49	0.44
Growth duration, d	117	117	116	118
<u>Wet season</u>				
Grain yield†	5.60ab	6.00a	5.98a	5.40b
Biomass, g m ⁻²	1339	1413	1317	1409
Harvest index	0.36	0.38	0.41	0.37
Growth duration, d	113	122	113	121

† Yields followed by different letters significantly different at *P* < 0.05.

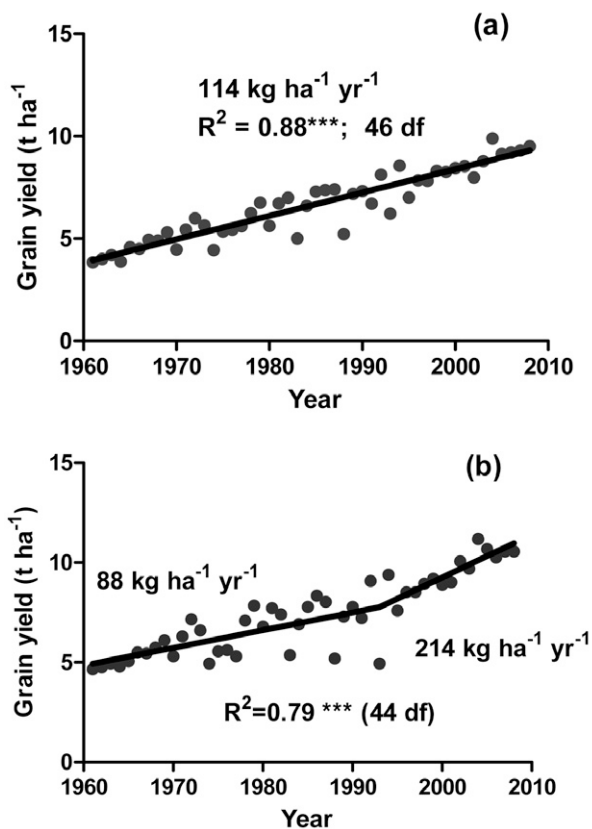


Fig. 6. Maize grain yield vs. year of harvest for (a) the United States and (b) the state of Iowa; yields at 15.5% moisture. Linear rates of yield increase are shown separately for 1961 to 2008 period. Split line regression resulted in a significantly improved fit for the Iowa yield data. Source: http://www.nass.usda.gov/Data_and_Statistics/Quick_Stats/ (verified 1 Jan. 2010).

the use of large high-speed planters. A second significant factor is the continuing rise in plant densities in the Corn Belt at a rate of about 1000 plants ha⁻¹ yr⁻¹ over the last 25 yr, and this trend to higher densities continues despite the rising price of seed. Improved plant-to-plant uniformity arising from the greater use of precision planters has also

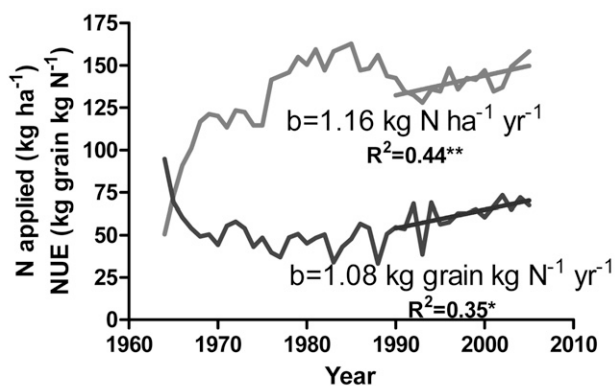


Fig. 7. Nitrogen applied to maize in Iowa (upper curve) and the ratio of grain yield to N applied (lower curve), 1964 to 2005. Linear rates of increase for each variable are shown for 1990 to 2005 periods. Source: <http://www.ers.usda.gov/Data/FertilizerUse/> (verified 23 Dec. 2009).

resulted in a small increase in yield (Liu et al., 2004), and it is likely that reduced plant-to-plant variation observed in newer vs. older hybrids has had a similar effect (Edmeades et al., 2006). Finally, a recent factor is the increasing use of foliar fungicide in disease-prone situations (maize after maize, conservation tillage, and/or high temperature and humidity), even when disease is not very evident.

Older research on the sources of productivity gains in the Corn Belt have suggested that about 40 to 50% of increased yields can be attributed to genetic improvement (Cardwell, 1982; Duvick, 2005). In recent years, however, as mean yield levels rise, the easy gains from better management practices alone such as applied N and improved weed control often are fully exploited, and the proportion of gain due to improved genetics that address genotype × management practice and yield potential rises (Edmeades and Tollenaar, 1990). Thus the full benefits of changed growing practices are only seen when complemented with cultivars developed to exploit those practices—the ubiquitous positive genotype by management interaction—and that complementation becomes increasingly important as yield levels rise. An important example is the optimum plant density of maize hybrids developed over the past 70 yr. This has risen substantially, exploiting the positive interaction between improved hybrids and plant density; it now averages around 80,000 plants ha⁻¹ in Iowa. A second example relates to date of planting. Genetic improvements in tolerance to cold and waterlogged soils have played an important part in allowing the earlier planting of maize and the expansion of conservation tillage practices that themselves favor earlier planting. The growing importance of genetic improvement makes an interesting parallel with wheat in the United Kingdom, mentioned earlier, but the continuing contribution of genotype by agronomic management interaction appears to be greater with maize in Iowa.

