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RESEARCH

Yield Responses to Planting Density for US Modern Corn Hybrids: A Synthesis-Analysis

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ABSTRACT

Identifying an optimal plant density is a critical management decision for corn (*Zea mays* L.) production. The main objectives of this study were to: (i) investigate the grain yield responses to plant density (yield–density relationship), (ii) identify best fitted yield–density response curves, and (iii) explore genotype (G) × environment (E) interaction effect on yield–density response models. Analysis was conducted on meta-data (124,374 observations) gathered from 22 US states and 2 Canadian provinces, diverse sites (E), for years from 2000–2014 on multiple hybrids (G). Yield data were further grouped into four yield environments (low [LY], <7 Mg ha^{-1}; medium [MY], 7–10 Mg ha^{-1}; high [HY], 10–13 Mg ha^{-1}; and very high [VHY], >13 Mg ha^{-1} yielding groups). Primary outcomes from this analysis were: (1) strong G × E interaction; (2) a quadratic model best fitted yield–density relationship; (3) four contrasting yield–density responses identified as dominant in each yield productivity environment, i.e., a declining, a constant, an increasing, and ever-increasing type; (4) the yield productivity environment varied for the different corn comparative relative maturity (CRM) groups, i.e., the LY environment for long-maturing hybrids matched with a MY or HY environment for short maturing hybrids; and (5) maximum yielding plant density (MYPD) was lower but maximum yield was greater for long- versus short-maturing hybrids. In summary, optimal plant density should be decided based on detailed G × E analysis of production conditions that include factors such as CRM, yield productivity environment (weather–soil × management practices), and site information.

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Abbreviations: CRM, corn relative maturity; E, environment; G, genotype; HY, high yielding; LY, low yielding; M, management; MY, medium yielding; VHY, very high yielding; MYPD, maximum yielding planting density; RMSE, root mean square error.

Plant density (number of plants per unit area) is among the four grain yield components (i.e., ear number per unit area, seed number per ear, seed weight) exerting a large impact on attainable corn (*Zea mays* L.) yield. Corn yield responds highly to changes in plant density when compared to similar crops such as sorghum (Norwood, 2001; Blumenthal et al., 2003; Stanger and Lauer, 2006). However, many yield to plant density (herein termed yield–density) responses with positive (yield increase with increasing plant density), neutral, and negative effects on corn yield were documented (Duncan, 1958; Prior and Russell, 1975; Hashemi et al., 2005; Bruns and Abbas, 2005; Tollenaar, 1992; Ciampitti et al., 2013a, 2013b; Ciampitti and Vyn, 2012, 2013). A better understanding on the yield–density relationship by dissecting factors influencing yield–density model responses such as genotype (G) (e.g., comparative relative maturity, CRM) and environment (E) should be pursued. Identifying major yield–density response curves are among crucial elements to consult with producers and to further advance the science in understanding plant density effect on yield and its components.

Corn grain yield has significantly increased in the hybrid era (Duvick, 1984; Castleberry et al., 1984; Eghball and Power, 1995;

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Assefa et al., 2012; Ciampitti and Vyn, 2012, 2014) and increase in the number of plants per unit area is suggested as one of the main contributors to yield improvement (Tokatlidis and Koutroubas, 2004; Duvick, 1997; Carlone and Russell, 1987; Tollenaar and Wu, 1999; Ciampitti and Vyn, 2012). Many of these authors claimed increased tolerance to stress (competition) and responsiveness to inputs achieved through breeding as the main reason for increase in plant density. However, advances in crop management techniques such as increased use of inorganic fertilizer, irrigation area, and enhanced weed and pest control techniques were also critical factors for increase in both plant density and yield.

Multiple factors affect the yield–density relationship. Genotype (e.g., type of hybrid), maturity group, available irrigation or rainfall amount (water supply), available plant nutrients (soil plus fertilizer), and planting date are among the main factors influencing the yield–density relationship (Keating et al., 1988; Abbas et al., 2012; Sangoi, 2001; Sangakkara et al., 2004; Nik et al., 2011; Tajul et al., 2013; Lindsey and Thomison, 2016). For example, previous research reports suggest that optimal plant density for maximizing yield varied relative to the water supply (Averbeke and Marais, 1992), hybrid (Stanger and Lauer, 2006), and soil type (Woli et al., 2014). Due to dependence on many environmental factors, the best yield–density model describing the association has always been debatable. Researchers have described equations and possible curves to describe the yield–density relationship (Holliday, 1960; Bleasdale and Nelder, 1960). An exponential or asymptotic model (Duncan, 1958; Carmer and Jackobs, 1965; Overman and Scholtz, 2011) and a parabolic or quadratic model (Stanger and Lauer, 2006; Coulter et al., 2010; Van Roekel and Coulter, 2011) were proposed. Impact of resource or environment in determining these models were also reported. For example, Averbeke and Marais (1992) noted that increased level of water deficit changed the yield–density relationship model from parabolic to asymptotic. An asymptotic model depicts a yield increase with increasing plant density to a maximum, without decreasing afterward. A parabolic model portrays increases in yield with density to a maximum density, with lower yields as density increases further (Holliday, 1960).

Most cereal crops have a stable yield for wide range of plant density because they can respond to availability of resources by adjusting the number of productive tillers (Darwinkel, 1978; Lafarge et al., 2002). Unlike most cereals, corn does not have the same ability to adjust yield for possible occasional inadequacy or availability of resources because modern corn hybrids cannot effectively tiller and often produce one ear per plant (Tokatlidis, 2013). Therefore, corn yield, particularly that of modern hybrids, is highly dependent on plant density (Van Roekel and Coulter, 2011; Tokatlidis et al., 2001, 2011).

A clear understanding on the yield–density relationship, accounting for major factors, and identifying conclusive yield–density response curves are, therefore, crucial to consult corn production. The objectives of this research study were to: (i) investigate the yield–density relationship, (ii) identify typical response models, and (iii) explore the G $\times$ E interaction via investigation of the influence of the productivity environment and CRM factors on yield–density response models.

