

# Can Changes in Canopy and/or Root System Architecture Explain Historical Maize Yield Trends in the U.S. Corn Belt?

Graeme L. Hammer,\* Zhanshan Dong, Greg McLean, Al Doherty, Carlos Messina, Jeff Schussler, Chris Zinselmeier, Steve Paszkiewicz, and Mark Cooper

## ABSTRACT

Continuous increase in the yield of maize (*Zea mays* L.) in the U.S. Corn Belt has involved an interaction with plant density. A number of contributing traits and mechanisms have been suggested. In this study we used a modeling approach to examine whether changes in canopy and/or root system architecture might explain the observed trends. A maize crop model was generalized so that changes in canopy and root system architecture could be examined. A layered, diurnal canopy photosynthesis model was introduced to predict consequences of change in canopy architecture. A two-dimensional root exploration model was introduced to predict consequences of change in root system architecture. Field experiments were conducted to derive model parameters for the base hybrid (Pioneer 3394). Simulation studies for various canopy and root system architectures were undertaken for a range of sites, soils, and densities. Simulated responses to density compared well with those found in field experiments. The analysis indicated that (i) change in root system architecture and water capture had a direct effect on biomass accumulation and historical yield trends; and (ii) change in canopy architecture had little direct effect but likely had important indirect effects via leaf area retention and partitioning of carbohydrate to the ear. The study provided plausible explanations and identified testable hypotheses for future research and crop improvement effort.

G.L. Hammer, The University of Queensland, School of Land, Crop, and Food Sciences, Agricultural Production Systems Research Unit (APSRU), Brisbane, QLD 4072, Australia; Z. Dong, C. Messina, J. Schussler, C. Zinselmeier, S. Paszkiewicz, and M. Cooper, Pioneer Hi-Bred International, Johnston, IA 50131-0552; G. McLean and A. Doherty, Dep. of Primary Industries and Fisheries, APSRU, Toowoomba, QLD 4350, Australia. C. Zinselmeier, current address: Syngenta, Slater, IA 50244. Received 17 Mar. 2008. \*Corresponding author (g.hammer@uq.edu.au).

**Abbreviations:** ASI, anthesis–silking interval; EFV, extraction front velocity; LAI, leaf area index.

CONTINUOUS INCREASE in the yield of maize (*Zea mays* L.) in the U.S. Corn Belt over the past 70+ years has been demonstrated in a series of field studies that contrast successful hybrids released by Pioneer Hi-Bred International since 1930—the so-called “ERA hybrid studies” (Duvick, 1977, 1984, 1992; Duvick et al., 2004). A key feature of the yield advance has been the interaction with plant density: yield has increased more rapidly at high density (Fig. 1a). Reworking of these data (Fig. 1b) indicates that for hybrids released up to the 1960s yield increased up to a density of only about 3 plants  $m^{-2}$ , whereas the (higher) yield plateau for hybrids released in the 2000s would not be reached until a density of about 5 to 6 plants  $m^{-2}$ .

Associated change in a number of traits and underlying physiological determinants has been observed. Duvick et al. (2004) reported that the yield advance was associated with increase in ears per 100 plants, leaf angle score, and stay-green score, and decrease in anthesis–silking interval (ASI) and tassel size scores. Importantly though, the yield increase has not been associated

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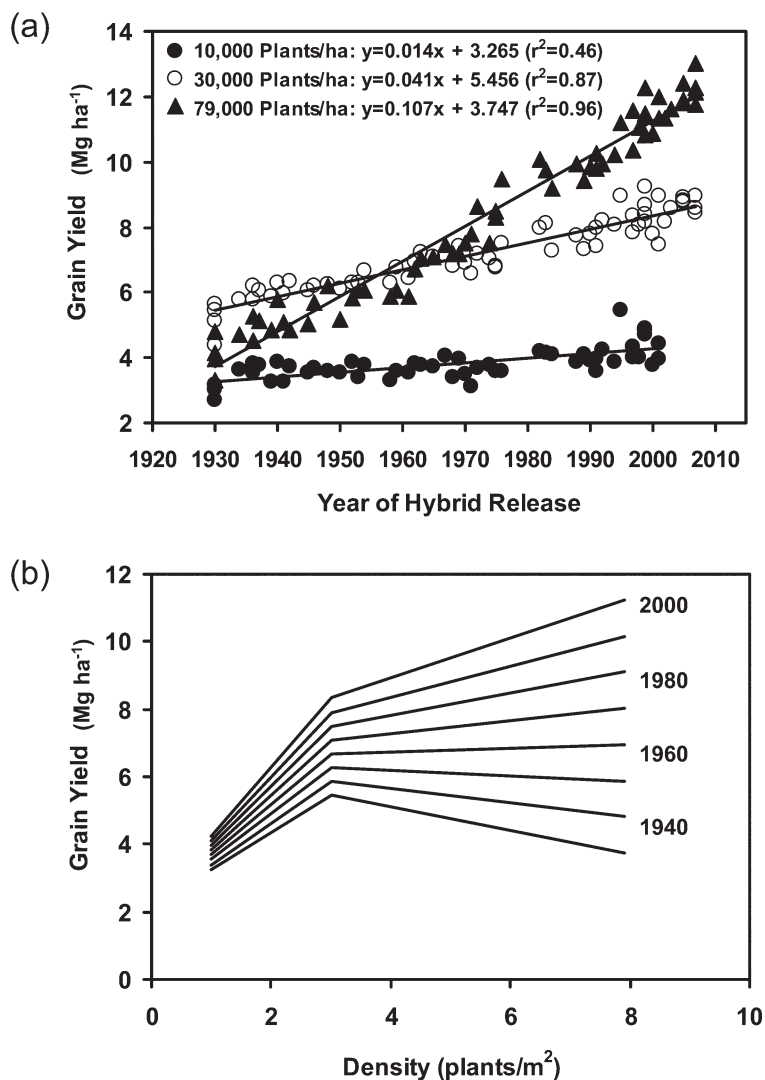


Figure 1. (a) Grain yield per hybrid regressed (base year = 1930) on year of hybrid release based on trials grown from 1990 to 2007 at each of three plant densities (updated from Duvick et al., 2004). (b) Idealized response of grain yield to planting density for hybrids differing in year of release (yield levels calculated from regressions in [a]; note that only three densities are used in deriving the responses, so they are indicative only).

with a change in maximum harvest index (Duvick et al., 2004; Tollenaar and Lee, 2006). Increase in total biomass accumulated via sustained photosynthesis during grain-filling and increased partitioning to the kernels during the known sensitive period for kernel number determination around silking and early ear growth (Andrade et al., 1993, 1999; Otegui and Bonhomme, 1998) have been implicated as the major physiological determinants of the yield increase (Tollenaar and Lee, 2006). In the ERA hybrid studies the partitioning effect is reflected in increased kernel number per unit area via reduced barrenness (i.e., increased ears per 100 plants) rather than by increased kernel number per ear (Duvick et al., 2004).

A similar partitioning effect has been related to genetic gains in maize yield for a range of water-limited conditions (Campos et al., 2006). When a subset of the

ERA hybrids was subjected to targeted water stress conditions invoked from before flowering to late grain filling, positive genetic gains for yield were observed. The yield gains under stress at flowering were associated with increased kernels per ear and reduced ASI and barrenness. So, in this case, yield advance was also underpinned by increased kernel number per unit area as in the ERA hybrid studies. However, changes in kernel number per ear also contributed here. The association with ASI is consistent with it being a reporter trait for ear and plant growth rates during the flowering period (Edmeades et al., 1993, 2000; Vega et al., 2001). Silking dynamics and kernel set have been related to ear growth rate, which can be influenced by both plant growth rate and assimilate partitioning to the ear (Echarte et al., 2004; Campos et al., 2004; Borrás et al., 2007).