It has not been easy to get a measure of maize PY and its progress in Iowa. First, hybrids must be tested at their optimum density. Studies of Pioneer hybrids released in each decade from 1930 to 2002 at their best density showed remarkably linear yield growth of 79 kg ha⁻¹ yr⁻¹, or 1.5% of mean yields of 1930 hybrids, but only 0.8% of 2002 hybrid yields, which were 10.2 t ha⁻¹ (Cooper et al., 2004). This rate of yield growth is about 66% of the increase in Iowa yields over the same period. A later look at this Pioneer hybrid set with releases to 2007 showed yield had almost reached 12 t ha⁻¹ and was increasing at 116 kg ha⁻¹ yr⁻¹ or 1.0% per annum (Hammer et al., 2009; see Fig. 8). The yield of the best three hybrids for each maturity class in each of the five districts in Iowa Crop Improvement Association trials in 2007 and 2008 averaged 11.8 t ha⁻¹ and could be considered another valid estimate of PY. However it is not possible to measure genetic progress with these trials, and all of the above PY estimates seem low for a region where FY averages 10.5 t ha⁻¹. Thus it is important to note that the same Pioneer hybrids as used by Cooper et al. (2004), when grown under

irrigation in a very favorable Chilean environment, showed PY progress at around 200 kg ha⁻¹ yr⁻¹ or 1%, with the highest yields close to 20 t ha⁻¹ (Campos et al., 2004).

Near Iowa, in Nebraska, higher yields have been reported in experiments to calibrate a maize simulation model (Hybrid-Maize [University of Nebraska, Lincoln, NE; Yang et al., 2004]), where, with irrigation, around 100,000 plants ha⁻¹ and 225 to 298 kg N ha⁻¹, yields of the latest hybrids in 1999 to 2002 averaged about 16 t ha⁻¹ (Yang et al., 2004). Annual crop contest winners report even higher yields: for rain-fed maize in Iowa, contest-winning yields are approaching 17 t ha⁻¹ (R.W. Elmore, personal communication, 2009), and for irrigated maize in Nebraska, contest-winning yields have averaged 18.8 t ha⁻¹ over the period 1984 to 2002 with little apparent increase over time (Cassman et al., 2003). Contest yields for rain-fed maize in Nebraska over the same period have risen steadily, reaching 15 t ha⁻¹ in 2002 (Cassman et al., 2003). Competition-winning yields arise from excellent management and very favorable and often unpredictable genotype × environment interactions, so as an estimate of overall PY for the region they must be treated with caution. Thus, as with contest-winning rice yields in Japan in the 1960s, we are forced to regard maize contest yields as not being representative of PY for the whole state.

It would be good to have data from other breeding sources, but on the basis of the published Pioneer data, we conclude that the breeders are still increasing maize PY in Iowa but at only 1% per annum. Regarding the current PY for rain-fed Iowa we conclude that the best estimate is the average yield simulated by Hybrid-Maize above using 20 yr weather from Ames, Iowa; that was 15.5 t ha⁻¹ (Grasini et al., 2009); it may be less than that of irrigated corn in Nebraska, because of subtle water stress (see also Hammer et al. [2009], below). It can now be calculated that the yield gap in Iowa is moderate (around 50%) and closing quickly as suggested in Fig. 8—not surprising given modern farmers, attractive prices, and a substantial investment in extension by private seed companies. Also, because of the uncertainty about contest-winning yields, we cannot agree with Cassman et al. (2003) that progress in maize FY in the Corn Belt may be approaching a limit, as reflected in Nebraska contest-winning irrigated PY; we do believe contest-winning crops are worthy of further careful study. Also, we agree that the rate of return to research on increasing maize yields in the Corn Belt appears to be declining, since research investments increased substantially in real terms during the 1970s through 1994 (Duvick and Cassman, 1999) while national yield increases have remained essentially linear with time through 2008 (Fig. 6(a)).

Significant changes in many traits have occurred as yields have increased in temperate maize, pointing to the physiological bases of improved PY. The late Don Duvick led the systematic evaluation of these changes, summarized in Duvick (2005) (Table 3). Most of the trait changes apart from

yield, lodging resistance, speed of dry down, and disease and insect resistance were not subject to direct selection pressure. The changes, however, can be better understood when solar radiation capture and competition for light are considered. In the 1930s hybrids were strongly single eared, tended to tiller, and had large branching tassels. They were well adapted to the low density and wide rows required for interrow weed control using animals, and light interception was relatively low. As a consequence they were sensitive to light competition, which caused individual plants to go barren. Breeding has reduced this sensitivity to such an extent that much higher densities are now tolerated and little light is wasted. A marked increase in leaf erectness and a reduction in tassel size is parallel to the changes due to selection in wheat and rice.

