

Similarity of maize seed number responses for a diverse set of sites

James R. KINIRY^{a,*}, Yun XIE^b, Thomas J. GERIK^c

^a USDA, Agricultural Research Service, 808 E. Blackland Rd., Temple, TX 76502, USA

^b Beijing Normal University & Open Res. Lab. of Environmental Change and Natural Disaster
of the State Education Commission, Beijing, China

^c Blackland Agric. Exp. Station, Texas, Agric. Exp. Sta., 808 E. Blackland Road, Temple, TX 76502, USA

(Received 14 June 2001; revised 5 October 2001; accepted 20 October 2001)

Abstract – Accurate modeling of maize (*Zea mays* L.) yields in diverse environments requires realistic simulation of seed numbers. Response of maize seed number to growth or light interception soon after pollination has been described with different types of functions. The objective of this study was to compare maize seed number responses to intercepted solar radiation or growth with data from a diverse set of sites. Pioneer hybrid 3394 planted near Temple, TX in 1999 at 2.5 to 20 plants·m⁻² showed a linear function for seed number responses to light intercepted per plant in the 11 d following silking and to ear growth rate in these 11 d. Similar linear seed number responses were found for three hybrids in Canada at 4 to 13 plants·m⁻². Likewise, the function for Pioneer 3394 in Temple was found to be similar to a regression for the same hybrid grown in Pennsylvania, and was similar to a function developed in Kenya. Thus, under the diverse environmental conditions of these studies, linear seed number functions appeared reasonable at these sites. Such seed number functions are critical to the understanding of optimization of planting density to maximum seed production per unit ground area. In the absence of drought stress, the optimum density will be the minimum planting density which could attain near-complete light interception at silking. As the probability of drought stress increases due to decreased soil water holding capacity or decreased expected rainfall, the optimum density would decrease accordingly.

crop modeling / maize / seed number / photosynthetically active radiation / harvest index

Résumé – **Similarité des réponses du nombre de grains par épi de maïs pour un jeu de sites variés.** La modélisation précise des rendements du maïs (*Zea mays* L.) dans divers environnements nécessite une simulation réaliste du nombre de grains par épi. La réponse du nombre de grains à la croissance ou à l'interception de la lumière aussitôt après la pollinisation a été décrite avec différents types de fonctions. L'objectif de cette étude était de comparer les réponses du nombre de grains par épi au rayonnement solaire intercepté ou à la croissance de l'épi avec les données provenant d'un ensemble de sites variés. L'hybride Pioneer 3394 planté près de Temple (Texas, USA) en 1999 avec 2,5 à 20 plants/m² a montré une relation linéaire entre le nombre de grains et la lumière interceptée durant les 11 jours qui ont suivi la sortie des soies ainsi qu'avec le taux de croissance de l'épi durant ces mêmes 11 jours. Des réponses linéaires similaires ont été trouvées pour trois hybrides au Canada avec 4 à 13 plants/m². De même, la relation pour Pioneer 3394 à Temple a été trouvée similaire à celle obtenue pour le même hybride cultivé en Pennsylvanie ainsi qu'au Kenya. Ainsi, sous diverses conditions d'environnement de ces études, une relation linéaire avec le nombre de grains apparaît comme raisonnable dans ces sites. De telles relations linéaires avec le nombre de grains sont critiques pour appréhender l'optimisation de la densité de plantation afin d'atteindre le maximum de production de grains par unité de surface de sol. En l'absence de stress dû à la sécheresse, la densité optimale sera la densité de plantation minimale qui permettrait d'atteindre l'interception pratiquement complète du rayonnement au moment de la sortie des soies. Comme la probabilité de stress hydrique augmente avec la décroissance de la capacité de rétention en eau du sol ou décroît avec les précipitations escomptées, la densité optimale devra décroître en tenant compte de ces facteurs.

modélisation de la culture / maïs / nombre de grains / rayonnement photosynthétiquement actif / indice de récolte

Communicated by Jean-François Ledent (Louvain-La-Neuve, Belgium)

* Correspondence and reprints
kiniry@brc.tamus.edu

1. INTRODUCTION

Crop models can be valuable tools for replanting decisions when plant stands are reduced [28] and for planting density optimization in a wide range of conditions including under nitrogen and drought limitations [25]. An important aspect of optimizing maize planting density is maximizing the number of seeds per unit ground area. Increased planting density causes less light to be intercepted per plant and more rapid soil moisture depletion due to greater transpiration. Understanding the mechanism of seed set in maize is critical to balancing the increase in light interception by the crop against the decreased growth per plant and decreased number of seeds per plant, in optimizing plant density. If a crop model such as CERES-Maize [12] accurately predicts seed number, it can dynamically evaluate optimum planting densities with different soils, different rainfall conditions, and different maize hybrids.