MATERIALS AND METHODS

A meta-database (124,374 observations) was synthesized from observations collected from plant density trials with corn hybrids, developed by DuPont Pioneer, conducted from 2000–2014 in 22 states in the United States and 2 provinces in Canada. These trials were conducted in a randomized complete block design with a split-plot arrangement. Plot size was 3.05 m (4-rows) by 5.4 m long (with a 0.76-m row spacing) and there were two to three replicates at each location. Plots were uniformly fertilized with all recommended nutrients for their respective area. Plant density was the whole plot treatment, and hybrids were in the subplot level. Five target plant densities (44,475; 59,306; 74,132; 88,958 and 103,784 plants ha^{-1}, over-planted and thinned) were used from 2000–2010. Planting density increments were widened for the 2011–2014 trial period, with targets of 44,475; 64,247; 84,016; 103,784; and 123,553 plants ha^{-1}. For the 2011–2014 trial period, planting was done based on target densities, actual stand count data were collected at harvest, and these actual stand count data were utilized for the validation analysis. Within each state or province, field research was conducted in one or more counties. Not all counties, states, provinces, or hybrids were present every year. Crop yield and plant density were recorded on the central two rows of the plot. Maximum grain moisture value at harvest in our meta-database was 450 g kg^{-1}; however, 99.7% of all observations (n = 124,374) were below 350 g kg^{-1}, which has been reported to be an indicator that all hybrids have achieved physiological maturity (Rench and Shaw, 1971; Brooking, 1990; Sala et al., 2007). Yield was adjusted to 155 g kg^{-1} moisture. Corn hybrid CRM ratings were obtained from DuPont Pioneer. These ratings are based on hybrid comparisons with maturity checks, the harvest moisture level of the hybrid, and maturity checks at flowering.

The yield–density data collected from 2000–2010 (91,855 observations) were used for the main analysis (‘training-data’), while data collected from 2011–2014 (32,519 observations) were employed for validation purposes (‘validation-data’). The separation of data into the training and validation datasets was necessary to self-test model replicability irrespective of the difference between the two datasets in space, time, or methods of measurement. Due to differences in plant density data availablity (i.e., training data used corn which was planted to target density then thinned, whereas validation data used corn planted to a target density validated by stand count at harvest), the 2000–2010 and 2011–2014 datasets were analyzed separately. The largest dataset (2000–2010) was used for main analysis while the smaller and more recent dataset (2011–2014) was employed as validation dataset to the prediction models.

This analysis approach, i.e., the use of training and validation datasets for development of a predictive model, is a common statistical practice (Sheridan, 2013; Gholap et al., 2012; Gonzalez-Sanchez et al., 2014). The 2000–2010 dataset was used for all analysis in the present paper unless validation data are mentioned.

Descriptive statistics such as minimum, maximum, mean, standard deviation, variance, yield distribution, and variation were analyzed using PROC MEANS and PROC GLM procedures of SAS (SAS Institute, 2012) and R program (R Development Core Team, 2012) for both validation and training data. Yield variation accounted by known factors such as year, location (county), hybrid, plant density, and interaction of these factors and with unknown factors was estimated using PROC VARCOMP procedure (SAS Institute, 2012). A correlation analysis between yield and continuous variables (crop maturity, location [latitude, longitude], plant density) was conducted on PROC CORR procedure (SAS Institute, 2012).

Data analysis on the yield–density relationship was conducted in SAS and R programs. Hierarchal approaches were followed for data analysis. At first, data were analyzed as one pool of information regardless of county, state, year, and other management differences. Analysis of the average yield–density relationship was conducted on PROC MIXED procedure (SAS Institute, 2012). At this first step of the analysis, yield was the response variable, and plant density was the fixed effect variable. Factors such as replication, state, year, and hybrid were treated as random variables. Linear, quadratic, exponential, and hyperbola models were fitted to the raw data (unadjusted data) and to the least square means (adjusted data) to identify the best model that explain the general (global) and environment specific yield–density relation using PROC NLMIXED and PROC RSREG procedures (SAS Institute, 2012).

As a second step, the yield–density relationship was analyzed for latitude-based groups. Four latitude groups were identified based on the latitude of experimental sites, i.e., sites with latitude range between 30 and 35, 35 to 40, 40 to 45, and 45 to 50° N. At this step of the analysis, the yield–density relationship was modeled in PROC MIXED, with yield as the response variable and plant density as the fixed effect variable. Factors such as replication, year, and hybrid were treated as random variables. The same model was fit in PROC RSREG to identify the best quadratic model that fit the yield–density relationship at each location.

Third, the yield–density relationship was analyzed at each latitude-based group for each hybrid CRM groups. Hybrid CRM groups in the study were: (i) very early maturing (CRM < 78 d), (ii) early maturing (78 d < CRM < 88 d), (iii) medium to early maturing (88 d < CRM < 98 d), (iv) medium maturing (98 d < CRM < 105 d), (v) late maturing (105 d < CRM < 115 d), and (vi) very late maturing (CRM > 115 d). The following CRM groups are characterized as dominant within latitude group evaluated (DuPont Pioneer, 2016). Very early and early maturing (CRM < 88 d) hybrids are dominant in latitude range between 45 and 50° N. Medium to early maturing (88 d < CRM < 98 d) groups are dominant northern portion of latitude range between 40 and 45° N and medium maturing (98 d < CRM < 105 d) are dominant to the southern portion of the same 40 to 45° N latitude. Late maturing groups (105 d < CRM < 115 d) are dominant within the 35 to 40° N latitude and very late maturing (CRM > 115 d) groups are dominant within the 30 to 35° N latitude. Similar to the above steps, the yield–density relationship was modeled in PROC MIXED, with yield as the response variable and plant density as the fixed effect variable. Factors such as replication, year, and hybrid were random variables. The same model was fit in PROC RSREG to identify the best quadratic model that fits the yield–density relationship for each latitude group.

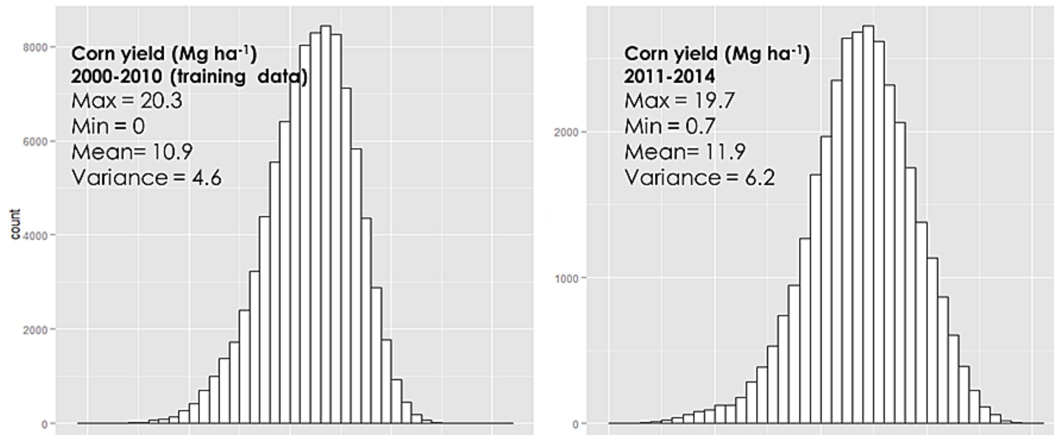
Due to strong relationships noted between productivity of the environments and yield, the fourth and fifth steps of our analysis on the yield–density relationship was conducted on bases of four yielding environments, i.e., low yielding, LY (<7 Mg ha^{-1}), medium yielding, MY (7–10 Mg ha^{-1}), high yielding, HY (10–13 Mg ha^{-1}), and very high yielding, VHY (>13 Mg ha^{-1}). Two approaches were used to define these productivity environments. The first approach utilized each experimental subplot yield (hybrids were subplots in the main plot) to determine the yield productivity environment for each observation. The reasoning behind this approach is that irrespective of the overall productivity of each site, every subplot has a microenvironment that explains its yield. The second approach utilized the mean yield in each site–year combination to determine the "productivity environment" for all observations within the site. This approach acknowledges the site and environmental conditions within a year are uniform, therefore variation is only due to treatments.