Tollenaar and coworkers, evaluating a smaller set of early-maturing temperate hybrids in Ontario, Canada, have also identified a number of underlying changes in plant architecture and function that have accompanied selection. Their studies have confirmed most of the changes shown in Table 3 (Tollenaar and Lee, 2006) but showed that selection has resulted in greater crop growth rate, especially during grain filling, arising from somewhat greater leaf area index (LAI), prolonged staygreen, and more erect leaves. P_{max} did not appear to change, although its rate of decline during grain filling was slower with newer hybrids (better functional staygreen) and it suffered less depression after cool nights in modern hybrids. Increased grain number of modern hybrids was related to greater dry matter accumulation around silking, to increased dry matter partitioning to the ear, and to greater ear fitness resulting in more kernels per unit ear dry weight (Tollenaar and Lee, 2006; Echarte and Tollenaar, 2006). More kernels, amounting to a greater grain-filling sink, may also be increasing photosynthesis and dry weight accumulation during this period through feedback mechanisms.

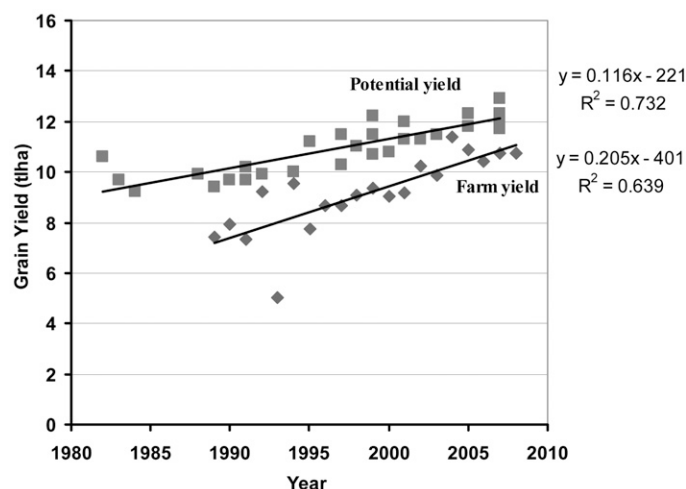


Fig. 8. Iowa maize farm yield vs. time and potential yield (at optimum density) vs. time of hybrid release; yields at 15.5% moisture. Sources: http://www.nass.usda.gov/Data_and_Statistics/Quick_Stats/ (verified 1 Jan. 2010); Hammer et al. (2009).

Breeders' trials conducted in Argentina show similar PY progress as in Iowa (I. Colonna, personal communication, 2009). For example, with a set of maize hybrids released between 1965 and 1997 there was an overall yield increase of over 60%, closely associated with increased grain number, and irrigated yield levels with the best hybrid of 17 t ha⁻¹ (Luque et al., 2006). Results from extensive research on the physiology of yield progress also showed that selection resulted in increases in crop growth rate and dry matter allocation to the ear during the critical period 1 wk before silking to 20 d after. It was during this period that the difference in favor of the more modern hybrids began to appear, and it was from this period that differences in kernel number and ultimately the progress in yield were derived. In addition RUE during this critical period showed a significant increase in response to year of hybrid release, while canopy extinction coefficient showed no clear tendencies (Luque et al., 2006). This is highly suggestive of an increase in P_{max} and establishes a clear parallel with PY progress in wheat and rice.

There is ample evidence to show good progress in maize yield under conditions of less water supply, as in dry years in Iowa (Duvick and Cassman, 1999) or under restricted irrigation where sometimes, especially with stress at flowering, the relative progress was actually greater under the less favorable conditions (Campos et al., 2004). Several key traits indicate increased water stress tolerance in modern hybrids, such as a reduced anthesis-silking interval and better tolerance of oxidative stress, as pointed out by Tollenaar and Lee (2006). These authors suggested that the modern hybrids are not only more resistant to high density and drought stresses but also to multiple minor stresses such as short dry spells, hot or dry windy days, cool nights, sudden radiation changes with cloud passage, oxidative herbicides, and brief waterlogging.

Hammer et al. (2009) have recently proposed that modern hybrids acquire more soil water through deeper roots, which could explain part of their improved density and drought tolerance. They argue also that progress is driven also by greater transpiration at a constant transpiration efficiency (TE), amounting to a TE of 44 kg DM ha⁻¹ mm⁻¹ (4.4 mg g⁻¹) at a mean vapor pressure deficit of 2 kPa. At prevailing HI values, this equates to 45 mm of transpiration per ton of grain or more than 600 mm crop evapotranspiration for a 12 t ha⁻¹ yield. A fixed TE could be seen to contrast with the notion that increased biomass is related to greater RUE and photosynthetic rate. Such changes, however, can occur without a change in TE, depending on changes in stomatal vs. internal leaf conductance and on the extent to which canopy gas exchange is coupled to the atmosphere. Cassman's group in Nebraska recently presented simulations and measurements that supported a higher TE and hence a steeper response of yield to water use, amounting to only 27 mm evapotranspiration per ton of grain (Grassini et al., 2009). Currently there is not enough information to resolve the important issues of change in rooting depth, TE, and the extent to which water supply may ultimately limit rain-fed maize yield in Iowa.

We cannot leave the Corn Belt without comment on the likely impact on yield of widespread adoption of GM (genetically modified) hybrids, commencing in 1996 and currently approaching 90% adoption in Iowa. Although the traits involved (herbicide resistance and insect resistance) do not increase PY per se, many observers point to yield increases at the farm level when GM hybrids are deployed. This is because weed control is generally better, timely planting is facilitated, and insect control is improved, particularly with respect to corn root worm. Damage from corn root worm was often not fully appreciated before transgenic sources of resistance became available, and the resulting complete root systems are

Table 3. Changes in yield and associated traits in Pioneer maize hybrids released between 1930 and 2002 (Duvick, 2005).