A potentially useful approach to understanding maize yields in many environments is the assumption that the number of seeds that develop on an ear is proportional to the available nonstructural carbohydrate (NCO) in the ear during early seed development following pollination. During the first 10–11 d after silking, plants abort seeds if drought or interplant competition for light reduces NCO supply to the ear [26]. This has been supported by shading and drought stress studies [8,17] and with supplemental NCO fed into plants under drought stress [4,29].

If seeds each required the same amount of NCO to support their early development, the responsiveness of seed number to amount of NCO in the ear soon after pollination would be linear. Growth per plant and light intercepted per plant have been used as surrogates for NCO in the ear. Linear seed number responses have been demonstrated for sorghum (*Sorghum bicolor* (L.) Moench) growth rate [24], for wheat (*Triticum aestivum*) incident solar radiation [6], and for wheat photothermal quotient [1] when nitrogen supply was adequate.

Likewise, many maize data sets show linear seed number responses. Hawkins and Cooper [10] analyzed results from a wide range of experiments in Kenya, including planting densities of 1.7 and 11.1 plants·m⁻². They found a linear relationship between seeds per plant and growth rate per plant from spikelet initiation to silking. Barbieri et al. [3] reported a linear response of seeds per m² to intercepted photosynthetically active radiation (IPAR) per m² with different nitrogen and row spacing treatments. Kiniry and Knievel [15] found linear relationships for a wide range of population studies in the

literature. With data in Iowa [27], they showed linear seed number responses to IPAR per plant for all their plant density data, from 4.0 to 8.5 plants·m⁻². Including all the seed number data of a study in Britain [11], there was also a linear response of seed number to IPAR. These treatments were plant densities of 8 to 32 plants·m⁻². Using all the results from a maize study in Zaire [18] the seed number response was also linear. These treatments were 4 to 10 plants·m⁻². Data from Massachusetts [9] had a linear seed number response for shaded plant values at 3 to 12 plants·m⁻² pooled with unshaded plant values at 7.5 and 12 plants·m⁻². Only the 3 plants·m⁻² unshaded treatment failed to be close to the response line. Using shading treatments and variable N treatments, Uhart and Andrade [23] derived linear equations for seed number as a function of IPAR. They derived linear equations with a plateau for seed number as a function of crop growth rate and ear growth rate. Finally, the response of seed number to IPAR per plant was linear, with a positive y-intercept for data collected in Texas and Pennsylvania [15]. A general linear function was adequate for 10 hybrids with population densities ranging from 2.5 to 10 plants·m⁻².

Other researchers have reported nonlinear seed number responses. Edmeades and Daynard [5] fit a rectangular hyperbola to single-plant results of seeds per plant as a function of assimilate flux, for planting densities of 5, 10, and 15 plants·m⁻².

Similarly, by combining treatments ranging from 2.5 to 13 plants·m⁻² with a defoliation treatment at 10 plants·m⁻², Tollenaar et al. [22] fit rectangular hyperbolas to seed number as a function of plant growth rate for three single-eared hybrids. Likewise, Andrade et al. [2] used data from several experiments, with plant densities of 2.1 to 16.2 plants·m⁻², to provide a nonlinear response of seeds per plant as a function of plant growth rate. Rationale for observed nonlinear responses at low growth (or assimilate flux) per plant is that plants have a threshold needed to support minimal seed development. When values per plant fall below this threshold, seed number decreases rapidly to zero (barrenness). However, such nonlinearity due to barrenness is not supported by the shading and plant density data of Hashemi-Dezfouli and Herbert [9] (Fig. 1). When only plants with seeds were analyzed, the seed number per plant response to IPAR in MJ·plant⁻¹·d⁻¹ was

$$\text{SEEDS} = 703 \times \text{IPAR} - 70, r^2=0.998. \quad (1)$$

Including barren plants in the results caused the regression to change to

$$\text{SEEDS} = 797 \times \text{IPAR} - 159, r^2=0.999. \quad (2)$$

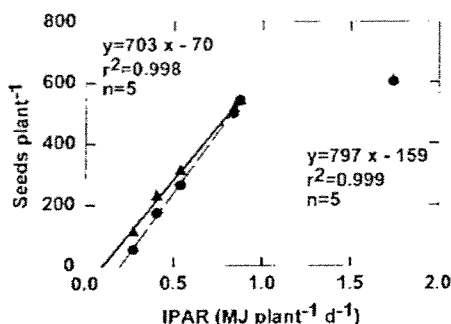


Figure 1. Seed number response to intercepted PAR per plant (IPAR) in Massachusetts [9]. Treatments included planting densities of 3, 7.5, and 12 plant·m⁻² and zero or 50% shading. Only the unshaded, 3 plants·m⁻² treatment was not included in the regressions. Triangles and solid line are for data without considering barren plants and circles and dotted line are for data when barren plant results were included.