For the fourth step, the yield–density relationship was investigated for each productivity environment delineated by single yield or average yield approaches. For each productivity environment data were analyzed as one pool of information regardless of county, state, year, and other management practices. An average yield–density response was drawn. Fifth, the yield–density relationship was investigated for each productivity environment delineated by single yield approach for six hybrid CRM groups. For each hybrid CRM group by productivity environment, the yield–density relationship change was analyzed regardless of the county, state, year, and other management differences.

RESULTS

For the training meta-database, corn yield ranged from 0.1 to 20.3 Mg ha^{-1} and was normally distributed with a mean of 10.9 Mg ha^{-1} and variance of 4.6 Mg ha^{-1}. Overall mean, minimum, maximum, and standard deviation varied by state (Fig 1; Table 1). Among the known factors, year accounted for 2%, location (county) for 17%, and year × location interaction (E) for 25% of the variation in the yield factor. The 56% remnant of the yield variance was explained by hybrid (10%), plant density (16%), and higher level interactions or unknown (error) factors (30%).

A significant positive correlation was documented between yield and hybrid CRM factors ($r = 0.36$). There was also a significant but negative correlation between latitudinal location and yield ($r = -0.27$). Overall, yield increased with hybrid CRM but decreased with increasing latitude. In general, yield increased with increasing plant density (positive correlation). However, the linear yield–density relationship was stronger (improved *r*) when G × E were considered. The latter concept is further demonstrated and discussed in the next sections of this manuscript.



Statistics		
Median	11.10	12.00
Mode	11.50	12.20
SD	2.14	2.48
range	20.30	19.0

Fig. 1. Descriptive statistics and distribution of the DuPont Pioneer hybrid test data for years 2000–2010 ('training data') and for years 2011– 2014 ('validation data').

Table 1. Descriptive statistics, location (state or province), and total data points for corn grain yield in DuPont Pioneer hybrid test from 2000 to 2014. In total, there were 124,374 observations gathered from 22 US states and 2 Canadian provinces (91,855 data points in 2000–2010; 32,519 data points in 2011–2014).

2000 to 2010							2011 to 2014						
Location	County latitude	Data points	Yield				Location	County latitude	Data points	Yield			
			Mean	Min.	Max.	SD				Mean	Min.	Max.	SD
	°N	No.	Mg ha^{-1}					°N	No.	Mg ha^{-1}			
GA	30–35	693	12.30	7	17.7	2.03	GA	30–35	410	12.88	8.5	17.2	1.56
AR	35–40	409	11.66	7.5	16.3	1.80	MS	30–35	160	12.83	7.3	17.5	2.18
DE	35–40	636	12.43	7.7	16.2	1.51	TX	30–40	817	12.86	4.9	19.7	2.95
KS	35–40	4061	11.57	4.4	20	2.06	KS	35–40	2607	11.86	2.7	17.8	2.71
MO	35–40	5638	11.19	2.9	18.4	2.12	MO	35–40	824	11.01	1.7	18.1	3.67
TN	35–40	1756	11.47	2.9	16.9	1.79	TN	35–40	393	11.36	0.7	18.2	3.77
IN	35–45	6677	11.34	4	16.8	1.90	IN	35–45	3149	12.18	3.8	19.1	2.47
OH	35–45	3571	11.66	2.8	18.4	2.14	OH	35–45	3178	12.50	1.6	18.5	2.03
PA	35–45	2297	11.82	6.3	17.6	1.97	MD	35–40	219	13.08	8.7	17.2	1.79
CO	40–45	2905	11.43	2.1	17.2	1.88	NC	35–40	400	8.43	2.6	13.7	2.44
IA	40–45	12728	11.24	0.4	17.6	1.96	IL	35–45	4213	12.52	1.4	19.1	2.38
IL	40–45	7923	11.31	1.5	16.9	1.86	CO	40–45	1225	12.63	4.1	17.2	1.77
MI	40–45	2727	10.45	4.7	16.5	2.05	MI	40–45	1049	11.96	6.1	16.5	1.79
NE	40–45	13312	11.39	0.8	20.3	2.34	NE	40–45	3205	13.25	4.8	19.3	2.37
SD	40–45	3251	9.78	2.4	15.9	2.18	SD	40–45	1565	10.52	3.5	15.8	2.01
MN	40–50	9394	10.31	0	18.5	1.80	MN	40–50	1251	10.42	6.2	14.8	1.49
ON	40–50	4327	9.37	1.3	15.9	2.46	ON	40–50	649	11.31	6.4	15.5	1.81
WI	40–50	4625	10.65	2	15.9	2.07	WI	40–50	846	11.20	3.7	16	2.49
ND	45–50	2913	9.35	2.1	15.3	1.79	IA	40–45	4505	11.18	1.4	17.8	2.07
QC	45–50	2012	9.51	3.1	15.2	2.03	PA	40–45	755	10.99	4.4	16.4	2.60
							ND	45–50	952	10.41	5	15.1	1.59
							QC	45–50	147	10.34	5.1	14.4	1.73

Grain-Yield Response to Plant Density

Overall Yield–Density Relationship

Averaged across all variables (site, year, and hybrid), yield response to plant density varied significantly as density increased from ~45 to 100 thousand plants ha^{-1} (Fig. 2a, b). Average yield increased significantly, with a slope of 90 g plant^{-1}, with a density increase from ~45 to 60 thousand plants ha^{-1}. A moderate yield increase, 39 g plant^{-1}, was documented when density increased from ~60 to 75 thousand plants ha^{-1}, but with a less proportional increase, 10 g plant^{-1}, when density increased from ~75 to 90 thousand plants ha^{-1}. For the upper density data, when density increased from ~89 to 100 thousand plants ha^{-1}, average yield declined by 5 g plant^{-1}. Compared with the best linear, exponential, and hyperbola models fitted to the data, the quadratic model best explained the yield–density relationship based on all statistical model selection criterions considered (Table 2). When the quadratic model was fitted to the raw data (unadjusted to any factor) the R^2 = 0.13 (13%), a value close to the percentage (%) of variance of yield explained by plant density. When the quadratic model was fitted to the least square means (adjusted mean for other factors), the R^2 = 0.99. Based on the quadratic model from the training dataset, an optimal plant density for agronomically maximum yields was ~90 thousand plants ha^{-1}.