Trait	Change in trait	Comment
Yield at optimum density	Linear increase	Around 80 kg ha ⁻¹ yr ⁻¹
Optimum density	Increase to >80,000 plants ha ⁻¹	Started at 30,000 plants ha ⁻¹
Biomass	Steady increase	
Harvest index	Slight increase, now 50–55%	Older hybrids may go barren at high density
Kernel number per square meter	Steady increase	More plants ha ⁻¹ , less barrenness
Kernel weight	Small increase	
Grain protein	Consistent decline	Consistent rise in starch percentage
Days to flowering	Unchanged	No change in leaf number
Grain fill duration	Longer	
Grain dry down	Faster	
Plant height	No trend	
Ear height	Slight reduction	
Root lodging	Large reduction	Not completely eliminated
Canopy	Much more erect	Maximum leaf area index (LAI) generally unchanged
Staygreen	Markedly increased	Little change under terminal drought
Leaf rolling	More	More obvious with upright leaves
Tassel size	Much reduced	
Anthesis-silking interval	Reduced to near zero	Indicator of stress tolerance at flowering

now seen to contribute to drought tolerance. Part of the rapid farm level yield progress (Fig. 6) could reflect this.

Sub-Saharan Africa

Maize in sub-Saharan Africa occupies lowland, mid-altitude, and highland tropical and sub-tropical zones with moderate to good rainfall; these are the key agro-ecologies of maize in most developing countries. Notwithstanding its critical importance for feeding poor people, we give limited attention to the region because it is covered in another paper in this issue (Keating et al., 2010), and because it is clear that FY is constrained by many factors besides progress in PY and PY_w . These include low soil fertility, low fertilizer use, inadequate plant density, weeds, poor tillage, and labor shortages, as well as serious infrastructural and institutional constraints limiting the adoption of improved technologies for maize (Keating et al., 2010). Improved open-pollinated cultivated and hybrids show moderate PY and PY_w gains (e.g., Bänziger et al. [2006] in southern Africa), but improved management, especially soil fertility, brings larger gains (Keating et al., 2010), and combining improved germplasm with improved agronomy delivers even greater gains. For illustration we have taken yields from on-farm trials with improved cultivars and best-bet management to show AYs across the region (Table 4); FY is much lower and is growing only slowly; there is no doubt that the PY–FY yield gap is at least 200%.

SYNTHESIS AND CONCLUSIONS

This paper has traced progress in breeding for PY in favorable or irrigated environments that have attracted substantial research and development investment in breeding and agronomy (sub-Saharan Africa is the exception to this). We have shown that progress in FY closely tracks progress in PY. Potential yield and FY progress are summarized in Table 4, but it should be noted that PY progress was measured under modern agronomy and therefore reflects genetic progress per se plus that derived from any positive cultivar by management interactions.

None of the regions shown in Table 4 recorded gains in PY exceeding 1% per annum, although some uncertainty surrounds the estimate for PY and gains for rice in Japan and for maize PY in Iowa. Breeding progress in PY_w in industrialized countries (e.g., wheat in Australia, Great Plains of the United States) seems to be steady at about 0.5% per annum (Fischer, 2009; Fischer et al., 2009). These relative rates augur poorly for the future, for FY tends to follow PY progress, and all the rates of progress are below those needed to prevent real price rises (Tweeten and Thompson, 2008). There is a ray of hope in the rapid maize FY progress in Iowa, but worrying also because it amounts to notable yield gap closing and may become exhausted. Higher yield gaps persisted in developing countries despite major research and development efforts (in the Yaqui Valley of Mexico and in

the Philippines). Even higher yield gaps are to be found in most rain-fed situations with limited rainfall (data not shown) and with maize in sub-Saharan Africa (Fischer et al., 2009; Lobell et al., 2009). Clearly the cereal yield growth that the world needs must, to a significant extent, derive from a focus on closing these large yield gaps, though this challenge has not been the major focus of this paper. Suffice to say that breeding can also help farmers close yield gaps by improving, for example, disease and pest resistance, nutrient extraction, tolerance to manageable soil toxicities, weed competitiveness, or adaptation to conservation tillage.

The physiology of recent past progress in PY may point the way to future gains. Harvest index is approaching 0.5 and increasingly PY progress is associated with increasing yields of biomass, especially for maize. Progress in both HI and biomass was associated with more efficient partitioning of dry matter to, and utilization within, the growing reproductive structures around flowering. This has led to a greater number of grains per square meter, a change that has always accompanied PY increase—with the exception of tropical rice—and to greater sink strength during grain fill. Effective staygreen during grain filling was an important contributor to PY increases in maize. In all three crops and considering only field plot data, there was good evidence that two or all three of the following—crop growth rate, RUE, and P_{max} —were higher around flowering in the highest yielding cultivars; there have been numerous earlier reports of increases during grain filling (e.g., Evans, 1993), but this may simply reflect increased sink strength.