Thus, the r^2 values were large for both equations. In this experiment barrenness increased from zero for the shaded and unshaded treatments with 3 plants·m⁻² to 51% with the highest density (12 plants·m⁻²) and 50% shading.

The form of the seed number response function of maize hybrids is critical for yield simulation. Increased density and environmental stress reduce the number of seeds set per plant. Dryland maize planting densities are typically 40 000 to 60 000 plants·ha⁻¹, with irrigated densities ranging up to 80 000. Thus, the most important region of a seed number response is for 40 000 to 80 000 plants·ha⁻¹. Assuming nearly complete canopy closure, each plant intercepts approximately 25% to 12.5% of the light for 1 m² of ground area in this range of plant densities. If the seed number response is truly nonlinear with a negative y-intercept at low light per plant or low growth per plant, increasing density sufficiently would cause decreases in seeds·m⁻² ground area. In contrast, a linear response with a positive y-intercept or through the origin would not show such a decrease in seeds·m⁻² ground area, in the absence of drought stress.

The objective of the present study was to compare seed number responsiveness among studies with nonprolific maize hybrids at a diverse range of sites. Responses for such hybrids are critical for simulating large areas, due to the prevalence of nonprolific hybrids for modern commercial production in temperate regions. Seed number of one such maize hybrid at Temple, TX in

1999 was measured on a wider range of planting densities than in previous studies reporting nonlinear responses. For this hybrid, seed number response to ear growth rate in the 11 d following silking was also investigated.

2. MATERIALS AND METHODS

This study involved both new field data on seed number at one location in Texas and previously-published data from other locations. Thus, we used a broad database to investigate seed number responses. Using a nonprolific hybrid, we measured seed number response to IPAR·plant⁻¹, with carefully thinned plant density plots. The seed number response to IPAR for this hybrid was used as the standard for all subsequent analyses. Next we compared our response function derived with the Temple, TX data, to data from Canada [22]. Finally, we compared our standard response function to a function from Kenya [13] and to data from Pennsylvania [15] for two hybrids.

For all data sets, regressions were tested for significant linear slopes, significant second-order terms (to test for significant nonlinearity), and significant y-intercepts (to see if the y-intercepts were significantly different from zero). In all analyses, a 95% confidence level was used.

Additional analyses were done to test for nonlinearity using rectangular hyperbolas similar to those of Tollenaar et al. [22]. The linear regressions indicated y-intercept values not significantly different from zero. For the nonlinear, rectangular hyperbolas, the y-intercepts were assumed to be zero. Thus, the form of the equations was

$$\text{SEEDS} = A \times \text{IPAR} / (1 + B \times \text{IPAR}) \quad (3)$$

where SEEDS is the number of seeds per plant, IPAR is the intercepted photosynthetically active radiation (MJ·plant⁻¹·d⁻¹) and A and B are fitted constants. A and B were fit iteratively with both the Marquardt and Gauss-Newton procedures of Proc NLIN [19]. When the 95% confidence limit for a fitted constant included zero, that constant was not significantly different from zero. A value of B not significantly different from zero would indicate the response was not significantly nonlinear. Since the Marquardt and Gauss-Newton methods gave the same results for all the data sets, only the Marquardt results will be presented.

Responses for this project were determined with means of several plants within a plot, not with individual plant values as done in some studies [2,5]. Use of single plant values can cause problems because treatment effects can become confounded with plant-to-plant variability due to uneven seedling emergence dates or within-field soil differences. Also, use of single plant data can be difficult to interpret when plants within a plot are inadvertently planted too close together, and appear overly responsive to a treatment. Such plants can be relatively small because of inter-plant competition, not as a result of the applied treatment, such as shading. Thus, for the analyses in this project, individual data points were plot means. Interplant variability within plots was not included in the statistical analysis.