The quadratic model obtained from the training dataset was superimposed on the validation dataset (Fig. 2c). The model fit, Root Mean Square Error (RMSE) of 1.46 Mg ha^{-1}, under predicted the mean perhaps due to the genetic gain over the 2011–2014 period as compared with training set of 2000–2010. Despite the under prediction, estimates remained within the standard deviation of the actual mean (Fig. 2c; Table 1) for most of the data points, particularly for those points that have a large population (>100 observations). Extremely low or high densities, data at the edges, had relatively few observations (<100 observations) for the 2011–2014 dataset, resulting in large standard deviation and being far from the fitted model.

Yield–Density Relationship by Location (Latitude)

The average yield–density relationship in the four latitude-based groups followed a similar trend despite significant differences in actual yield levels (Fig. 3). As latitude increased, at a comparable density level yield response to plant density decreased. However, in all four latitude groups, yield increased significantly when density increased from ~45 to 60 thousand plants ha^{-1} and continued to increase moderately when plant density changed from ~60 to 75 thousand plants ha^{-1}. However, when plant density increased from ~75 to 89 thousand plants ha^{-1},

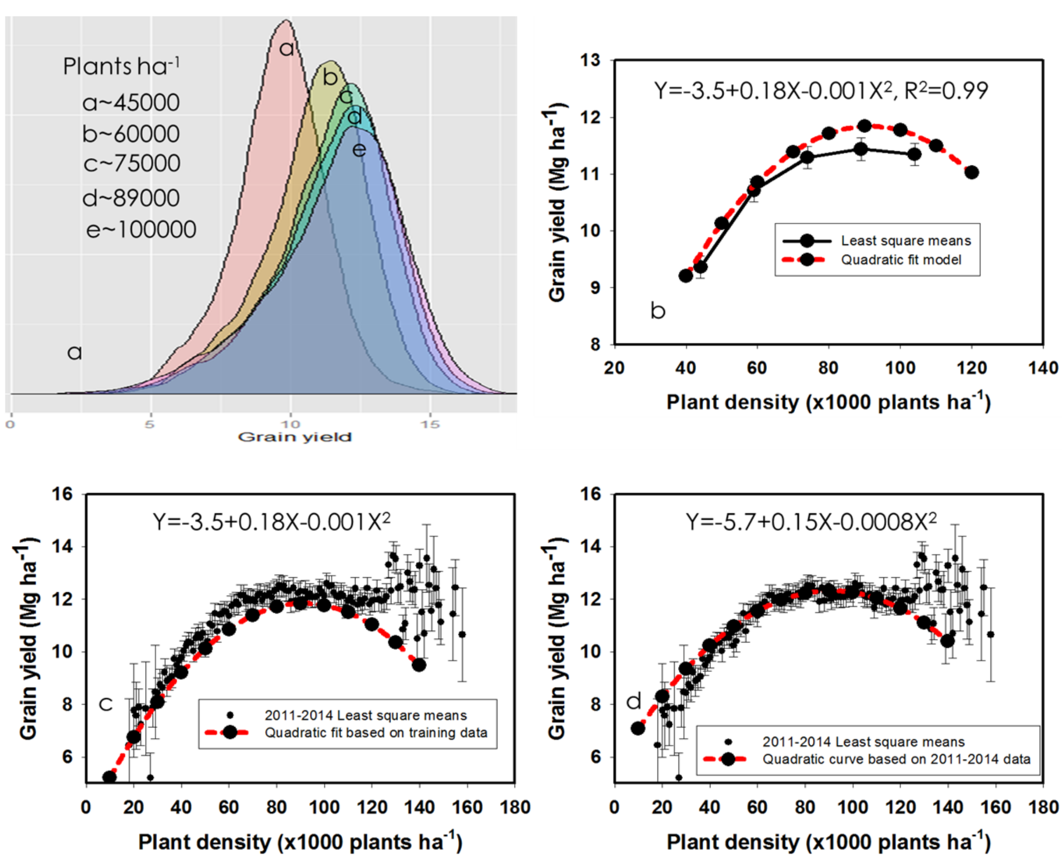


Fig. 2. Grain yield distribution for five plant densities, (a) mean response at each density level, (b) quadratic fitted model for the grain yield–density relationship calculated from the training database, (c) training dataset superimposed on validation dataset, and (d) validation data set and its best quadratic fit. Vertical bars in the graph are the standard error.

Table 2. Comparison of linear, quadratic, exponential, and modified hyperbola models on the training dataset using four model selection criterion, i.e., coefficient of determination (R^2), Akaike Information Criterion (AIC), Corrected Akaike Information Criterion (AICC), and Bayesian Information Criterion (BIC). For AIC, AICC, and BIC, the smaller the value the better the model. The selection criterion for the four different models fitted on the entire data (unadjusted) and on the least square mean (adjusted for other factors) were presented for the global yield–density relationship. Models fit on the least square mean values were presented for enviroment specific models (models for each of four yielding environments). Values in boldface indicate cases where the performance of selected model (quadratic model) is better than the rest of the models.