Prospects for further PY progress must build on this physiological understanding, and the study by Sylvester-Bradley et al. (2005) on wheat yield prospects in the United Kingdom does just this. There appears to be only limited scope for lifting HI when it is already at 50%; for example, even with the best designed wheat plants, HI seems unlikely to exceed 0.60 or even 0.55 if the risk of lodging is to be kept at a reasonable level (Berry et al., 2007). More biomass production, therefore, must be the main way forward, and this usually means greater crop growth rate, since extensions of crop duration have other limitations. Greater crop growth rate is a question of RUE because most crops grown under high yield potential conditions intercept >95% of the incident solar radiation for much of their life cycles. Under such conditions, RUE is a function of P_{max} and of light distribution in the canopy, but light distribution appears to already have already been optimized in the erect-leaf canopies of most modern cereal cultivars.

Evidence to support increased photosynthetic rate and crop growth rate is provided by CO_2 fertilization experiments that show yield responds to greater crop growth rate at key stages of development, at least in C_3 crops, in which P_{max} responds more strongly to CO_2 increase above current ambient. It is noteworthy that P_{max} rates in modern wheat cultivars in the field are clearly below the highest rates of

P_{max} found in the wild relatives of wheat (Evans, 1993). And although Evans (1993) gives reasons why P_{max} may not have changed initially with breeding, and why selection for P_{max} itself has not delivered higher yields, there seems no strong physiological reasons why it cannot be pushed higher without insurmountable trade-offs. Finally, we are well below the theoretical photosynthetic limit, which is commonly taken from the response of photosynthesis to radiation at low levels of radiation; according to Zhu et al. (2008), for C_3 crops this amounts to the capture (net of respiration) of 4.6% of intercepted total solar radiant energy as carbohydrate energy or about 2.7 g DM MJ⁻¹ intercepted total solar radiation. The highest recorded conversion rates for the full crop life cycle are around half of this; for shorter periods 2 g DM MJ⁻¹ have been recorded. The corresponding theoretical limit for C_4 crops is 6.0% or 3.5 g DM MJ⁻¹ of total incident solar energy (Zhu et al., 2008). Actual rates found in maize fall well short of this. Lindquist et al. (2005) reported one of the highest conversion rates for maize, namely 1.8 g DM MJ⁻¹, over the crop cycle. It may take more leaf N or it may not, but RUE must remain the focus of any major yield initiative if we are to improve, complement, or even maintain the rates of progress currently derived largely from conventional breeding. Surely the easiest way forward is to look at the natural variation we have within our crop species and their close relatives while bearing in mind the complexity of source-sink relationships in modern cultivars. The availability of untapped genetic diversity within each crop species for almost every trait is considerable; its efficient utilization remains a major breeding challenge. A related way forward could be to explore and exploit the apparent differences observed among modern cultivars in response to environmental changes, for example, CO₂ increase experienced over the past 40 yr (Ziska, 2008).

This paper does not have space to discuss in depth several other important issues surrounding breeding. Increased PY also results in increased resource use efficiency, not only for solar radiation but also water, nitrogen (Fig. 7), phosphorus,

energy, and labor. Breeding offers some scope to counteract the negative effects of higher temperature on yield, which are expected to accompany climate change in most current cropping locations. The breeding resources diverted from yield breeding to maintenance of disease resistance and improvement of grain quality are substantial, especially in wheat and rice, and may account for a significant part of the differences in rate of global yield increase between maize and the two self-pollinated cereals. The advent of new tools including molecular markers, genomic selection, association mapping, marker-aided recurrent selection, bioinformatics, biometrics, robotics, and remote sensing are beginning to aid breeding for yield. These specialized techniques, as they mature, have considerable potential to increase rates of progress and may even reduce the unit cost of yield gains.

The possibilities for genetic engineering to increase PY per se is obviously an important subject, but skepticism has been expressed about many of the claims and assumptions made by its proponents with respect to progress at the crop level in the medium term (e.g., Fischer, 2008). At the very least there needs to be much more attention to the physiology that links processes at the molecular level to crop performance in the field, a recurring theme in recent crop science literature (e.g., Edmeades et al., 2004; Sinclair and Purcell, 2005; Spiertz et al., 2007). Recent developments suggest there is credible evidence of field progress in PY_w through the use of transgenics (Castiglioni et al., 2008; Zhang, 2009); in general this seems to be related to countering the well-known sensitivity of seed number to drought around flowering in cereals, although in the case of maize it appears to have a positive effect on drought-affected yields throughout the crop lifecycle. The next few years must clearly validate the success of these claims of genetic engineering for increased PY and PY_w and reveal the underlying physiological mechanisms if we are to place any reliance on this approach to improving yield per se.

Finally, a strong and competitive plant breeding and seed industry, fostered by hybrid cultivars and other forms

Table 4. Summary of rates of recent progress in yield expressed relative to measured or predicted yield in 2007 or 2008. See text for sources.

Region and Period	Potential yield (PY)			Farm yield (FY)		Yield gap
	2007	Change	Progress	2007	Progress	% of FY
	t ha ⁻¹	kg ha ⁻¹ yr ⁻¹	% per annum	t ha ⁻¹	% per annum	
Wheat						
United Kingdom, 1989–2008	10.4	61	0.6	8	0.7	30
Yaqui Valley, 1979–2008	9	23	0.3	6	0.4	50
Rice						
Japan, 1978–2007	11	104	0.9	6.5	0.4	70
Central Luzon, 1978–2007 wet season	6	0	0	3.8	0.6	58
Central Luzon 1978–2007 dry season	9	0	0	4.5	0.6	100
Maize						
Iowa, 1990–2008	15.5	116	1.0	10.5	2.0	48
Sub-Saharan Africa 1989–2007	4 [†]	?	?	1.6	0.8	>200

[†] Attainable yields with best bet management averaged for Malawi, Ethiopia, Nigeria, Uganda, Mali, and Mozambique (Source: C. Dowsell of Sasakawa Global 2000, personal communication, 2009).

of cultivar protection, appears to be a major factor in the remarkable progress in maize yields in the United States and surely has lessons for elsewhere.