Plant growth rate is determined by the ability to capture resources and convert them to biomass. In the absence of nutrient and pest limitations, and assuming stable  $\text{CO}_2$  concentration, the key varying environmental resources to capture and convert are radiation and water. On any given day, the amount of radiation intercepted and its efficiency of conversion depend on leaf attributes and the nature of the crop canopy. Erect leaf angle can increase crop growth rate and radiation use efficiency by distributing light more effectively through canopies (Duncan et al., 1967). The effect is most pronounced when the canopy has reached a high leaf area index (LAI). There are known genomic regions controlling leaf angle in maize (Mickelson et al., 2002) and evidence suggesting that differences in photomorphogenic regulation of auricle growth generate differing leaf angles (Fellner et al., 2003). There is also evidence indicating increased radiation use efficiency in modern maize hybrids (Lindquist et al., 2005; Tollenaar and Aguilera, 1992). However, whether changes in leaf erectness contribute significantly to the increased biomass accumulation of modern maize hybrids remains uncertain (Luque et al., 2006).

The potential amount of water captured by a crop will influence plant growth rate when water becomes limiting. In such situations, given any specific soil condition, crop water uptake depends on the nature of each plant's root system and its spatial arrangement. Campos et al. (2004) observed differences in water extraction between old and modern maize hybrids. During a period of water limitation, the old hybrid extracted more water from shallow soil depth, whereas the new hybrid appeared to be more effective at depth. There are known genomic regions affecting root architecture in maize (Giuliani et al., 2005). Giuliani et al. (2005) hypothesized that regulation of root angle might account for their observation that the lines with a

more horizontal root system, and thus a greater concentration of roots in shallow soil layers, had increased leaf abscisic acid concentration causing reduced stomatal conductance. Studies on root architecture in wheat (*Triticum aestivum* L.) (Manschadi et al., 2006) have also indicated a relationship between encompassing seminal root angle, root system architecture, and consequent water extraction from the soil. Root angle is also known as the gravitropic set point angle (Firn and Digby, 1997), and genetic variation in the gravitropic set point angle of lateral roots has been found among *Arabidopsis* mutants (Mullen and Hangarter, 2003). While these observations on root angle and root system architecture are consistent with the findings on water extraction reported by Campos et al. (2004), whether this effect contributes significantly to the increased biomass accumulation of modern maize hybrids remains unknown.

In this study we adopted a systems modeling approach to examine the question of whether changes in canopy and/or root system architecture might explain the observed maize yield trends in the U.S. Corn Belt. We used average leaf and root angles as quantitative indicators of canopy and root system architecture and modified the APSIM crop modeling platform (Keating et al., 2003) to incorporate their potential effects on plant growth rate via effects on light and water capture. We then generated a hypothetical set of genotypes varying in leaf and root angle and simulated the emergent consequences on yield response to planting density for representative sites in the U.S. Corn Belt. The general benefits and pitfalls of employing such a systems modeling approach to explore consequences of trait and management variation in evidence-based hypothetical situations are discussed by Hammer et al. (2002) and several examples are presented. Recently, Sinclair et al. (2005), Manschadi et al. (2006), and Lyon et al. (2003) have used this approach in studies on crop adaptation to water-limited environments associated with manipulating maximum transpiration rate in sorghum [*Sorghum bicolor* (L.) Moench], root architectural traits in wheat, and plant density in maize, respectively.

## MATERIALS AND METHODS

### Maize Model Description

The maize module of the APSIM cropping system simulation platform (Keating et al., 2003) was adapted for this study. A general description and validation of the model is given by Robertson et al. (undated). The model is based on enhancements to CERES-Maize (Jones and Kiniry, 1986; Carberry and Abrecht, 1991) combined with modifications to simulate biomass accumulation based on resource capture concepts (Monteith, 1986). Biomass increment depends on whether the crop is limited more by light or water and is calculated using the switching approach implemented by Chapman et al. (1993). In light-limited situations, crop growth is dependent on radiation intercepted and radiation use efficiency, and the demand for water as transpiration is determined from the ratio of crop growth and transpiration

efficiency, with the latter adjusted for the effect of daytime vapor pressure deficit. Water-limited situations occur when the potential supply of water from root uptake cannot meet this transpiration demand. In that situation, crop growth is calculated as the product of the transpiration supply and transpiration efficiency. The supply of water from the soil depends on the depth of the root system, which is derived using a constant extraction front velocity (EFV), and the amount of water that can be extracted from each occupied layer. The extraction potential is determined via an exponential decay equation (Passioura, 1983), which depends on the moisture content of the layer and the crop soil water extraction coefficient (kl) that quantifies its relevant soil-root system attributes. This approach, first outlined by Monteith (1986), has been applied successfully in a number of species (Meinke et al., 1993; Robertson et al., 1993; Thomas et al., 1995; Dardanelli et al., 1997).

For this study, coefficients suitable for the Pioneer maize hybrid 3394 were determined either from relevant literature or by fitting to data from experiments (Campos et al., 2004; this study) that included this hybrid as one of the modern contrasts. Thermal time from emergence to floral initiation was set at 265 degree days, leaf initiation rate at 23.2 degree days, and leaf appearance rates at 65 and 30 degree days for leaves appearing before and after leaf number 11, respectively. Cardinal temperatures for the calculation of thermal time were not changed from those used in the base version of the model. Radiation use efficiency was increased to  $1.85 \text{ g m}^{-2} \text{ MJ}^{-1}$  on a total radiation basis based on findings of Lindquist et al. (2005) for modern corn hybrids. Coefficients defining the leaf size distribution were derived for this hybrid from experiments conducted during this study (see below). The EFV was set at  $2.5 \text{ cm d}^{-1}$  up to flowering and kl values ranged from 0.08 in the surface layers to 0.03 below 150-cm soil depth. These values are consistent with those found for maize by Dardanelli et al. (1997) who observed maize rooting depth of greater than 2 m.

### Quantifying Leaf Size Distribution and Density Effects on Leaf Area

Field experiments to measure growth and development responses to density for a range of maize hybrids were conducted at the Pioneer Johnston Research Farm, Johnston, IA ( $41^{\circ}40' \text{ N}$ ,  $93^{\circ}42' \text{ W}$ ) over a number of years. Hybrid 3394 was included in experiments in 1997, 1999, and 2004. The soil type at Johnston Research Farm is Wiota silty clay loam (fine-silty, mixed, superactive, mesic Pachic Argiudoll). For all experiments, the row spacing was 76 cm and planting depth was 5 cm. Experiments were planted on 6 May 1997, 3 May 1999, and 7 May 2004. The accumulated rainfall from May to October was 381, 606, and 599 mm for 1997, 1999, and 2004, respectively. Levels of plant density were 1.0 and 8.1 plants  $\text{m}^{-2}$  for the experiments in 1997 and 1999, and 1.0, 7.4, and 10.3 plants  $\text{m}^{-2}$  for the experiment in 2004. Leaf length and width of all fully expanded leaves of tagged plants were measured before flowering in the 2004 experiment. Total plant leaf area of selected representative plants at various V stages was measured destructively using a LI-3000 leaf area meter (LiCor Inc., Lincoln, NE). Samples of leaf blade and stem at various V-stages were dried to constant weight at  $70^{\circ}\text{C}$  and dry weights were recorded in all three experiments.

Data from these experiments was used to quantify the potential leaf size distribution for hybrid 3394 and any responses in partitioning and specific leaf area associated with density. Available data on LAI over the crop cycle were then used to test the capacity of the model to regenerate leaf area responses to density. The bell-shaped curve for individual leaf area ( $LA_N$ ) against leaf number ( $N$ ) was defined by the equation (Dwyer and Stewart, 1986; Birch et al., 1998):

$$LA_N = LA_{\max} \left\{ \exp \left[ a(N - x_o)^2 + b(N - x_o)^3 \right] \right\} \quad [1]$$

where  $LA_{\max}$  is the area of the largest leaf,  $x_o$  is the position (leaf number) of the largest leaf, and  $a$  and  $b$  are fitted coefficients.

The curve was fitted using standard iterative nonlinear curve fitting techniques that minimize residual sums of squares.