Global model		Fitted on the entire data				Fitted on the mean			
	Criterion	Linear	Quadratic	Exponential	Hyperbola	Linear	Quadratic	Exponential	Hyperbola
	R^2	0.10	**0.13**	0.12	0.12	0.73	**0.99**	0.94	0.88
	AIC	392659	**389451**	392848	390675	11.1	**–5.7**	44.0	7.0
	AICC	392659	**389451**	392848	390675	35.1	**18.3**	68.0	31.0
	BIC	392688	**389480**	392876	396704	9.9	**–6.9**	42.9	5.8
Environment-specific model fitted on the mean		Low yielding environment				Medium yielding environment			
		Linear	Quadratic	Exponential	Hyperbola	Linear	Quadratic	Exponential	Hyperbola
	R^2	0.70	**0.80**	0	0.49	0.17	**0.93**	0.71	0.39
	AIC	–4.8	–6.9	–	–8.1	–7.4	**–19.7**	42.1	–9.0
	AICC	19.2	**17.1**	–	21.9	16.6	**4.3**	66.1	15.0
	BIC	–6.0	**–8.1**	–	–3.3	–8.6	**–20.9**	41.0	–10.1
		High yielding environment				Very high yielding environment			
		Linear	Quadratic	Exponential	Hyperbola	Linear	Quadratic	Exponential	Hyperbola
	R^2	0.71	**0.97**	0.98	0.89	0.96	**0.98**	0.82	0.96
	AIC	2.9	**–10.4**	44.5	–1.9	–10.8	1.5	46.3	–11.2
	AICC	26.9	**13.6**	68.5	22.1	13.2	25.5	70.3	12.8
	BIC	1.7	**–11.5**	43.3	–3.1	–12.0	0.4	45.1	–12.4

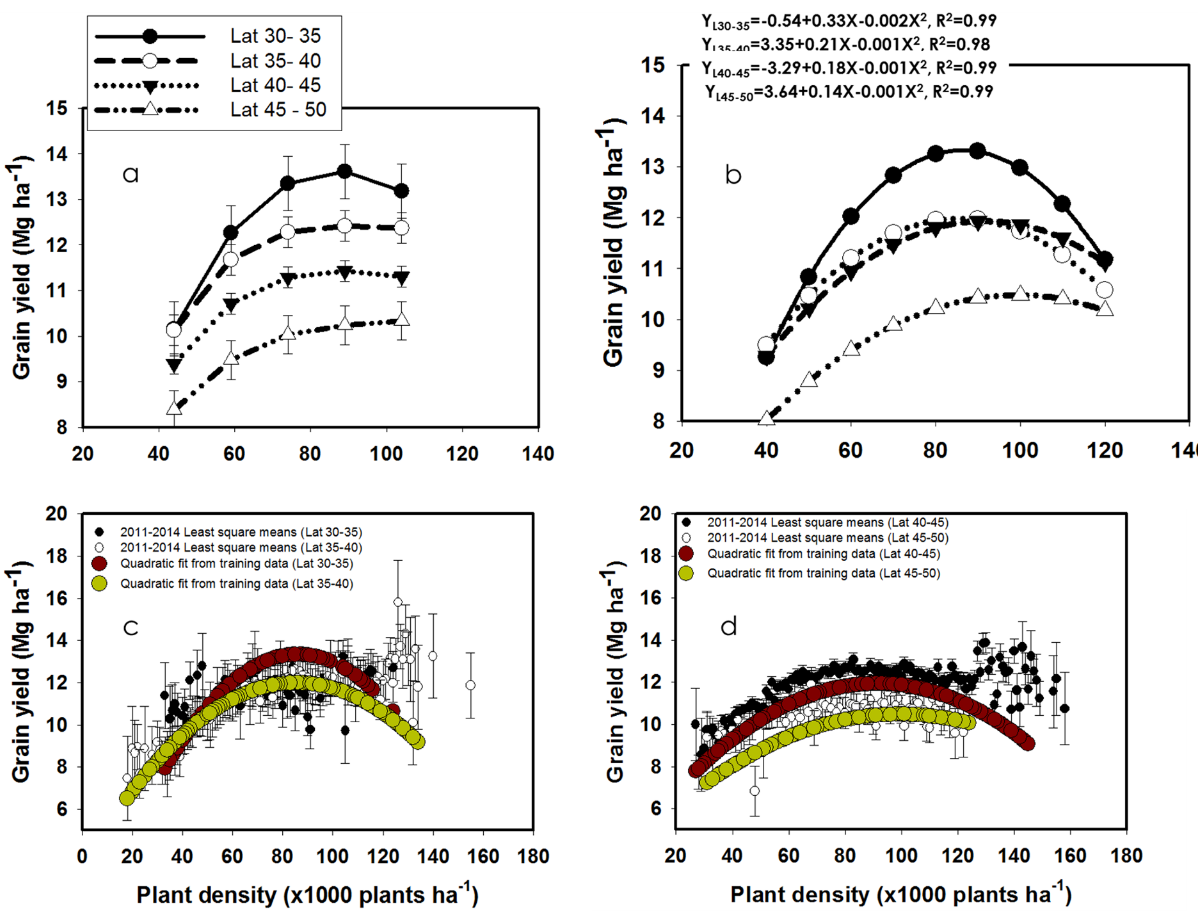


Fig. 3. Average corn grain yield under five plant densities 2000–2010 (a), the quadratic models that best fit this training data (b), and quadratic model superimposed on validation data set (c and d) by latitude groups in the United States and southeast Canada. Vertical bars in the graph are the standard error.

yield response to plant density increased with higher latitude (Lat. 45–50° N) but not significantly with the lowest latitude (Lat. 30–35° N). For a planting density increase from ~89 to 100 thousand plants ha^{-1}, yield declined in the lowest latitude group but did not significantly change for the other latitude groups (Fig. 3a). Maximum yields of 13.5, 12.4, 11.7, and 10.2 Mg ha^{-1} were estimated at about 87, 89, 89, and 95 thousand plants ha^{-1} for latitude ranges 30–35, 35–40, 40–45, 45–50° N, respectively (Fig. 3b).

The quadratic equations derived from the 2000–2010 training dataset were superimposed on the 2011–2014 dataset (Fig. 3c, d). A RMSE of 1.49, 1.55, 1.57, and 1.04 Mg ha^{-1} were obtained for latitude ranges 30–35, 35–40, 40–45, 45–50° N, respectively. These RMSE are within the ranges of the standard deviation reported for the yield factor (Table 1), thus, it can be postulated that the quadratic model has an adequate fit to the validation data. Model performance could further be improved with better genetic gain estimation as well as substantial data points at either edges (low/high) of the density factor.

Yield–Density Relationship by Hybrids

Overall, there was a tendency for yield, at each plant density, to decline as hybrid CRM decreases within a location (Fig. 4). However, in all four latitude groups, there was no significant difference in the yield response curve between very long- (CRM > 115 d) and long-maturing (106 d < CRM < 115 d) corn hybrids. In addition, unlike the generalization that yield was lower with decreasing hybrid CRM in the higher latitudes, yield of very long- (CRM > 115 d) and long-maturing (106 d < CRM < 115 d) were lower than the medium-maturing (95 d < CRM < 105 d) hybrids. This is likely due to the shorter length of the crop growing season. In the lower latitudes (30–40° N), yield of all maturity groups increased sharply at lower density range (~45 to ~75 thousand plants ha^{-1}), moderately at medium density range (~75 to ~89 thousand plants ha^{-1}), but did not change at the highest density range (~89 to ~100 thousand plants ha^{-1}). A similar conclusion can be drawn for higher latitudes, except that the yield gain due to increased plant density is relatively low as the latitude factor increases.