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REFERENCES

- Austin, R.B. 1982. Crop characteristics and the potential yield of wheat. *J. Agric. Sci. (Cambridge)* 98:447–453.
- Bänziger, M., P.S. Sentinela, D. Hodson, and B. Vivek. 2006. Breeding for improved stress tolerance in maize adapted to southern Africa. *Agric. Water Manage.* 80:212–224.
- Bell, M.A., and R.A. Fischer. 1994. Using yield prediction models to assess yield gains: A case study for wheat. *Field Crops Res.* 37:149–160.
- Bell, M.A., R.A. Fischer, D. Byerlee, and K.D. Sayre. 1995. Genetic and agronomic contributions to grain yields. *Field Crops Res.* 44:55–65.
- Berry, P.M., R. Sylvester-Bradley, and S. Berry. 2007. Ideotype design for lodging resistant wheat. *Euphytica* 154:165–179.
- British Society of Plant Breeders. 2008. New varieties underpin growth in UK cereal yields – NIAB study. p. 1–2. *In* British Society of Plant Breeders Newsletter, Nov. 2008. British Society of Plant Breeders Ltd., Ely, UK.
- Bueno, C.S., and T. Lafarge. 2009. Higher crop performance of rice hybrids than of elite inbreds in the tropics: 1. Hybrids accumulate more biomass during each phenological phase. *Field Crops Res.* 112:229–237.
- Campos, H., M. Cooper, J.E. Habben, G.O. Edmeades, and J.R. Schussler. 2004. Improving drought tolerance in maize: A view from industry. *Field Crops Res.* 90:19–34.
- Cassman, K.G. 1999. Ecological intensification of cereal production systems: Yield potential, soil quality, and precision agriculture. *Proc. Natl. Acad. Sci. USA* 96:5952–5959.
- Cassman, K.G., A. Dobermann, D.T. Walters, and H. Yang. 2003. Meeting cereal demand while protecting natural resources and improving environmental quality. *Annu. Rev. Environ. Resour.* 28:315–358.
- Cardwell, V.B. 1982. Fifty years of Minnesota corn production: Sources of yield increase. *Agron. J.* 74:984–990.
- Castiglioni, P., D. Warner, R.J. Bensen, D.C. Anstrom, J. Harrison, M. Stoecker, M. Abad, G. Kumar, S. Salvador, R. D’Ordine, S. Navarro, S. Back, M. Fernandes, J. Targolli, S. Dasgupta, C. Bonin, M. Luethy, and J.E. Heard. 2008. Bacterial RNA chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions. *Plant Physiol.* 147:446–455.
- Condon, A.G., M.P. Reynolds, G.J. Rebetzke, M. van Ginkel, R. Richards, and G. Farquhar. 2007. Using stomatal aperture-related traits to select for high yield potential in bread wheat. p. 617–624. *In* H.T. Buck et al (ed.) *Wheat Production in Stressed Environments*. Proc. 7th Int. Wheat Conference, Mar del Plata, Argentina, 27 Nov–2 Dec, 2005. Springer, New York, NY.
- Cooper, M., O.S. Smith, G. Graham, L. Arthur, L. Feng, and D.W. Podlich. 2004. Genomics, genetics, and plant breeding: A private perspective. *Crop Sci.* 44:1907–1913.
- Duvick, D.N. 2005. The contribution of breeding to yield advances in maize (*Zea mays*). *Adv. Agron.* 86:83–145.
- Duvick, D.N., and K.G. Cassman. 1999. Post-green revolution trends in yield potential of temperate maize in the north-central United States. *Crop Sci.* 39:1622–1630.
- Echarte, L., and T. Tollenaar. 2006. Kernel set in maize hybrids and their inbred lines exposed to stress. *Crop Sci.* 46:870–878.
- Edmeades, G.O., M. Bänziger, H. Campos, and J. Schussler. 2006. Improving tolerance to abiotic stresses in staple crops: A random or planned process? p. 293–309. *In* K.R. Lamkey and M. Lee (ed.) *Plant breeding*. The Arnel R. Hallauer International Symposium. Blackwell, Ames, IA.
- Edmeades, G.O., G.S. McMaster, J.W. White, and H. Campos. 2004. Genomics and the physiologist: Bridging the gap between genes and crop response. *Field Crops Res.* 90:5–18.
- Edmeades, G.O., and T. Tollenaar. 1990. Genetic and cultural improvement in maize production. p. 164–180. *In* S.K. Sinha et al (ed.) *Proc. Intl. Congr. Plant Physiol.* Vol. 1. IARI, New Delhi, India.
- Estudillo, J., and K. Otsuka. 2001. Has the Green Revolution ended? A review of long-term trends in MV adoption, rice yields, and rice income in central Luzon, 1966–99. *Jpn. J. Rural Econ.* 3:51–64.
- Evans, L.T. 1993. *Feeding the ten billion*. Cambridge Univ. Press, Cambridge, UK.
- Fischer, R.A. 2008. Improvements in wheat yield: Farrer, physiology and functional genomics. *Agric. Sci. NS* 1/08:6–18.
- Fischer, R.A. 2009. Farming systems of Australia: Exploiting the synergy between genetic improvement and agronomy. p. 23–54. *In* V. Sadras and D. Calderini (ed.) *Crop physiology: Applications for genetic improvements and agronomy*. Elsevier, Amsterdam, The Netherlands.
- Fischer, R.A., D. Byerlee, and G.O. Edmeades. 2009. Can technology deliver on the yield challenge to 2050? Paper prepared for expert meeting on “How to Feed the World in 2050.” 24–26 June 2009. FAO, Rome.
- Fischer, R.A., D. Rees, K.D. Sayre, Z.-M. Lu, A.G. Condon, and A. Larque-Saavedra. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Sci.* 38:1467–1475.
- Fischer, R.A., and P.C. Wall. 1976. Wheat breeding in Mexico and yield increases. *J. Aust. Inst. Agric. Sci.* 42:139–148.
- Goto, A., H. Sasahara, A. Shigemune, and K. Miura. 2009. Hokuriku 193: A new high-yielding indica rice cultivar bred in Japan. *JARQ* 43:13–18.
- Grassini, P., H. Yang, and K.G. Cassman. 2009. Limits to maize productivity in western Corn Belt: A simulation analysis for fully irrigated and rainfed conditions. *Agric. For. Meteorol.* 149:1254–1265.
- Hammer, G.L., Z. Dong, G. McLean, A. Doherty, C. Messina, J. Schussler, C. Zinselmeier, S. Paszkiewicz, and M. Cooper. 2009. Can changes in canopy and/or root system architecture explain historical maize yield trends in the U.S. Corn Belt? *Crop Sci.* 49:299–312.
- Horie, T., T. Shiraiwa, K. Homma, K. Katsura, S. Maeda, and H. Yoshida. 2005. Can yields of lowland rice resume the increases that they showed in the 1980s? *Plant Prod. Sci.* 8:259–274.
- Jennings, P.R. 1964. Plant type as a rice breeding objective. *Crop Sci.* 4:13–15.
- Katsura, K., S. Maeda, T. Horie, and T. Shiraiwa. 2007. Analysis of yield attributes and crop physiological traits of Liangyoupeiju, a hybrid rice recently bred in China. *Field Crops Res.* 103:170–177.
- Katsura, K., S. Maeda, T. Horie, and T. Shiraiwa. 2009. Estimation of respiratory parameters for rice based on long-term and intermittent measurement of canopy CO₂ exchange rates in