## Model Adaptations for Canopy and Root System Architecture Simulation

To simulate effects of variation in canopy architecture a layered canopy photosynthesis model (Hammer and Wright, 1994; Spitters, 1986) was introduced and crop growth calculated throughout the diurnal cycle. Briefly, the canopy model partitions leaf area in each canopy layer into sunlit and shaded fractions, determines direct and diffuse light extinction through the canopy and thus incident light flux for each leaf fraction, calculates photosynthesis from the known light response curve, makes allowance for respiration and biochemical conversion efficiencies, and integrates over the canopy. The model allows for variation in incident direct and diffuse radiation associated with latitude, time of year, time of day, and atmospheric condition, based on the degree of transmission of extraterrestrial radiation. The diurnal cycle of radiation input is estimated from readily available daily totals and calculated daylength. For maize, maximum photosynthetic rate was set at  $2.07 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and the overall conversion efficiency at  $0.41 \text{ mg}$  of biomass per milligram of  $\text{CO}_2$  as found by Massignam (2003) and Sinclair and Horie (1989).

Average canopy leaf inclination relative to the horizontal ( $\alpha$ ) was used as an indicator of leaf erectness and overall canopy architecture. In the canopy model, the proportion of radiation intercepted ( $F$ ) by a layer was calculated via the standard negative exponential equation on LAI, which involves the canopy extinction coefficient,  $k$ . The value of  $k$  at any time of day depends on the sun angle ( $\beta$ ) and the shadow projection coefficient ( $G$ ) at that time, which is a function of  $\alpha$  and  $\beta$  (Duncan et al., 1967) such that

$$F = 1 - \exp \left[ (-k) \text{LAI} \right] \quad [2]$$

and

$$k = G(\alpha, \beta) / \sin(\beta) \quad [3]$$

if a spherical leaf angle distribution with randomly distributed leaves is assumed. To consider a broad range of  $\alpha$  it was necessary to incorporate the equations for calculating  $G(\alpha, \beta)$  presented by Duncan et al. (1967). In other studies, where broad ranges of leaf angle are not considered, a value of 0.5 has been assumed for  $G$ , as that approximates the solution to  $G(\alpha, \beta)$  for a considerable range of  $\alpha$  and  $\beta$  (Sinclair and Horie 1989; McCree, 1988). Spitters (1986) showed that canopy photosynthesis models of the type implemented here could reproduce diurnal patterns of assimilation accurately and that only small errors resulted from use of

average leaf angle. This was reinforced by Massignam (2003) who generated accurate estimates of biomass accumulation over the crop cycle in maize using this approach.

A simulation of diurnal patterns of crop growth rate for a range of canopy LAI and average angle of leaf inclination was undertaken as a qualitative test of the revised canopy photosynthesis model. Results were compared with those reported by Duncan et al. (1967) who found increasing effect of leaf erectness on crop growth around solar noon as LAI increased. This trend was faithfully reproduced using the canopy photosynthesis model described above (Fig. 2). At leaf angle of  $40^\circ$  there was little increase in canopy photosynthesis around noon for increase in LAI beyond 4. However, with more erect average leaf angle ( $80^\circ$ ), growth rate at that time of day continued to increase with LAI. The simulations also show that the model captures the interactions between canopy radiation interception and use efficiency. At low LAI (L2), growth rate is greater with less erect leaves ( $40^\circ$ ) because the greater radiation interception has significant impact in that situation. However, at high LAI (L8) when interception is near complete, growth is greater with erect leaves because radiation is distributed better throughout the canopy resulting in higher use efficiency. The depression in growth rate around noon for L2 and L4 with erect leaves (Fig. 2b) is a consequence of the trade-off between these two factors that depends on the extent of canopy cover and the leaf and sun angles. Around solar noon in this case, the reduction in radiation interception for L2 and L4 more than offset the improved distribution of radiation through the erect-leaved canopy.

Average root system declination relative to the horizontal ( $\gamma$ ) was used as an indicator of overall root system architecture. The angle was used to calculate the shape of the space occupied by roots in a cross-sectional plane perpendicular to the crop row orientation (Fig. 3). To simulate the dynamics of soil water extraction observed in wide, skip row systems in sorghum (Broad and Hammer, 2004), McLean et al. (2003) implemented a two-dimensional model for root exploration with the extraction front progressing at the standard velocity (EFV) in all directions into the soil. This resulted in an expanding semicircular occupancy pattern for the root system (Fig. 3a;  $\gamma = 45^\circ$ ). For calculating potential water extraction, each soil layer was weighted by the fraction of the area of that layer occupied by the root system at that time. Although more complex root system models have been developed (Wu et al., 2005), this parsimonious approach adequately predicted the dynamics of water use, crop growth, and yield for a range of wide row configuration systems and environments (Whish et al., 2005). The approach has been generalized here by assuming root systems will expand to occupy the same area but not necessarily with the same shape. This has been implemented by forming ellipses of equivalent area to that of the standard circular occupancy pattern, but with dimensions of the axes dependent on the magnitude of  $\gamma$ . For  $45^\circ < \gamma < 90^\circ$  this implies a deeper but narrower root system than the standard at any given time (Fig. 3b). The circular form becomes one instance of this general form at  $\gamma = 45^\circ$ . There is some evidence to support enhanced EFV and water extraction from depth in modern maize hybrids over older hybrids from further analysis (J.R. Schussler, unpublished data, 2003) of experimental data on the ERA hybrid studies reported by Campos et al. (2004).

## Simulation of Canopy and Root System Architecture Effects

To examine canopy and root system architecture effects, a preliminary set of long-term simulations was conducted for maize crops planted at a range of densities at Johnston. A soil profile with water-holding capacity of 400 mm to 250-cm depth, which had 120 mm available water at sowing (Table 1), was assumed. A depth of 250 cm was used to allow for expression of potential differences in root depth associated with root angle. Sowing was simulated on 8 May using these initial conditions for each year of the 50-yr climate record (1956–2005). Conditions other than water availability (i.e., nutrition, pests, and weeds) were assumed to be nonlimiting. A hypothetical set of hybrids varying in average leaf and root angle was simulated. Average leaf angle ( $\alpha$ ) was varied from 20° (planophile) to 80° (erectophile) in 10° increments. This range extends to average leaf angles well beyond those normally associated with maize canopies (i.e., 40–70°). Average root angle ( $\gamma$ ) was varied from 45° (circular) to 70° (elliptical) in 5° increments. Density treatments simulated ranged from 1 to 12 plants m<sup>-2</sup> with increment of 1 plant m<sup>-2</sup>. The simulated yield responses to density were compared for this set of hypothetical hybrids.

A subset of the combinations of leaf angle and root angle used in these simulations was then employed in simulations at three representative locations throughout the Corn Belt to assess the degree of applicability of the results found for the preliminary study at Johnston. Starting conditions relevant to those locations were determined (Table 1). Three soils reflecting the known range in total available water-holding capacity in the U.S. Corn Belt (270, 330, and 400 mm to 250-cm depth) were used at each location. The water-holding capacity values were based on the geographic analysis of Corn Belt soils presented by Löffler et al. (2005). The soil water available at sowing was estimated from a 50-yr simulation of soil water accumulation through the fallow period (October–May) assuming a near dry profile at the beginning of the fallow. It was assumed that the corn crop was planted 8 May each year of the 50-yr simulation with the same starting soil condition.

An extra set of simulations was conducted at Johnston to examine the effect of varying average leaf angle in the canopy throughout the crop cycle as is commonly observed and is likely associated with shade avoidance responses (Smith and Whitelam, 1997; Ballaré et al., 1997; Maddonni et al., 2002). Maddonni et al. (2001) reported promotion of erectophile leaf habit with increase in plant population density in maize. This effect was implemented in the simulation by assuming planophile leaves until light interception reached a threshold level and then increasing the degree of erectness as light interception, and hence competition for light, increased. Three threshold levels and two levels of sensitivity of response were invoked (Fig. 4) and ranged within extremes from an early initiated and rapid shift from planophile to erectophile to a late initiated, slow shift.