Overall, maximum yield declined with both decreasing hybrid CRM and increasing latitude. In most cases, long- and very long-maturing hybrids reached their maximum yield within the plant density range of 84 to 87 thousand plants ha^{-1}. On the other hand, very early- to medium-maturing hybrids had their maximum yield usually at a higher density range of 90 to 97 thousand plants ha^{-1}.

Grain Yield Response to Plant Density by Productivity Environment

Yield–Density Relationship by Environment

The yield–density relationship was evaluated based on four productivity environments defined based on a single plot yield ('single yield' approach) for each hybrid–density–site

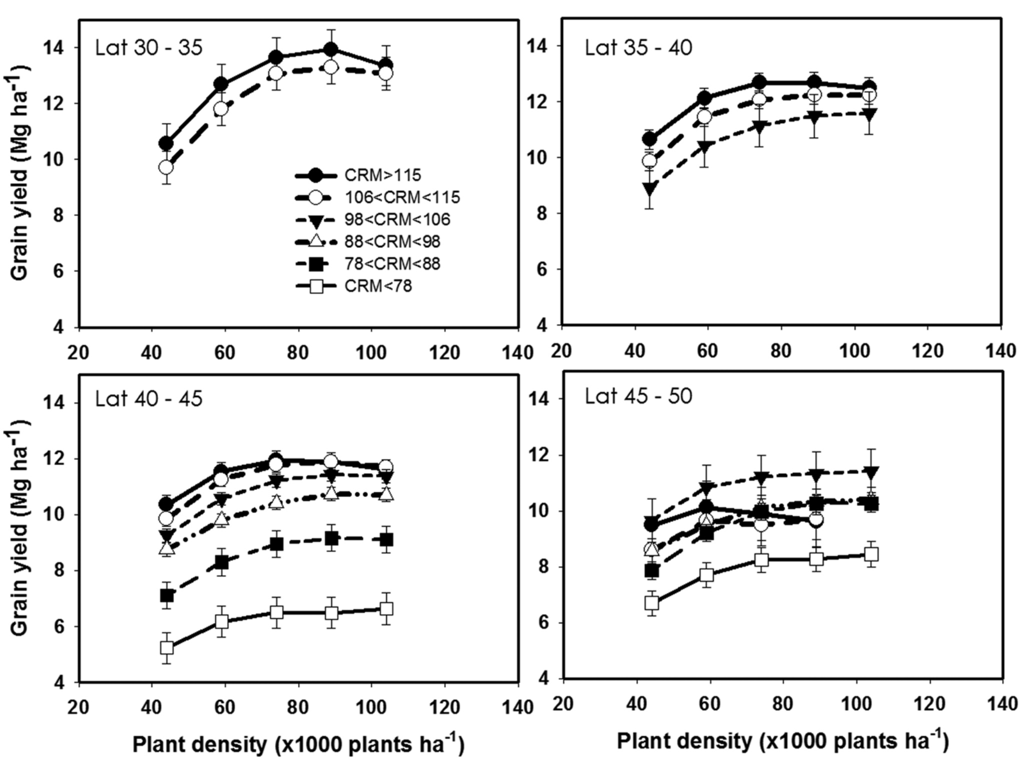


Fig. 4. Corn grain yield response to plant density for six hybrid crop comparative relative maturity groups under five plant density levels in four location (latitude) groups in the United States and southeast Canada. In lower latitudes (30–40° N), only hybrids with longer crop comparative relative maturity groups were in the trial and in higher latitudes (45–50° N), only medium and short maturing groups can yield due to the short growing season.

combination (low yielding, LY; medium yielding, MY; high yielding, HY; and very high yielding, VHY). For the training data set, the number of data points for each year of data collection that fall into each productivity environment are provided at the state scale (Table 3). Four different response models and optimal plant densities for maximum yield were identified (Fig. 5).

For the LY environment, a maximum yield of ~6.2 Mg ha^{-1} was attained at a plant density level of 60 thousand plants ha^{-1}. Further density increases resulted in yield reductions (Fig. 5a). For the MY environment, a maximum yield of about 9 Mg ha^{-1} was attained at 60 thousand plants ha^{-1}, plateauing afterward (Fig. 5b). In the HY environment, yield increased relatively sharply for plant density increases from

Table 3. Number of data points by year and state or province that fall into four yielding environments using subplot yield.