- the field. *Field Crops Res.* 111:85–91.
- Keating, B., P. Carberry, P. Bindraban, S. Asseng, and H. Meinke. 2010. Eco-efficient agriculture: Concepts, challenges and opportunities. *Crop Sci.* 50(2):109–119.
- Kucharik, C.J. 2008. Contribution of planting date trends to increased maize yields in the central United States. *Agron. J.* 100:328–336.
- Lindquist, J.L., T.J. Arkebauer, D.T. Walters, K.G. Cassman, and A. Dobermann. 2005. Maize radiation use efficiency under optimal growth conditions. *Agron. J.* 97:72–78.
- Liu, W., M. Tollenaar, G. Stewart, and W. Deen. 2004. Impact of planter type, planting speed, and tillage on stand uniformity and yield of corn. *Agron. J.* 96:1668–1672.
- Lobell, D.B., K.G. Cassman, and C.B. Field. 2009. Crop yield gaps: Their importance, magnitudes, and causes. *Annu. Rev. Environ. Res.* 34: 4.1–4.26.
- Lobell, D.B., and J.I. Ortiz-Monasterio. 2008. Satellite monitoring of yield responses to irrigation practices across thousands of fields. *Agron. J.* 100:1005–1012.
- Lobell, D.B., J.I. Ortiz-Monasterio, G.P. Asner, P.A. Matson, R.L. Naylor, and W.P. Falcon. 2005. Analysis of wheat yields and climate trends in Mexico. *Field Crops Res.* 94:250–256.
- Loomis, R.S., and D.J. Connor. 1992. *Crop ecology: Productivity and management in agricultural systems.* Cambridge Univ. Press, Cambridge, UK.
- Luque, S.F., A.G. Cirilo, and M.E. Otegui. 2006. Genetic gains in grain yield and related physiological attributes in Argentine maize hybrids. *Field Crops Res.* 95:383–397.
- Mae, T., A. Inaba, Y. Kaneta, S. Masaki, M. Sasaki, M. Aizawa, S. Okawa, S. Hasegawa, and A. Makino. 2006. A large-grain cultivar, Akita 63, exhibits high yields with high physiological N-use efficiency. *Field Crops Res.* 97:227–237.
- Ohsumi, A., A. Hamasaki, H. Nakagawa, H. Yoshida, T. Shiraiwa, and T. Horie. 2007. A model explaining genotypic and ontogenetic variation of leaf photosynthetic rate in rice (*Oryza sativa*) based on leaf nitrogen content and stomatal conductance. *Ann. Bot. (Lond.)* 99:265–273.
- Ortiz-Monasterio, J.I., and D.B. Lobell. 2007. Remote sensing assessment of yield losses due to sub-optimal planting dates and fallow period weed management. *Field Crops Res.* 101:80–87.
- Peng, S., K.G. Cassman, S.S. Virmani, J. Sheehy, and G.S. Khush. 1999. Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. *Crop Sci.* 39:1552–1559.
- Peng, S., G.S. Khush, P. Virk, Q. Tang, and Y. Zou. 2008. Progress in ideotype breeding to increase rice yield potential. *Field Crops Res.* 108:32–38.
- Peng, S., R.C. Laza, R.M. Visperas, A.L. Sanico, K.G. Cassman, and G.S. Khush. 2000. Grain yield of rice cultivars and lines developed in the Philippines since 1966. *Crop Sci.* 40:307–314.
- San-oh, Y., Y. Mano, T. Ookawa, and T. Hirasawa. 2004. Comparison of dry matter production and associated characteristics between direct-sown and transplanted rice plants in a submerged paddy field and relations to planting patterns. *Field Crops Res.* 87:43–58.
- Sayre, K.D., S. Rajaram, and R.A. Fischer. 1997. Yield potential progress in short wheats in northwest Mexico. *Crop Sci.* 37:36–42.
- Shearman, V.J., R. Sylvester-Bradley, R.K. Scott, and M.J. Foulkes. 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Sci.* 45:175–185.
- Shimshi, D., and J. Ephrat. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis and yield. *Agron. J.* 67:326–331.