Maize hybrid Pioneer 3394 (Pioneer Hi-Bred Int., Inc. Johnston, IA) was planted on 5 March 1999 at the Grassland, Soil and Water Research Laboratory near Temple, Texas (31° 6' N, 97° 20' W; 210 m above sea level) on a Houston Black clay (fine, montmorillonitic, thermic Udic Pellustert). Plots were overplanted in 0.5-m rows and thinned to the desired densities soon after seedling emergence. These densities were 2.5, 5.0, 10, 15, and 20 plants·m⁻². There were four replications, with each population density plot consisting of eight rows, 5 m long. We applied 1.48 kg a.i.·ha⁻¹ of atrazine (6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine) and 1.88 kg a.i.·ha⁻¹ metolachlor (2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl)acetamide) before planting. Fertilizer consisted of 134 kg N·ha⁻¹ (urea solution) and 45 kg P·ha⁻¹ (phosphoric acid) applied on 2 Dec. 1998, and 112 kg N·ha⁻¹ (urea solution) applied on 11 Jan. 1999. Rainfall was adequate to avoid drought stress during the season and fertilizer was applied in amounts to assure that even the highest planting densities had adequate soil nutrients.

We measured PAR interception at silking and 11 d later with a 0.8-m-long Sunfleck Ceptometer (Decagon, Pullman, WA 99163). In each replication, we took three series of measurements of each planting density in rapid succession. A series of measurements consisted of 10 PAR measurements above the canopy, 10 below the canopy, and 10 more above the canopy. The fraction of PAR intercepted was calculated with the mean of the above-canopy measurements and the mean of the below-canopy measurements. While taking the readings below the canopy, the light meter was moved across the plant rows. Measurements were taken between 1025 and 1400 h during times with relatively stable incident solar radiation (without intermittent clouds). IPAR per plant

was calculated from the fraction intercepted, the incident PAR and the plant density.

Five plants per replication were harvested for ear dry weight measurement at silking (21 May) and 11 d later (1 June). Five plants were also harvested after maturity, for determining seed number, stover biomass and harvest index. Plants were always harvested from the middle four rows. Plants were dried in a forced-air drying oven at 70 °C until the weight stabilized, and weighed.

A regression was fit with the treatment means for each replication. This regression was for seeds per plant as a function of mean IPAR per plant per day in the 11 days following silking and for ear growth rate in this interval. Fraction of PAR intercepted was measured from 3 June to 9 June. The final harvest was after maturity and seed number was determined for at least three plants per plot.

To investigate consistency in seed number responses, we also analyzed the data for three nonprolific hybrids in Canada [22]. The Canadian hybrids were Pride 5, Warwick 263 and United 106. Data were taken from the published figures and plant densities of 4 to 13 plants·m⁻² were included. The defoliation treatment data was not used because of the severity of the stress of such a treatment. The 2 plants·m⁻² data were not included because they appeared to be sink-limited, showing a similar number of seeds to the 4 plants·m⁻² treatment. To allow comparison with the Pioneer 3394 regression described below, we assumed there were 3.5 g of biomass produced per MJ of IPAR [14]. The response of seed number to IPAR was analyzed as described above. The standard equations for Pioneer 3394 were tested against data for each of the three hybrids [22], as described above.

As a final test, published seed number responses for hybrids Pioneer 3394 and Pioneer 3475 in Pennsylvania [15], and a published seed number response from Kenya [13] were compared to the standard response function of Pioneer 3394 in Temple. The objective was to see if the response could be applied to these locations. The Kenya response function provided accurate grain yield predictions for planting densities of 1 to 9 plants·m⁻² in irrigated and dryland conditions in Kenya.

3. RESULTS AND DISCUSSION

For Pioneer 3394 the relationship between seeds per plant and IPAR was linear. This was in spite of the severe impact of high planting density on plants (Tab. 1). Stover dry weight was decreased by 60 percent in the highest

Table I. Pioneer 3394 results for Temple, TX in 1999.

Population plants·m ⁻²	Harvest index		Stover dry wt. g·plant ⁻¹		Seed number seeds·m ⁻²		FPAR intercepted ^a	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2.5	0.54 a	0.02	167 a	51	1756 a	744	0.418 a	0.029
5.0	0.54 a	0.00	134 a	3	2925 b	210	0.695 b	0.043
10	0.49 b	0.02	92 b	9	3117 b	320	0.885 c	0.014
15	0.48 b	0.01	68 b	9	3735 bc	656	0.925 cd	0.012
20	0.44 c	0.01	67 b	13	4210 c	745	0.949 d	0.009

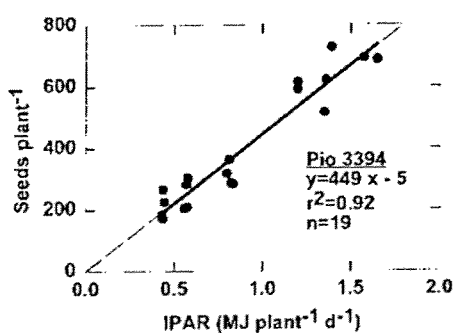
LSD (alpha=0.05) was 0.03 for harvest index, 42 for stover dry weight, 891 for seeds per m² ground area and 0.045 for FPAR intercepted.