Year	Number of data points that fall into each yield grouping by state or province			
	Low yielding	Medium yielding	High yielding	Very high yielding
2000	IA (14), IL (14), IN (26), MI (124), MN (107), MO (8), OH (71), PA (5)	IA (302), IL (338), IN (235), MI (114), MN (465), MO (36), ND (92), NE (29), OH (9), ON (107), PA (307)	IA (508), IL (276), IN (323), MI (146), MN (361), MO (107), ND (111), NE (92), ON (156), PA (383)	IA (63), IL (7), IN (9), MI (98), MN (8), MO (6), ND (2), NE (23), ON (17), PA (15)
2001	CO (1), IA (18), KS (15), MI (4), MN (50), ND (135), NE (125), ON (155), QC (144), WI (2)	CO (44), IA (288), IL (75), KS (130), MI (142), MN (220), MO (24), ND (288), NE (202), OH (50), ON (144), PA (28), QC (185), WI (67)	CO (102), IA (463), IL (334), KS (158), MI (12), MN (157), MO (125), ND (101), NE (511), OH (65), ON (314), PA (122), QC (11), WI (223)	CO (15), IA (119), IL (106), IN (174), KS (28), MN (11), MO (9), NE (121), OH (5), ON (43), PA (103), WI (60)
2002	IL (6), IN (82), KS (5), MN (15), MO (159), NE (102), ON (163), QC (39), WI (110)	CO (47), GA (4), IA (171), IL (94), IN (276), KS (113), MI (22), MN (331), MO (73), NE (470), ON (258), PA (12), QC (144), TN (39), WI (69)	CO (170), GA (32), IA (713), IL (173), IN (132), KS (130), MI (208), MN (386), MO (156), NE (702), ON (46), PA (67), QC (19), TN (64), WI (143)	CO (23), GA (74), IA (322), IL (92), IN (4), KS (66), MI (37), MN (7), MO (42), NE (272), PA (20), TN (3), WI (71)
2003	IA (6), IL (1), IN (31), MN (7), MO (74), ND (19), NE (33), ON (40), QC (25), WI (62)	CO (39), DE (9), IA (353), IL (27), IN (286), KS (9), MI (185), MN (245), MO (187), ND (220), NE (285), OH (2), ON (149), QC (161), TN (13), WI (118)	CA (103), DE (75), IA (713), IL (441), IN (251), KS (145), MI (69), MN (355), MO (74), ND (86), NE (671), OH (116), ON (90), QC (154), TN (77), WI (121)	CO (44), DE (5), IA (113), IL (182), IN (2), KS (64), MN (18), MO (184), ND (1), NE (438), OH (62), ON (37), QC (2), TN (66), WI (3)
2004	CO (1), IA (1), MN (6), ND (55), NE (9), ON (190), QC (7), TN (2), WI (4)	CO (101), DE (3), GA (45), IA (40), IL (98), IN (41), MI (171), MN (353), MO (92), ND (300), NE (210), OH (6), ON (344), PA (2), QC (74), TN (58), WI (123)	CO (200), DE (76), GA (153), IA (523), IL (499), MN (551), MO (642), ND (8), NE (447), OH (91), ON (62), PA (77), QC (123), TN (186), WI (219)	CO (46), DE (71), GA (52), IA (331), MN (14), MO (75), NE (328), OH (203), PA (112), QC (13), TN (89), WI (47)
2005	CO (9), IA (3), MN (2), MO (3), ND (12), NE (163), OH (4), ON (106), QC (20), TN (6)	CO (87), DE (12), IA (331), IL (121), IN (75), KS (62), MI (22), MN (193), MO (87), ND (154), NE (134), OH (286), ON (125), PA (8), QC (80), SD (56), TN (54), WI (79)	CO (98), DE (55), IA (601), IL (446), IN (300), KS (354), MI (174), MN (459), MO (183), ND (190), NE (824), OH (261), ON (252), PA (84), QC (85), SD (210), TN (146)	CO (2), DE (27), IA (244), IL (166), IN (45), KS (53), MI (104), MN (18), MO (25), ND (1), NE (563), OH (1), ON (54), PA (47), QC (5), SD (67), TN (20), WI (77)
2006	IL (24), MN (17), ND (7), NE (114), ON (18), QC (3), SD (88), TN (1), WI (3)	CO (35), DE (1), IA (176), IL (253), IN (93), MI (11), MN (216),MO (216), ND (109), NE (308), OH (102), ON (63), QC (68), SD (193), TN (49), WI (81)	CO (202), DE (45), IA (902), IL (624), IN (550), MI (113), MN (386), MO (373), ND (176), NE (697), OH (500), ON (110), QC (114), SD (99), TN (190), WI (274)	CO (66), DE (71), IL (377), IL (57), IN (19), MI (32), MO (157), MN (31), ND (54), NE (509), OH (69), ON (94), QC (4), SD (33), TN (15), WI (88)
2007	IA (1), IL (8), MN (82), ND (12), NE (1), OH (6), ON (9), SD (155), WI (1)	CO (93), DE (16), GA (10), IA (257), IL (178), IN (79), MI (55), MN (341), MO (158), ND (128), NE (507), OH (164), ON (115), PA (12), QC (31), SD (167), TN (18), WI (141)	CO (316), DE (85), GA (45), IA (606), IL (480), IN (452), MI (155), MN (435), MO (519), ND (97), NE (765), OH (256), ON (46), PA (76), QC (50), SD (136), TN (89), WI (349)	CO (65), DE (85), GA (109), IA (241), IL (149), IN (199), MI (9), MN (76), MO (143), ND (1), NE (249), OH (184), PA (178), QC (5), TN (55), WI (48),
2008	IA (38), KS (1), MI (10), MO (3), ND (9), NE (22), ON (17), SD (16), WI (6)	AR (49), CO (23), IA (200), IL (22), IN (45), KS (271), MI (168), MN (160), MO (152), ND (103), NE (417), OH (48), ON (119), PA (10), QC (41), SD (317), TN (37)	AR (144), CO (260), IA (626), IL (281), IN (296), KS (496), MI (69), MN (676), MO (551), ND (101), NE (526), OH (238), ON (160), PA (76), QC (125), SD (356),TN (113), WI (363)	AR (28), CO (165), IA (318), IL (217), IN (412), KS (255), MN (174), MO (246), NE (414), OH (162), ON (55), PA (125), QC (10), SD (15), TN (92), WI (50)
2009	IL (5), MN (30), MO (10), ND (10), ON (35), SD (111), TN(3), WI (81)	AR (35), CO(5), GA (33), IA (234), IL (73), IN (148), KS (23), MI (38), MN (639), MO (97), ND (94), NE (72), OH (3), ON (246), PA (60), QC (71), SD (430), TN(52), WI (198)	AR (73), CO (150), GA (117), IA (1074), IL (281), IN (756), KS (338), MI (215), MN (885), MO (287), ND (62), NE (760), OH (179), ON (11), PA (194), QC (97), SD (399), TN(124), WI (430)	AR (80), CO (109), GA (19), IA (323), IL (192), IN (277), KS (292), MI (62), MN (120), MO (200), ND (1), NE (505), OH (370), PA (25), SD (12), TN(13), WI (32)
2010	CO (29), IA (257), IL (82), MN (30), ND (6), NE (26), ON (34), TN(3)	CO (83), IA (356), IL (313), IN (13), KS (126), MI (68), MN (309), MO (38), ND (68), NE (161), OH (13), ON (112), PA (8), QC (12), SD (61), TN(22), WI (95)	CO (99), IA (443), IL (844), IN (96), KS (485), MI (50), MN (434), MO (83), ND (98), NE (279), OH (40), ON (183), PA (70), QC (67), SD (267), TN(55), WI (216)	CO (43), IA (59), IL (174), IN (10), KS (347), MN (14), MO (30), ND (4), NE (226), OH (5), ON (48), PA (71), QC (23), SD (54), TN(9), WI (20)