## Field Experiments and Model Sensibility Testing

Yield-density response field experiments have been conducted over a number of years for a range of hybrids by Pioneer. Yield response to density measured in these experiments was contrasted with simulation results as a qualitative sensibility test of the

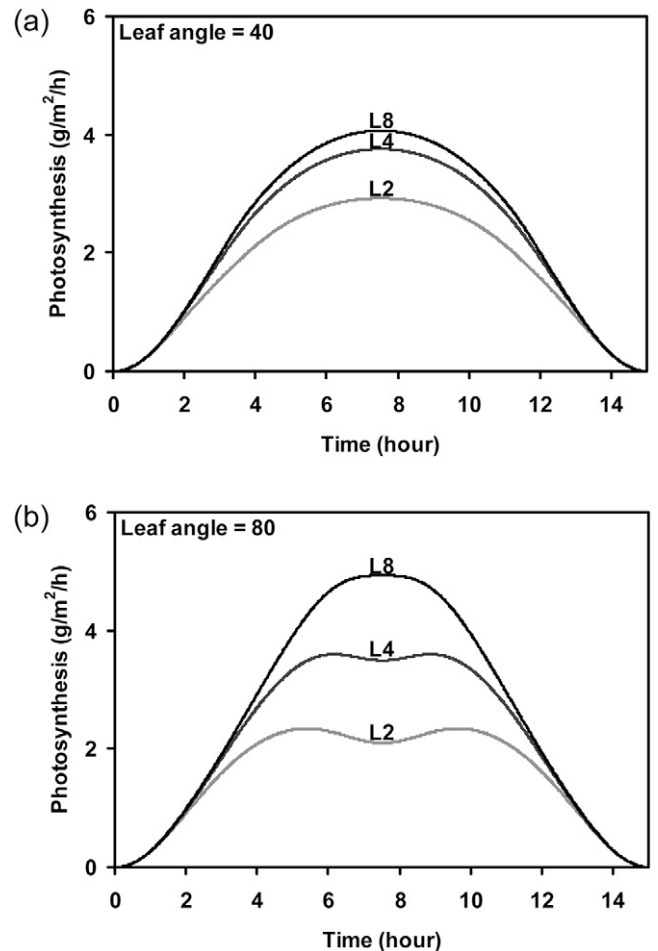


Figure 2. Simulated diurnal time course of net canopy photosynthesis for a maize crop having leaf area index (L) of 2, 4, or 8 and average leaf inclination from the horizontal of (a) 40° or (b) 80°. Simulation conducted for Day 180 of the year at Johnston, IA (41°40' N lat).

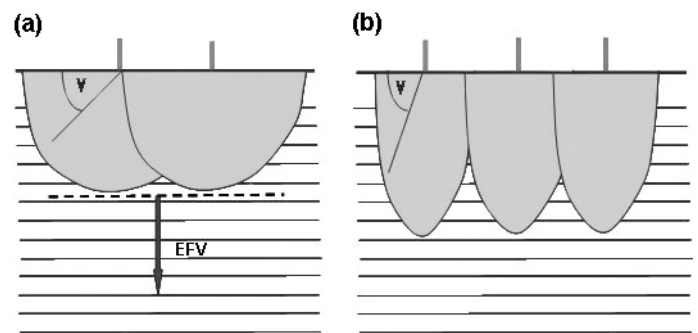


Figure 3. Schematic of procedure for simulating root system occupancy of soil profile layers dependent on average angle of root declination from horizontal  $\gamma$ . (a) Reference circular system where occupancy radiates at standard extraction front velocity (EFV);  $\gamma = 45^\circ$ . (b) Elliptical generalization based on assumption of equivalent occupancy area to reference circular system; example shown is for  $45^\circ < \gamma < 90^\circ$ .

simulated responses. Without detailed soil characterization at the experimental sites it is not possible to undertake more quantitative comparisons. Experiments were conducted at five and six locations in 2001 and 2003, respectively. Details of locations, soil type, rainfall amounts, and plant densities are given in Table 2. The

**Table 1. Representative locations throughout the Corn Belt, their average seasonal rainfall, and associated soil properties used in the simulation studies. The high, medium, and low water-holding capacity soils (HW, MW, and LW, respectively) have an available water range of about 16, 13, and 10%, respectively, giving available water capacity of 400, 330, and 270 mm, respectively, for a soil depth of 250 cm. The soil water available at sowing (median, wettest) was estimated from a 50-yr simulation of soil water accumulation through the fallow period (October–May) assuming a near dry profile at the beginning of the fallow.**

Location	Lat, long	Avg. rainfall (Oct–May)	Soil type	Soil water at sowing (median, wettest)
		mm		mm
Johnston, IA	41°40' N, 93°42' W	296.1	HW	120, 280
	41°40' N, 93°42' W	296.1	MW	120, 280
	41°40' N, 93°42' W	296.1	LW	120, 270
York, NE	40°52' N, 97°35' W	255.1	HW	100, 230
	40°52' N, 97°35' W	255.1	MW	100, 230
	40°52' N, 97°35' W	255.1	LW	100, 230
Princeton, IL	41°32' N, 89°35' W	407.5	HW	180, 280
	41°32' N, 89°35' W	407.5	MW	180, 280
	41°32' N, 89°35' W	407.5	LW	180, 270

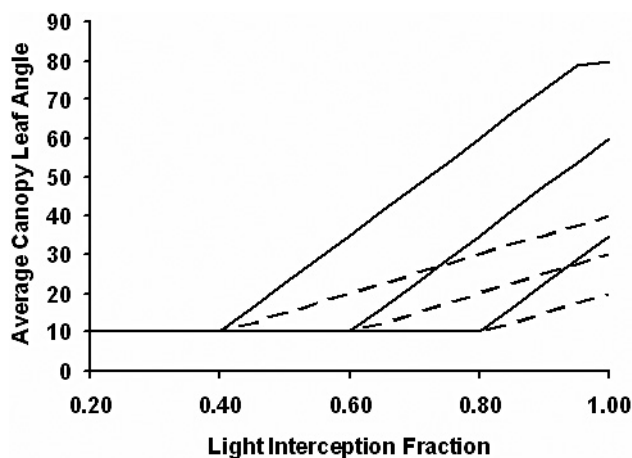


Figure 4. Assumed responsiveness of average canopy leaf angle relative to the horizontal ( $\alpha$ ) to canopy light interception for the additional simulation study at Johnston. Three levels of threshold light interception fraction (0.4, early; 0.6, mid; 0.8, late) required to trigger responsiveness in average leaf angle were considered. For each threshold level, two degrees of sensitivity of response [high-rapid (solid lines) and low-slow (broken lines)] were considered.

experimental design for each site-year was a randomized complete block in a split-plot arrangement with four replicates. Plant densities were the main plots and hybrids the subplots. Subplots consisted of four 0.76-m rows of 4.55-m length. The central two rows were mechanically harvested and grain weight and grain moisture were determined by load cell and capacitance moisture meter, respectively. Grain yield was adjusted to 15% moisture content.

## RESULTS

### Simulating Density Effects on Canopy Development

The relationship between individual leaf size and leaf number fitted experimental data well (Fig. 5). A reduction

in leaf size at high density was evident after about leaf number 10. This was most likely caused by reduction in assimilate availability per plant for the high density treatments. This competition effect is indicated by the significant increases in both SLA and biomass partitioning to leaves at high density (Table 3). Although such changes would tend to maintain leaf size at high density, they cannot fully compensate for the reduced assimilate availability so that leaf size is reduced. The competition effect on SLA is captured in the model as it is calculated as a consequence of temperature-regulated potential leaf area growth and biomass allocation to leaves, and it can move between specified upper and lower boundary values. However, while partitioning to leaf varies with progress in development through the vegetative phase in the model, it is not affected by the degree of competition. Hence, the partitioning function was modified slightly to increase potential allocation of biomass to leaf, especially late in the vegetative stage. This enabled credible simulation of leaf area dynamics for a wide range of density (Fig. 6).