Means followed by the same letter are not significantly different (Duncan's Multiple Range Test, alpha=0.05).

^a Fraction of photosynthetically active radiation (PAR) intercepted by the plant canopy at silking.

Table II. Comparison of the relationship between seeds per plant and different variables for equation [1]. Fitted constants are the initial slope (A) of the kernel per plant responses and the nonlinear constant (B). CL are the 95% confidence limits for the fitted constants. IPAR is the intercepted PAR in the 11 d after silking (MJ·plant⁻¹·d⁻¹), plant growth rate is the plant growth from 1 wk before silking until 3 wk postsilking (g·plant⁻¹·d⁻¹).

Hybrid	Independent variable	A	CL	B	CL
Pioneer 3394	IPAR	433	333 to 534	- 0.02	- 0.2 to 0.15
Pride 5	Plant growth rate	126	61 to 192	- 0.01	- 0.14 to 0.12
Warwick 263	Plant growth rate	125	95 to 156	0.03	- 0.03 to 0.10
United 106	Plant growth rate	145	67 to 223	0.07	- 0.11 to 0.26

**Figure 2.** Seed number response to intercepted PAR per plant (IPAR) in the 11 d following silking for maize hybrid Pioneer 3394. The hybrid was grown in the field near Temple, TX at planting densities from 2.5 to 20 plants·m⁻². The solid line is the regression and the dashed line is the regression forced through the origin.

density relative to the lowest density. Likewise, harvest index values decreased from 0.54 to 0.44 as planting density increased. Similar harvest index values were reported by Tollenaar [21]. The two most recently released hybrids (Warwick 263 and United 106) in that study had mean harvest index values of 0.52 at 1 plant·m⁻², 0.51 at 2, 0.49 at 4, 0.50 at 8, 0.49 at 12, 0.44 at 18 and 0.41 at 24.

Using all the population treatments for the Temple study, the regression for seed number per ear as a function of IPAR per plant (Fig. 2) did not have a significant y-intercept or a significant second-order term, but had a significant slope. Likewise, the rectangular hyperbola failed to show significant nonlinearity (Tab. II). The linear regression for this data, forced through zero, was:

$$\text{Seeds per plant} = 444 \times \text{IPAR (MJ·plant}^{-1}\text{·d}^{-1}\text{)}. \quad (4)$$

Similarly, the relationship between seeds per plant and ear growth rate in the 11 d following silking (Fig. 3)

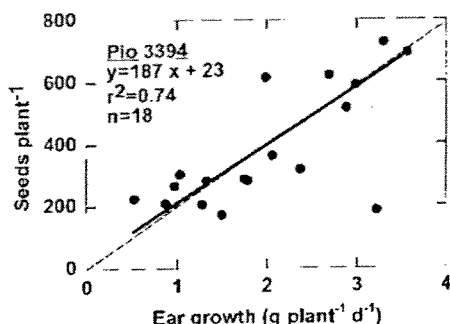


Figure 3. Seed number response to ear growth rate in the 11 d following silking for maize hybrid Pioneer 3394. The hybrid was grown in the field near Temple, TX at planting densities from 2.5 to 20 plants·m⁻². The solid line is the regression and the dashed line is the regression forced through the origin.

had a significant slope, a nonsignificant y-intercept, and a nonsignificant second order term.