- Sinclair, T.R., and L.C. Purcell. 2005. Is a physiological perspective relevant in a “genocentric” age? *J. Exp. Bot.* 56:2777–2782.
- Spiertz, J.H.J., P.C. Struik, and H.H. van Laar (ed.). 2007. *Scale and complexity in plant systems research: Gene-plant-crop relations.* Springer, New York, NY.
- Sylvester-Bradley, R., J. Foulkes, and M. Reynolds. 2005. Future wheat yields: Evidence, theory and conjecture. p. 233–260. *In* R. Sylvester-Bradley and J. Wiseman (ed.) *Yields of farmed species.* Nottingham Univ. Press, Nottingham, UK.
- Takai, T., S. Matsuura, T. Nishio, A. Ohsumi, T. Shiraiwa, and T. Horie. 2006. Rice yield potential is closely related to crop growth rate during late reproductive period. *Field Crops Res.* 96:328–335.
- Taylaran, R.D., S. Ozawa, N. Miyamoto, T. Ookawa, T. Moto-bayashi, and T. Hirasawa. 2009. Performance of a high-yielding modern rice cultivar Takanari and several old and new cultivars grown with and without chemical fertilizer in a submerged paddy field. *Plant Prod. Sci.* 12:365–380.
- Tollenaar, M., and E.A. Lee. 2006. Dissection of physiological processes underlying grain yield in maize by examining genetic improvement and heterosis. *Maydica* 51:399–408.
- Tubiello, F.N., J.S. Amthor, K.J. Boote, M. Donatelli, W. Easterling, G. Fischer, R.M. Gifford, M. Howden, J. Reilly, and C. Rosenzweig. 2007. Crop response to elevated CO₂ and world food supply. *Eur. J. Agron.* 26:215–223.
- Tweeten, L., and S.R. Thompson. 2008. Long-term agricultural output supply-demand balance and real farm and food prices. Working Paper AEDE-WP 0044-08, Ohio State University, Columbus, OH.
- van Ittersum, M.K., and R. Rabbinge. 1997. Concepts in production ecology for analysis and quantification of agricultural input-output combinations. *Field Crops Res.* 52:197–208.
- Watanabe, N., J.R. Evans, and W.S. Chow. 1994. Changes in the photosynthetic properties of Australian wheat cultivars over the last century. *Aust. J. Plant Physiol.* 21:169–183.
- Yang, H.S., A. Dobermann, J.L. Lindquist, D.T. Walters, T.J. Arkebauer, and K.G. Cassman. 2004. Hybrid-Maize – a maize simulation model that combines two crop modeling approaches. *Field Crops Res.* 87:131–154.
- Yang, W., S. Peng, R.C. Laza, R.M. Visperas, and M.L. Dionisio-Sese. 2007. Grain yield and yield attributes of new plant type and hybrid rice. *Crop Sci.* 47:1393–1400.
- Yoshinaga, S., Y. Arai (San-oh), T. Ishimaru, A. Ohsumi and M. Kondo. 2009. Characteristics of dry matter production and grain filling in new rice cultivar “Momiroman” suitable for grain feed use. *Japan. J. Crop Sci.* 227: 212–213 (in Japanese).
- Zhang, Q. 2009. Strategies for developing super green rice. *Proc. Natl. Acad. Sci. USA* 104:16402–16409.
- Zhang, Y., Q. Tang, Y. Zou, D. Li, J. Qin, S. Yang, L. Chen, B. Xia, and S. Peng. 2009. Yield potential and radiation use efficiency of “super” hybrid rice grown under subtropical conditions. *Field Crops Res.* 114:91–98.
- Zhu, X.-G., S.P. Long, and D.R. Ort. 2008. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Curr. Opin. Biotechnol.* 19:153–159.
- Ziska, L.H. 2008. Three-year field evaluation of early and late 20th century spring wheat cultivars to projected increases in atmospheric carbon dioxide. *Field Crops Res.* 108:54–59.