### Effects of Variation in Canopy Architecture

There was considerable year-to-year variability in the simulated yield response to density in the preliminary long term simulations conducted at Johnston (Fig. 7). In the best yielding years ( $\sim 16 \text{ Mg ha}^{-1}$ ) yield increased with density up to about 6 plants  $\text{m}^{-2}$ . However, in median-yield years ( $\sim 10 \text{ Mg ha}^{-1}$ ) yield reached a plateau at 4 to 5 plants  $\text{m}^{-2}$  and in low-yielding years, yield mostly peaked at even lower density (3–4 plants  $\text{m}^{-2}$ ) and often declined at high density.

When change in canopy architecture and leaf erectness was simulated by varying average leaf angle, no differences in yield response to density were predicted (Fig. 8a). This nonresponsiveness was predicted for all soil types and all starting water conditions. There was also no effect on this density response at the median yield level associated with varying responsiveness in leaf angle throughout the crop cycle (data not shown). Only at the higher yield level associated with the best years, was the density response found to be affected by leaf angle responsiveness (Fig. 8b). In this situation, early and rapid onset of transition from a planophile to an erectophile canopy resulted in an extended response to density (up to 8 plants  $\text{m}^{-2}$ ) with slightly higher yields at high density.

There were no differences to these findings for the subset of simulations conducted across sites and soil conditions (data not shown). While the site and soil condition affected the level of simulated yield, the responses to density were similar to those found at Johnston. For a given soil condition, the simulated yield levels were greatest

at Princeton, followed by Johnston, and then York. At a given site, the simulated yield levels aligned closely with the magnitude of stored soil water at sowing. The nature of the yield-density response at each site reflected that found for the differing yield levels at Johnston. However, at Princeton, there was a higher frequency of high yield years and at York there was a higher frequency of low yield years.

### Effects of Variation in Root System Architecture

When change in root system architecture was simulated by varying average root angle, significant shifts in median yield response to density were predicted but only for situations where the profile was wettest at sowing (Fig. 9a). There was no effect of root angle on the density response at the median yield level when the soil profiles were recharged only to the median level at sowing (Fig. 9b). These findings were similar across sites and soil types for similar starting soil conditions (data not shown) with differences among sites reflecting the same patterns as noted above for leaf angle simulations.

### Qualitative Testing of Simulated Responses

The simulated responses of yield to density matched qualitatively those found in the field experiments (Fig. 10). There were no detailed soil data at each experiment to enable more quantitative comparison. However, the simulated data for individual years and the experimental data for specific hybrid treatments in each experiment showed similar density responses. Yield increased with density until the effect was saturated at 5 to 8 plants m<sup>-2</sup> depending on the yield level. Decline in yield at high density was predicted in only few years, but this was consistent with experimental observations over the range of density considered. At higher density, model adaptations to deal with plant barrenness, such as those presented by Ritchie and Alagarwamy (2003), would likely be required.

Change in the response of yield to density with hybrid age in the field experiments reflected simulated differences associated with root system architecture (Fig. 10). Both more recent hybrids in the field experiments and those simulated with more elliptical root systems showed slightly higher yield plateaus and a higher density at which that yield level was reached. This effect is clearer if the median yield values for both sets of data are examined (Fig. 11).

**Table 2. Location, soil and treatment details for the field experiments on yield response to density.**

Year	Location	No. of sites	Lat, long	Avg. rainfall (May–Oct)	Soil type	Density treatments
				mm		plants m <sup>-2</sup>
2001	Marion, IA	1	42°6' N, 91°37' W	632	Silty clay loam	4.4, 6.7, 8.9, 11.1
2001	Woodland, CA	1	38°40' N, 121°46' W	58	Silt loam	4.4, 6.7, 8.9, 11.1
2001	Johnston, IA	2	41°40' N, 93°42' W	596	Wiota silty clay loam	4.4, 6.7, 8.9, 11.1
2001	Macomb, IL	1	40°25' N, 90°29' W	607	Silty clay loam	4.4, 6.7, 8.9, 11.1
2003	Macomb, IL	1	40°9' N, 90°35' W	607	Silty clay loam	2.2, 4.4, 6.7, 8.9, 11.1
2003	Marion, IA	2	42°8' N, 91°35' W	632	Silty clay loam	2.2, 4.4, 6.7, 8.9, 11.1
2003	Johnston, IA	2	41°40' N, 93°42' W	596	Wiota silty clay loam	2.2, 4.4, 6.7, 8.9, 11.1

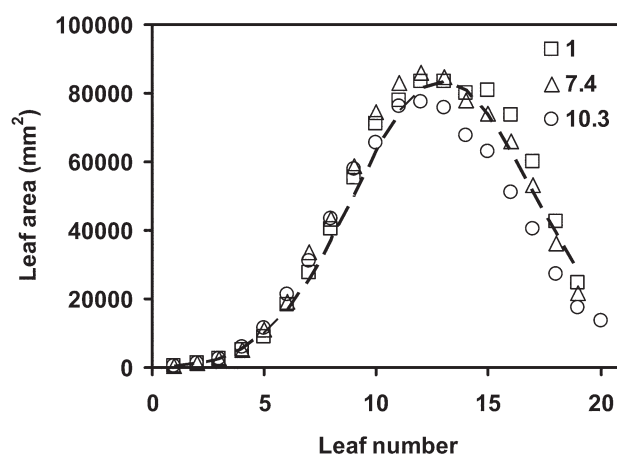


Figure 5. Individual leaf area ( $LA_N$ ) versus leaf number ( $N$ ) for maize hybrid 3394 grown at three population densities (plants m<sup>-2</sup>) at Johnston, IA. The dashed line has been fitted to the low density treatment and is defined by the equation  $LA_N = LA_{max} \{ \exp[a(N - x_0)^2 + b(N - x_0)^3] \}$  where  $LA_{max} = 83,600$  mm<sup>2</sup>,  $a = -0.0314$ ,  $b = 0.000317$ ,  $x_0 = 13.0$ , and  $R^2 = 0.99$ .

**Table 3. Average specific leaf area (SLA) and ratio of leaf to total above-ground biomass (L/TOT ratio) for maize hybrid 3394 grown under low and high density conditions at Johnston, IA. Values are averaged over harvests conducted at 8, 10, 12, and 16 fully expanded leaves. The value in parentheses is the standard error of the corresponding mean.**

Density	SLA	L/TOT ratio
plants m <sup>-2</sup>	cm <sup>2</sup> g <sup>-1</sup>	
Low (1.0)	155 (5)	0.432 (0.027)
High (7.4)	182 (5)	0.479 (0.027)

## DISCUSSION

### The Historical Maize Yield Trend Interaction with Density Is More Likely Related to Change in Root System Architecture than to Change in Canopy Architecture

The simulated change in root architecture generated increased biomass and yield at higher density when stored water was available at depth in the profile at sowing (Fig. 9). This shift in yield response to density was similar to

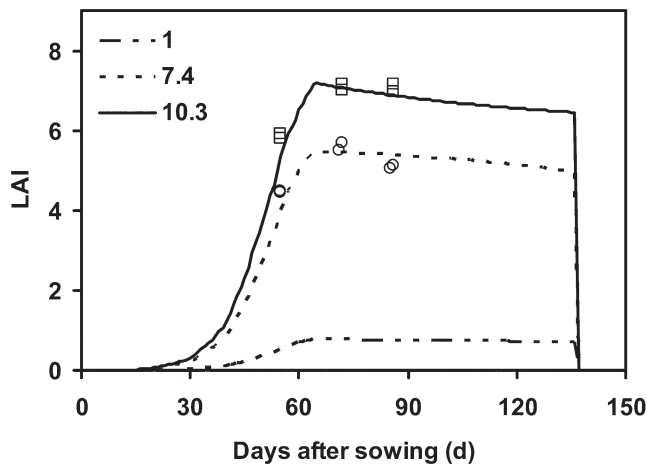


Figure 6. Simulated (continuous lines) and observed (open symbols) leaf area index versus time after sowing for a range of densities (1.0, 7.4, and 10.3 plants  $m^{-2}$ ) for the 2004 experiment at Johnston, IA. Note that observed data were not available for the lowest density treatment.