With the Canadian data, with planting densities of 4 to 13 plants·m⁻², the seed number responses were linear for all three hybrids (Fig. 4). Slopes for the three Canadian hybrids were always significant and the y-intercepts were never significant. The squared terms were never significant, indicating no significant nonlinearity. For each hybrid, the rectangular hyperbola failed to show significant nonlinearity (Tab. II). The regression from Pioneer 3394 (Eq. (4)), assuming 3.5 g of maize biomass is produced per MJ of IPAR [14], predicts seed number as:

$$\text{Seeds per plant} = 127 \times \text{Growth (g·plant}^{-1}\cdot\text{d}^{-1}). \quad (5)$$

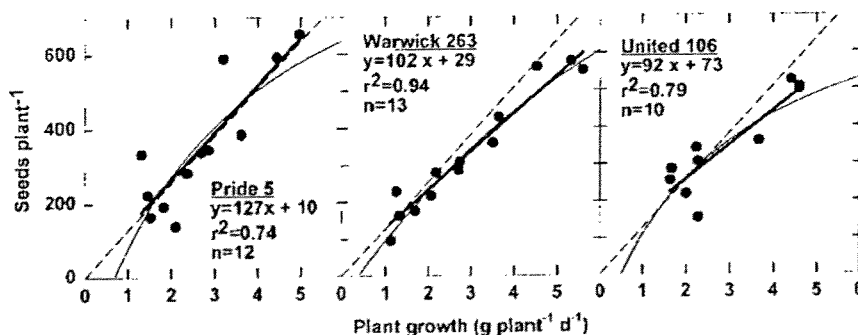


Figure 4. For three nonprolific hybrids grown in Canada [21], seed number response to plant growth rate. The hybrids were grown at planting densities from 4 to 13 plants·m⁻². The solid lines are the regressions fit to this data and the dashed line is the regression for Pioneer 3394 (Eq. (2), see text). The curves are the original published rectangular hyperbolas derived by Tollenaar et al. [21].

Using this function to predict the Canadian data, the slope of the errors as a function of growth was significant only for Warwick 263. The mean error of prediction for each linear function was not significantly different from zero for Pride 5 and United 106 but was significant for Warwick 263. Warwick 263 had a mean error of 42 seeds fewer than predicted. Within the range of data considered, the rectangular hyperbolas of Tollenaar et al. were similar to the fitted lines. The greatest divergence occurred at the upper range of data for Pride 5 and United 106. The nonlinear functions tended to underpredict seed numbers for these upper data points.

The response given by equation (4) was similar to published responses for two Pioneer hybrids in Pennsylvania (Fig. 5) [15]. The regressions for Pioneer 3394 and Pioneer 3475 are shown for the range of measured data. Predictions for Pioneer 3394 differed from those of equation (4) by 12 percent or less. Predictions for Pioneer 3475 differed from those of equation (4) by 4 percent or less.

Equation (4) predictions also closely agreed with those from the function used to simulate maize seed number in Kenya [13] (Fig. 5). That equation was:

$$\text{Seeds per plant} = G2 \times \text{PSKER}/5096 - 51.6 \quad (6)$$

where $G2$ is the potential number of seeds per plant of a hybrid and $PSKER$ is the mean plant growth in the period immediately following silking ($\text{mg}\cdot\text{plant}^{-1}\cdot\text{d}^{-1}$). They assumed 3.4 g of biomass were produced per MJ of IPAR. Thus, equation (6) becomes:

$$\text{Seeds per plant} = G2 \times \text{IPAR} \times 0.667 - 51.6 \quad (7)$$

where IPAR is in units of $\text{MJ}\cdot\text{plant}^{-1}\cdot\text{d}^{-1}$. Predicted seeds per plant was not allowed to exceed the potential number.

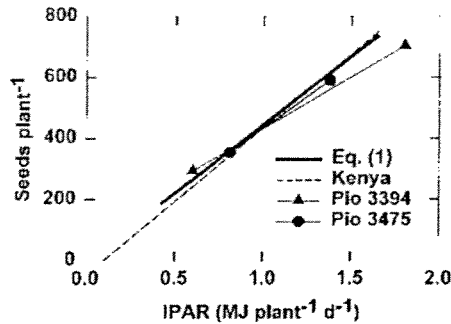


Figure 5. Comparison of four seed number response lines of maize. Equation (1) is for Pioneer 3394 in Temple, TX (see text). Pioneer 3394 and Pioneer 3475 functions were derived from data in Pennsylvania [15]. The Kenya function was used to simulate maize seed number in Kenya [13]. The symbols on the last two response functions indicate the end points of the lines, for the range of measured data in each case.

We assumed a potential of 750 seeds·plant⁻¹ for this analysis. Predictions from this equation differed from equation (4) predictions by 14% or less, over the range of the data for equation (4).

In conclusion, when plants received adequate moisture and nutrients, responses of seed number to IPAR and to ear growth rate were linear, with y-intercepts not significantly different from zero. This implies that plants set seeds in direct proportion to the amount of assimilate (carbohydrate) available in the ear following silking. Seeds require this carbohydrate to continue to develop after ovule fertilization. The amount of light intercepted per plant required to support each seed is remarkably stable for most of the sites in this study.