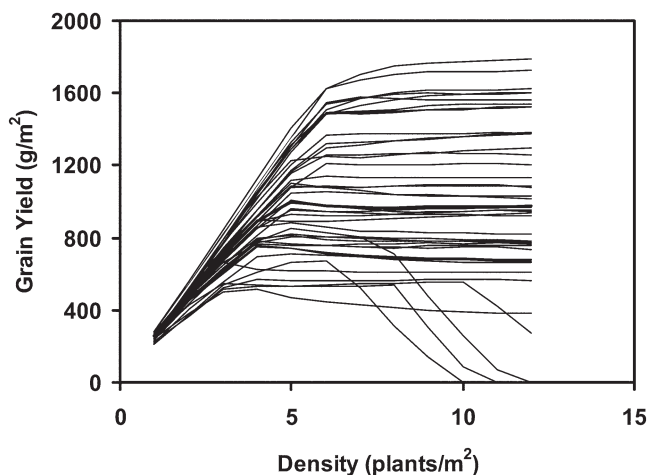


Figure 7. The simulated yield-density response for individual years for the preliminary simulation experiment at Johnston. The simulations shown are for average leaf angle ( $\alpha$ ) of  $50^\circ$  and average root angle ( $\gamma$ ) of  $45^\circ$ .

the more recent changes observed in the ERA and density response field studies (Fig. 1 and 11). Hybrids released after about 1980 showed this higher yield plateau at high density and the increased density required to reach that yield level (from about 5–6 plants  $m^{-2}$ ; Fig. 1b) was the same as that simulated for the specific set of conditions presented (Fig. 11a). In the field studies, the density at which the yield plateau was reached shifted the same amount, but from about 6 to 7 plants  $m^{-2}$ , for the experiments reported (Fig. 11b). These density ranges maximizing grain yield are consistent with similar field studies on Brazilian maize hybrids (Sangoi et al., 2002), where the yield plateau occurred between densities of 5 and 7.5 plants  $m^{-2}$ . Simulated changes in canopy architecture had no similar effects except for the extreme case in very high yielding situations and with changes in average leaf angle through the season (Fig. 8).

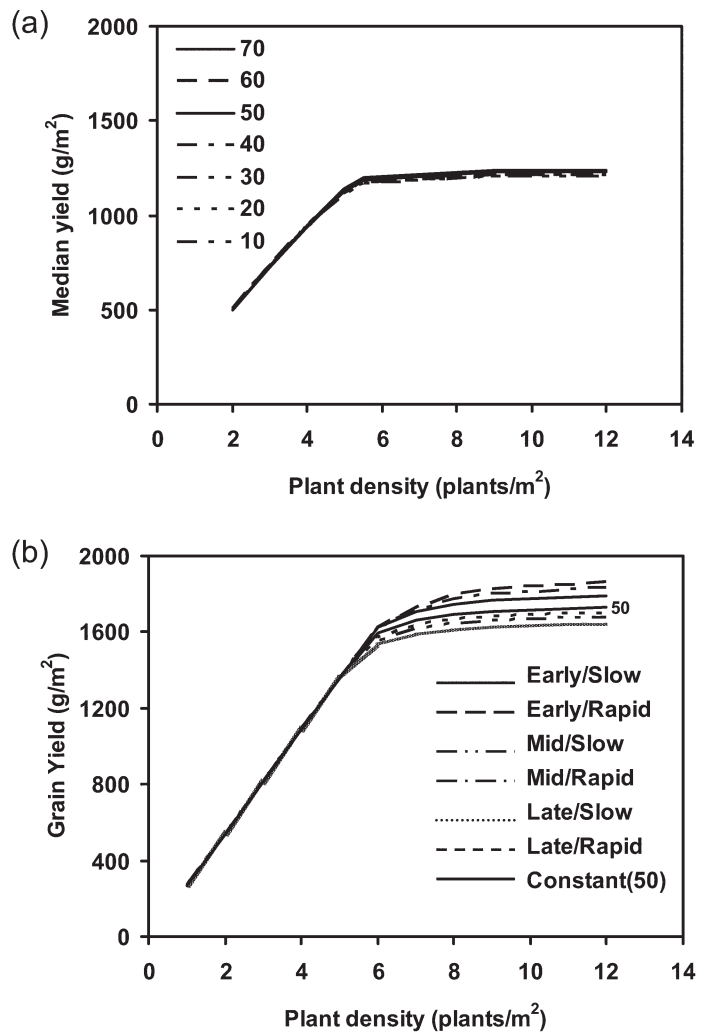


Figure 8. Simulated response to density in maize at Johnston for (a) median yield from a 50-yr simulation for a wide range in average leaf angle, and (b) yield in the highest yielding year for a range of changes in canopy architecture through the crop cycle (see Fig. 3). Simulations shown were conducted with a root angle of  $45^\circ$  for a high water-holding capacity soil with the median level of stored water at sowing (see Table 1).

These results indicated that root system architecture and associated capture of water was more important than canopy architecture and capture of light for increase in biomass and yield at high density. The root system modeling approach used in this study generated narrower and deeper root systems ( $>2$  m) as the root angle increased. Provided there was water available at depth, then the additional potential water use would generate more biomass once surface layers were exhausted. Studies in rice (*Oryza sativa* L.) (Kato et al., 2006) and wheat (Manschadi et al., 2006) have reported a link between root angle and root system architecture, particularly in relation to root exploration and efficacy in water capture at depth. This is supported by studies with detailed root models (Dunbabin, 2007) showing that parameters controlling the efficient distribution of roots through the soil (geotropism index, deflection index, branch angle) were most important for

water uptake. Hence, while the simulated effect here is associated with greater rooting depth, improved extraction capacity from enhanced occupancy of deep soil layers may likewise contribute. This alternative is consistent with observations that root systems of old corn genotypes were already able to explore soils in this region to depths beyond 2 m (Weaver, 1926).

### Access to Stored Soil Water at Depth Is Required if Change in Root System Architecture Is Responsible for the Continuing Maize Yield Trend Interaction with Density

When the median stored soil water predicted at sowing was used in the simulations, change in root angle did not generate any difference in the yield response to density. The profiles associated with the median stored water level were predicted to have little stored water at depth at sowing. Only with a wetter profile, which had been recharged to depth, was the effect generated. The starting soil water was predicted by simulating the soil water balance through the winter fallow, assuming only 10% available water in the profile at the end of the previous crop. This may have been an underestimate of the starting condition given the considerable possibility of late in-crop rainfall in the region. Continuous cropping system simulations that take account of crop rotations (e.g., previous crop of soybeans or corn) are required to generate more accurate estimates of the likely soil water store at sowing. As the APSIM platform has this capability, a more comprehensive simulation study could be executed to address this issue.

The continued increase in maize yield via enhanced biomass production requires increased amounts of water use as transpiration, given that there is little evidence supporting improvement in transpiration efficiency in C4 species (Tanner and Sinclair, 1983; Hammer et al., 1997). How much extra water can be captured? As each additional 1 Mg ha<sup>-1</sup> of grain requires about 2 Mg ha<sup>-1</sup> of aboveground biomass (assuming a harvest index of 0.5), and given the intrinsic transpiration efficiency of maize of 9 Pa (Tanner and Sinclair, 1983), then for an average vapor pressure deficit of 2 kPa, 45 mm additional transpiration is required. Hence the 6 Mg ha<sup>-1</sup> historical yield increase (Fig. 1) indicates that modern corn crops use about 270 mm more water than their early counterparts. Has this increased intensity of resource capture associated with yield advance positioned the corn crop near the limit of water resource availability so that water stress has become more frequent? In addition to better understanding of soil water recharge likelihood, more detailed study of root system attributes and possibilities for capture of water at depth are required to determine whether this remains a viable avenue for further genetic improvement.

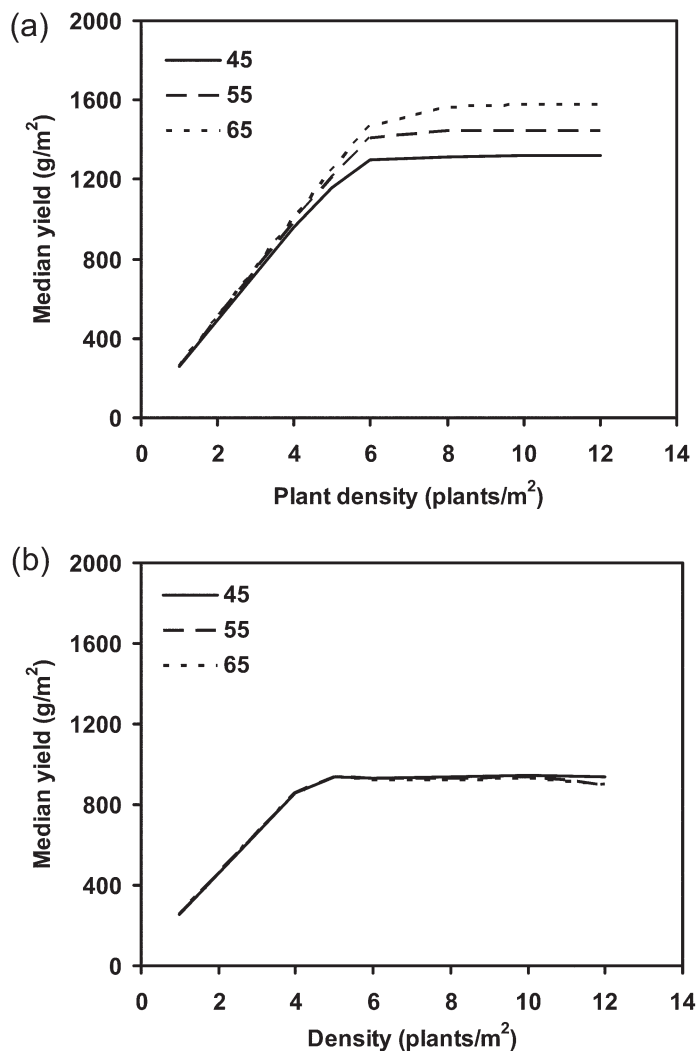


Figure 9. Simulated response to density in maize at Johnston for median yield from a 50-yr simulation for root angles of 45°, 55°, and 65° with (a) the wettest soil profile predicted at sowing, and (b) the median wetness soil profile predicted at sowing. Simulations shown were conducted with a leaf angle of 50° for a medium water-holding capacity soil (see Table 1).

### Canopy Architecture Change May Be Related to Other Critical Factors

Although change in canopy architecture did not generate sufficient effect on biomass accumulation to be significantly associated with change in the yield response to density, it may have had effects in other ways not captured in the modeling. In the canopy photosynthesis model, increased leaf erectness caused a reduction in the canopy light extinction coefficient, leading to greater penetration of light into the canopy, and more uniform distribution of photosynthesis throughout the canopy. Hence, leaves near the ear were contributing a greater proportion of total canopy photosynthesis.

It is plausible that the enhanced photosynthesis at ear height would increase carbohydrate supply to the developing ear, potentially contributing to reduced barrenness and increased kernels per ear. It is well known that the

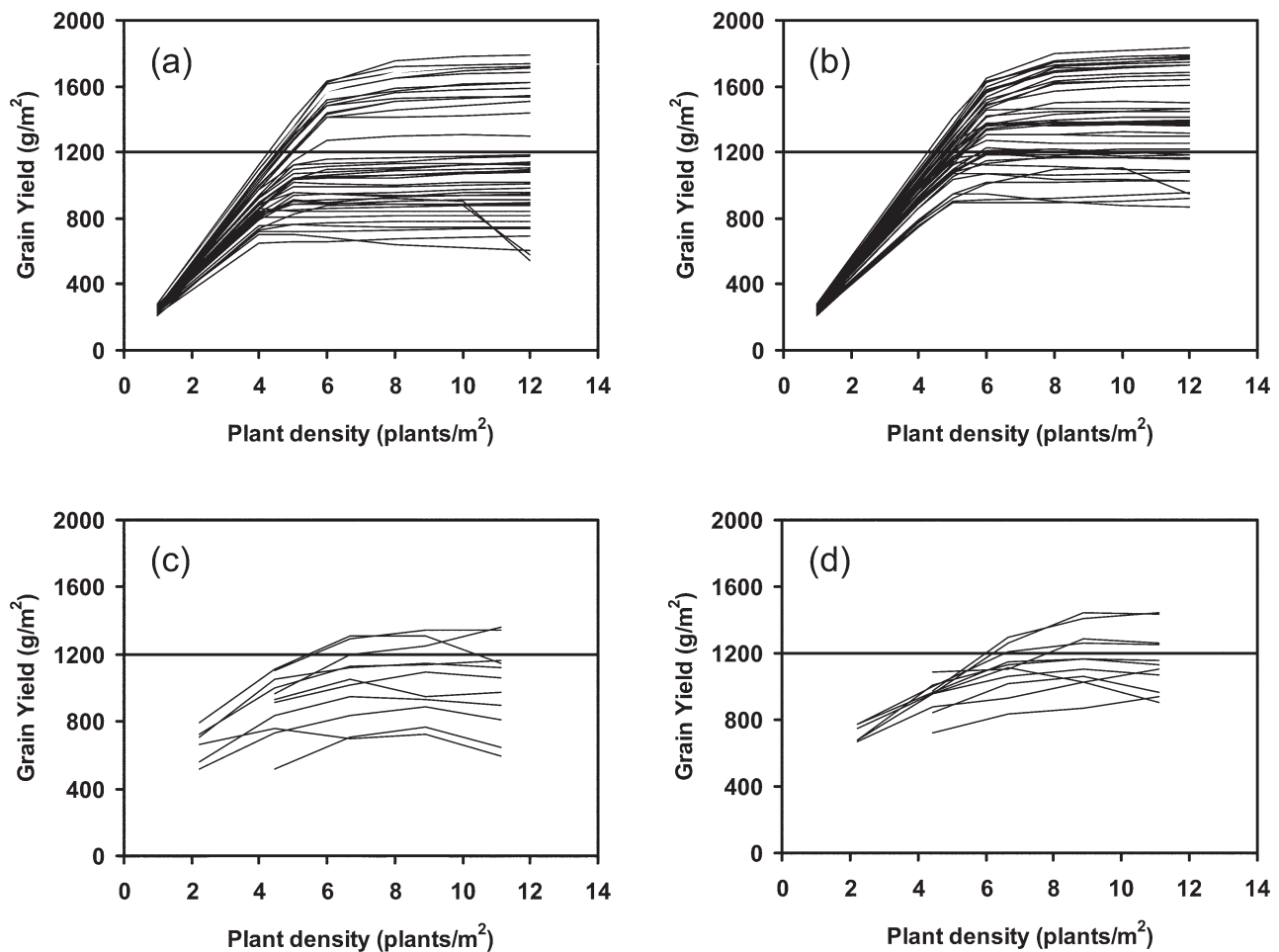


Figure 10. Yield versus plant density for (a, b) simulated and (c, d) experimental results. The simulated yields are for individual years of a 50-yr simulation at Johnston for root angle of either (a) 45° or (b) 65° assuming a low water-holding capacity soil and wettest starting condition (see Table 1). The experimental yields cover a range of sites and seasons (see Table 3) with individual site-season results shown for mean yield of hybrids released in (c) the 1990s or (d) the 2000s.

proximity to actively growing organs is a dominating factor in allocation of assimilate (Wardlaw, 1990). This possible link of leaf angle with grain set is supported by the simultaneous timing of the changes observed in leaf angle and barrenness in the ERA germplasm released between 1960 and 1989 (Duvick et al., 2004). There is also sound underpinning physiology to support the hypothesis. Maintenance of carbohydrate supply to the developing embryo is critical for seed set in maize (Zinselmeier et al., 1999) and the extent of barrenness has been related to the threshold plant growth rate required to initiate grain set (Campos et al., 2004). This threshold has been deconstructed into components related to both plant growth rate and partitioning to the ear (Echarte and Tollenaar, 2006; Borrás et al., 2007). It is thus plausible that leaf erectness might be associated with increased partitioning to the ear and consequential increase in grain set via the more locally available supply of carbohydrate. Increased grain set is a critical yield-determining factor in maize as there is limited capacity for adjustment in grain size during the grain filling period (Borrás et al., 2004).