The nonlinearity in the previous study [22] could be attributed partly to the choice of treatments used and partly to a plateau in the seed number response due to an upper limit on the number of seeds which can be set by some hybrids. At sufficiently low planting density, the number of ovules on an ear can become a limitation to seed number. In that study, nonlinearity at low growth rates was due to the defoliation treatment data, where four leaves were removed one week before silking. In their words, “(the defoliation treatment) represented an extreme stress (and) may have introduced factors additional to those involved in high plant densities...”. An apparent plateau existed at about 600 to 700 seeds per ear. This was evident for the 2 plants·m⁻² treatment. A crop model could simulate such a sink-limited situation by having an upper limit on the number of seeds per ear that

a hybrid could set. Hybrid Pioneer 3394 in the present study did not show such a plateau, even though planting density was decreased to 2.5 plants·m⁻².

A linear response of seed number to IPAR, through the origin, has important implications for optimizing planting density of nonprolific hybrids. With increasing planting density, seeds per unit ground area should increase as long as canopy-level PAR interception at silking increases, in well-watered conditions. Such is shown in Table I. Fraction of PAR intercepted by the plant canopy continued to increase throughout the range of planting densities. Likewise, seeds·m⁻² increased throughout the range of densities, but did not differ significantly between the two highest densities. In moisture-limited conditions, however, high planting density can have greater LAI and more rapid soil moisture depletion. Thus higher planting densities could have greater drought stress in the period following silking, resulting in reduced NCO in the ears and fewer seeds set. One could calculate the optimum density using Beer’s law, an extinction coefficient based on row spacing [7], and LAI values of a hybrid at different densities. The optimum density would be the minimum planting density that could attain near-complete light interception at silking. As the probability of drought stress increased due to decreased soil water holding capacity or decreased expected rainfall, the optimum density would decrease accordingly.

The discrepancy among studies as to the y-intercept deserves further attention. A y-intercept greater than zero would lead to greater seed number per unit ground area with increased planting density, when soil moisture and soil nutrients are not limiting. Data from several studies summarized by Kiniry and Knievel [15] often had positive y-intercepts. Such responses were found with treatments severe enough to reduce seeds·plant⁻¹ to 100 to 200 in some cases. In Britain [11], with planting densities of 8 to 32 plants·m⁻², the y-intercept was 40 seeds·plant⁻¹. In Zaire [18], with 4 to 10 plants·m⁻², the y-intercept was 52 seeds·plant⁻¹. Similar positive y-intercepts were demonstrated with data from Ontario, Canada and Pennsylvania, U.S. Of these, high densities decreased seed number to less than 200 seeds·plant⁻¹ for the study in Britain and for the three hybrids in the Canadian study [12]. In contrast, when shading and high density treatments affected seed number in Massachusetts [9], the y-intercept was -81 seeds·plant⁻¹. Seed number in this study was reduced to 110 seeds·plant⁻¹ in the most severe treatment.

For several hybrids with a wide range of maturity types, Kiniry and Knievel [15] found one common response of seed number to IPAR. Some hybrids, however,

differed significantly in their responses. The negative y-intercept of some studies could be attributed to hybrids that were intolerant of high planting density. Similarly, sufficiently high planting density could have depleted soil moisture or soil nutrients to such an extent that seed set was reduced.

Acknowledgments: The authors express their appreciation to the National Key Basic Research Special Foundation Project (G2000018605) in China for their support.