It has also been argued for rice (Sinclair and Sheehy, 1999) that erect leaves are required to maintain sufficient green leaf area to store the nitrogen required for retranslocation to grain during grain filling in modern high-yielding cultivars. The increased light penetration associated with erect leaves would maintain a more uniform canopy profile of leaf nitrogen (Wright and Hammer, 1994; Drouet and Bonhomme, 1999; Massignam, 2003) and avoid premature shade-induced leaf senescence. A similar argument applies to maize. Although stay-green score has been increasing in maize, there has been a continuing decline in grain nitrogen content and, the onset of increase in stay-green score preceded onset of the increase in leaf angle in the ERA series (Duvick et al., 2004). While there remains a high requirement for grain nitrogen in maize despite its progressive marginal decline, it appears that the increasing grain demand for nitrogen is being met by factors other than enhanced storage in the leaves associated with leaf erectness. Such factors would include an extended duration of nitrogen uptake during grain filling, as found for stay-green in sorghum (Borrell et al., 2001; Borrell and

Hammer, 2000), so that additional nitrogen could transit leaves without reducing their nitrogen content below critical levels for maximum photosynthesis. It appears that such mechanisms to enhance stay-green appeared before leaf erectness in maize. Hence, we hypothesize that the trend to more erect leaves in maize is more likely related to its effect via enhanced partitioning of carbohydrate to the ear during its early development than it is to storage of nitrogen for use later in grain filling. However, further experimentation, model development, and simulation analysis would be required to test this hypothesis.

### Effects on ASI Are Likely Consequent on Plant Growth Rate and Partitioning Effects Associated with Changes in Canopy and Root Architecture

Effects of root system architecture on enhancing water capture, and canopy architecture effects on increasing partitioning of carbohydrate to the developing ear, will both affect ASI. Under water-limited conditions around flowering, the more effective root system at accessing deep soil water will maintain a higher plant growth rate. This will translate to more rapid ear growth and silking (Borras et al., 2007) and, hence, reduced ASI. This effect can be observed by contrasting the simulations presented in Fig. 10a and 10b. The effect of more elliptical (deeper) root architecture on grain yield is most obvious in the lower-yielding, water-limited years. This would be associated with increased plant growth rate and grain number, and consequently lower ASI, in those years. These effects are diminished or absent in the higher-yielding years. Thus the simulations for root architecture change generate the known genotype  $\times$  environment interaction for grain number and ASI in maize (Bolaños and Edmeades, 1996).

A similar connection to ASI is likely for canopy architecture effects on increasing partitioning of carbohydrate to the developing ear, although this effect has not been incorporated in this modeling study. Increased partitioning to the ear (as suggested above for more erect canopy architecture) would contribute to reducing the threshold plant or ear growth rate required to initiate grain set (Borras et al., 2007). This would result in more rapid and effective silking and lower ASI in situations where carbohydrate supply to the developing ear was limiting, such as with water limitation or at high density.

Both of these scenarios support the notion of ASI as a reporter trait for ear and plant growth rates during the flowering period (Edmeades et al., 1993, 2000; Campos et al., 2004). However, the analysis identifies plausible mechanisms underpinning the expression of ASI. The mechanisms suggested are consistent with timing of changes observed in the ERA studies (Duvick et al., 2004). Anthesis-silking interval has decreased throughout the entire time period, but the period of its most rapid

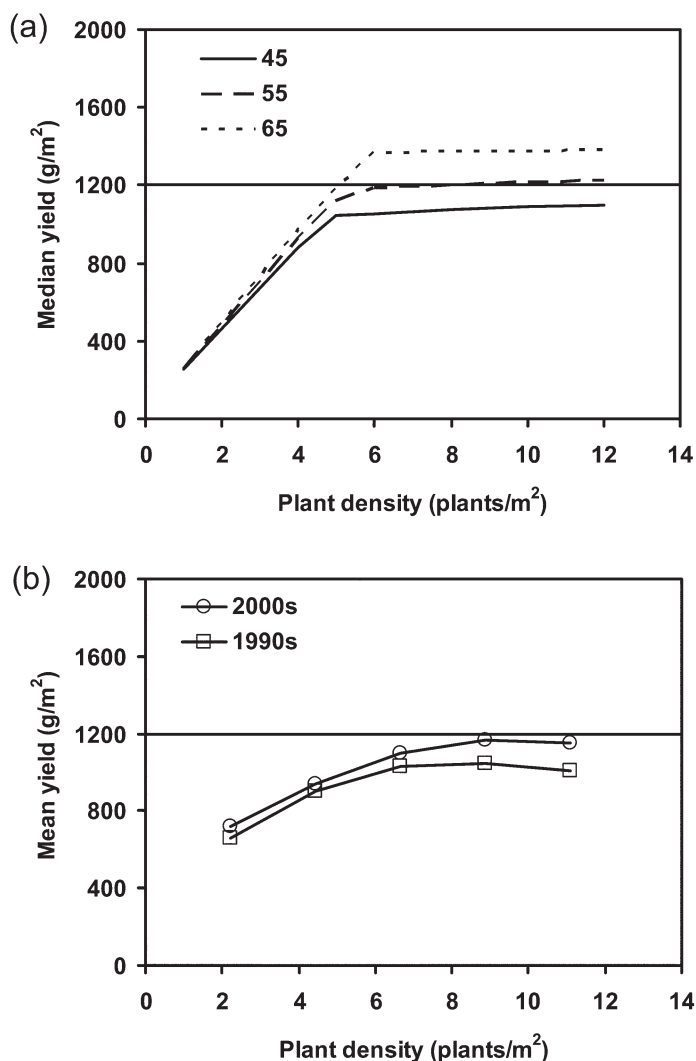


Figure 11. Median yield versus plant density for (a) simulated and (b) experimental results. The median simulated yields are derived from a 50-yr simulation at Johnston for each of three hypothetical root system architectures assuming a low water-holding capacity soil and wettest starting condition (see Table 1). The experimental yields cover a range of sites and seasons (see Table 3) with medians determined for two groups of hybrids based on decade of release.

decline (1960–1989) coincided with the times of most rapid increase in leaf erectness and reduction in barrenness. This is consistent with the enhanced partitioning hypothesis associated with more erect canopy architecture. Anthesis-silking interval has continued to decline (albeit less rapidly) since 1990, while leaf angle and barrenness have been stable. This is consistent with the suggestion of enhanced water capture associated with more effective root architecture occurring in that most recent period. However, it is also likely that these mechanisms are not the sole contributors to effects on ASI. Tassel size score has declined continuously with breeding effort (Duvick et al., 2004), indicating a likely important role for change in internal plant competition on partitioning of carbohydrate to support ear growth. Other studies (Welcker et al., 2007) have

also shown genetic differences in leaf and silk elongation rates under water limitation, which may involve mechanisms not connected to plant and ear growth rates.

## CONCLUSIONS

Modeling the evidence-based hypothetical situations that were structured to examine the question of whether changes in canopy and/or root system architecture might explain the observed maize yield trends in the U.S. Corn Belt suggests the following:

Change in root system architecture and water capture has greater direct effect than change in canopy architecture and light capture in explaining enhanced plant growth rate and biomass accumulation associated with historical yield increase and its interaction with density;

Change in canopy architecture may have important indirect effects associated with maintenance of green leaf area and partitioning of carbohydrate to the ear;

Both putative mechanisms contribute to the historical reduction in ASI and support the notion that ASI is an effective reporter trait for ear and plant growth rates during the ear development period;

Better quantification of the availability of soil water in the maize cropping system, and its extraction by maize roots at depth, are critical factors for ongoing yield advance.

We have used the best available knowledge and quantitative dynamic crop growth and development framework to generate enhanced understanding of complex trait interactions and develop testable hypotheses on historical changes. The ERA studies provided an invaluable source of information to learn from history. The evidence-based hypothetical situations provided plausible explanations that identify opportunities for future scientific research as well as rational targets for future crop improvement effort.

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