REFERENCES

- [1] Abbate P.E., Andrade F.H., Culot J.P., The effects of radiation and nitrogen on number of grains in wheat, *J. Agric. Sci. Camb.* 124 (1995) 351–360.
- [2] Andrade F.H., Vega C., Uhart S., Cirilo A., Cantarero M., Valentinuz O., Kernel number determination in maize, *Crop Sci.* 39 (1999) 453–459.
- [3] Barbieri P.A., Sainz Rozas H.R., Andrade F.H., Echeverria H.E., Row spacing effects at different levels of nitrogen availability in maize, *Agron. J.* 92 (2000) 283–288.
- [4] Boyle M.G., Boyer J.S., Morgan P.W., Stem infusion of liquid culture medium prevents reproductive failure of maize at low water potential, *Crop Sci.* 31 (1991) 1246–1252.
- [5] Edmeades G.O., Daynard T.B., The relationship between final yield and photosynthesis at flowering in individual maize plants, *Can. J. Plant Sci.* 59 (1979) 585–601.
- [6] Fischer R.A., Number of kernels in wheat crops and the influence of solar radiation and temperature, *J. Agric. Sci. Camb.* 105 (1985) 447–461.
- [7] Flénet F., Kiniry J.R., Board J.E., Westgate M.E., Reicosky D.C., Row spacing effects on light extinction coefficients of corn, sorghum, soybean, and sunflower, *Agron. J.* 88 (1996) 185–190.
- [8] Grant R.F., Jackson B.S., Kiniry J.R., Arkin G.F., Water deficit timing effects on yield components in maize, *Agron. J.* 81 (1989) 61–65.
- [9] Hashemi-Dezfouli A., Herbert S.J., Intensifying plant density response of corn with artificial shade, *Agron. J.* 84 (1992) 547–551.
- [10] Hawkins R.C., Cooper P.J.M., Growth, development and grain yield of maize, *Exp. Agric.* 17 (1981) 203–207.
- [11] Iremiren G.O., Milbourn G.M., Effects of plant density on ear barrenness in maize, *Exp. Agric.* 16 (1980) 321–326.
- [12] Jones C.A., Kiniry J.R., CERES-Maize: A simulation model of maize growth and development, Texas A&M Univ. Press, College Station, 1986.
- [13] Keating B.A., Wafula B.M., McCown R.L., Simulation of plant density effects on maize yield as influenced by water and nitrogen limitations, in: *Proc. Int. Congr. Plant Physiol.*, New Delhi, India, Soc. For Plant Physiol. & Biochem., 1988.
- [14] Kiniry J.R., Jones C.A., O'Toole J.C., Blanchet R., Cabelguenne M., Spanel D.A., Radiation-use efficiency in biomass accumulation prior to grain-filling for five grain-crop species, *Field Crops Res.* 20 (1989) 51–64.
- [15] Kiniry J.R., Kniewel, D.P. Response of maize seed number to solar radiation intercepted soon after anthesis, *Agron. J.* 87 (1995) 228–234.
- [16] Kiniry J.R., Otegui M.E., Processes affecting maize grain yield potential in temperate conditions, in: Slafer G.A., Otegui M.E. (Eds.), *Physiological Bases for Maize Improvement*, 1999, pp. 31–46.
- [17] Kiniry J.R., Ritchie J.T., Shade-sensitive interval of kernel number of maize, *Agron. J.* 77 (1985) 711–715.
- [18] Muleba N., Hart T.G., Paulsen G.M., Physiological factors affecting maize (*Zea mays* L.) yields under tropical and temperate conditions, *Trop. Agric. (Trinidad)* 60 (1983) 3–10.
- [19] SAS Institute, SAS/STAT User's Guide. SAS Inst., Cary, NC, 1988.
- [20] Schussler J.R., Westgate M.E., Assimilate flux determines kernel set at low water potential in maize, *Crop Sci.* 35 (1995) 1074–1080.
- [21] Tollenaar M., Is low plant density a stress in maize?, *Maydica* 37 (1992) 305–311.
- [22] Tollenaar M., Dwyer L.M., Stewart D.W., Ear and kernel formation in maize hybrids representing three decades of grain yield improvement in Ontario, *Crop Sci.* 32 (1992) 432–438.
- [23] Uhart S.A., Andrade F.H., Nitrogen deficiency in maize: II. Carbon-nitrogen interaction effects on kernel number and grain yield, *Crop Sci.* 35 (1995) 1384–1389.
- [24] Vanderlip R.L., Charles-Edwards D.A., Foale M.A., Ferraris R., Predicting tiller number and seed number in grain sorghum, *Agron. Abstr.* 1984, 138.
- [25] Wafula B.M., Applications of crop simulation in agricultural extension and research in Kenya, *Agric. Syst.* 49 (1995) 399–412.
- [26] Westgate M.E., Boyer J.S., Reproduction at low silk and pollen water potentials in maize, *Crop Sci.* 26 (1986) 951–956.
- [27] Whigham D.K., Woolley D.G., Effect of leaf orientation, leaf area, and plant densities on corn production, *Agron. J.* 66 (1974) 482–486.
- [28] Williams J.R., DeLano D.R., Heiniger R.W., Vanderlip R.L., Llewelyn R.V., Replanting strategies for grain sorghum under risk, *Agric. Syst.* 60 (1999) 137–155.
- [29] Zinselmeier C., Lauer M.J., Boyer J.S., Reversing drought-induced losses in grain yield: sucrose maintains embryo growth in maize, *Crop Sci.* 35 (1995) 1390–1400.