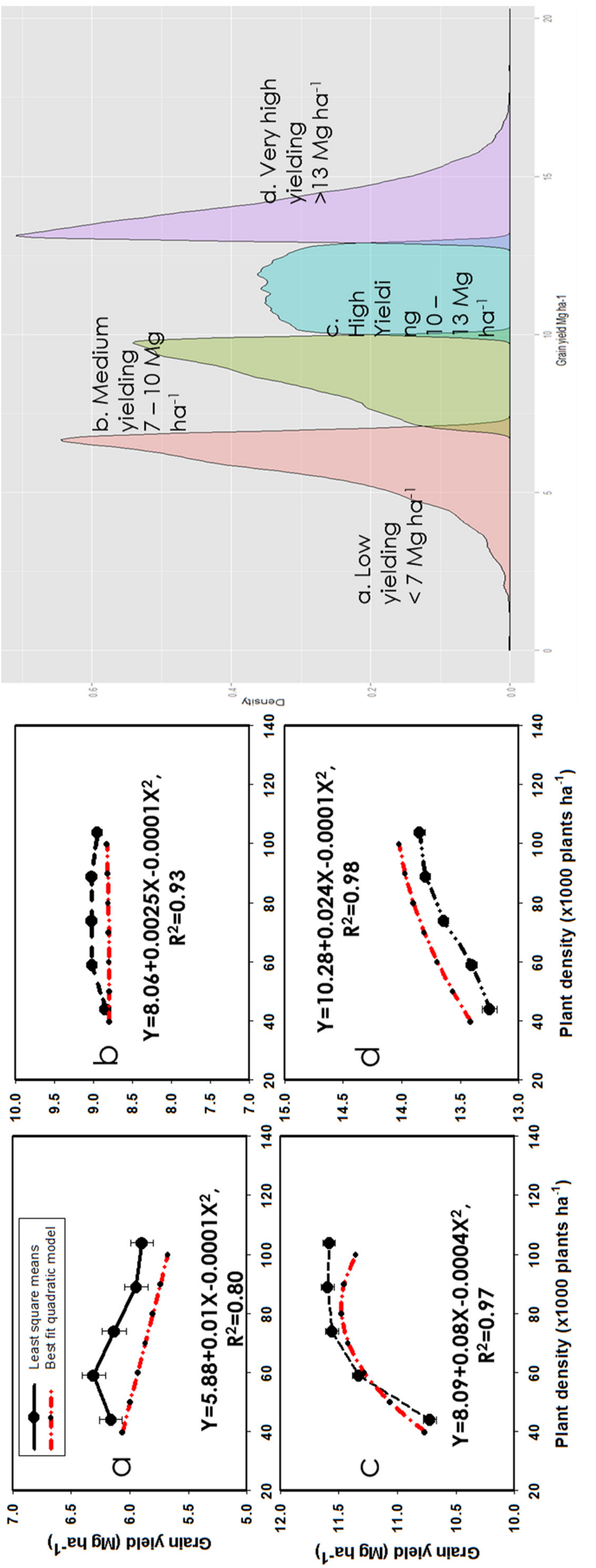


Fig. 5. Models for grain yield response to plant density in four productivity environments, i.e., (a) low yielding, (b) medium yielding, (c) high yielding, and (d) very high yielding. The frequency distribution plot on the right indicates the yield boundaries of each environment and grain yield frequency. Productivity environments are delineated by a single plot grain yield approach. This approach uses a single plot grain yield for each hybrid–density–site combination to determine its productivity environment. Vertical bars in the graph are the standard error.

45 to 75 thousand plants ha^{-1}, followed by a slow growth or stable yield when density overpassed 75 thousand plants ha^{-1} (Fig. 5c). Maximum yield was about 11.5 Mg ha^{-1} at 100 thousand plants ha^{-1}. In a VHY environment (>13 Mg ha^{-1}), yield response to plant density continued to increase even at 100 thousand plants ha^{-1} (Fig. 5d).

When the 'average site yield' approach was implemented for classifying the productivity environments (Table 4), only two types of responses were identified, that is, there was a decreasing response in LY and an 'increasing until maximum' response for the other environments (Fig. 6). For the LY environment, maximum yield (6.2 Mg ha^{-1}) was attained at a plant density level of 73 thousand plants ha^{-1} (Fig. 6a). For the MY, HY, and VHY environments, maximum yields of 9.4, 12.2, and 14.4 Mg ha^{-1} were attained with densities of 83, 90, and 92 thousand plants ha^{-1}, respectively (Fig. 6b). Maximum yield, maximum yielding plant density (MYPD), and coefficient of determination (R^2) value to fitted model increased with increase in the productivity environment (Fig. 6). As indicated in the materials and methods, productivity environments in the paper are based on yield. Rainfall is among one of the major environmental factors influencing yields, therefore, overall growing season, April to October (average across all latitudes), precipitation by state are presented in Table 5.

Yield–Density Relationship by Productivity Environment × Genotype

Evaluation of yield response of six hybrids CRM clusters in four productivity environment groups (with the 'single site yield' approach) resulted in different responses by CRM group and productivity environment (Fig. 7). In the LY environment, long- and very long-maturing hybrids reached their maximum yield with lower densities from 40 to 60 thousand plants ha^{-1}, declining as density increased. Short CRM hybrids reached MYPD at relatively greater density than the long CRM groups. In the MY environment, negligible yield responses were observed for very long- and long-maturing hybrids. Yield of long CRM were superior to short CRM groups but yield did not vary with changes in density. As CRM decreased, a yield response for increasing density was observed. As productivity improved from MY to VHY, yield increased across all densities and CRM groups. In the HY environment, the MYPD for long

Table 4. Number of data points by year and state or province that fall into four yielding environments using average site yield.

Year	Number of data points that fall into each yield grouping by state or province			
	Low yielding	Medium yielding	High yielding	Very high yielding
2000	OH (80)	IA (287), IL (635), IN (261), MI (482), ON (143)	IA (600), IN (332), MN (567), MO (157), ND (205), NE (144), ON (137), PA (710)	–
2001	NE (119), ON (236)	IA (238), KS (195), MI (158), MN (200), ND (524), QC (340)	CO (192), IA (490), IL (515), KS (136), MN (238), MO (158), NE (840), OH (120), ON (420), PA (253), WI (352)	IA (160)
2002	MO (200), ON (189), WI (140)	IN (315), KS (173), MN (530), NE (527), ON (278), PA (12), QC (202)	CO (240), IA (1056), IL (209), IN (179), KS (141), MI (267), MN (209), MO (230), NE (1019), PA (99), TN (106), WI (253)	GA (110), IA (150), IL (156)
2003	–	IA (229), IN (179), MI (254), MN (240), MO (259), ND (206), NE (483), ON (183), QC (114), WI (148)	CA (186), DE (89), IA (956), IL (651), IN (391), KS (218), MN (385), ND (120), NE (552), OH (180), ON (133), QC (228), TN (156), WI (156)	MO (260), NE (392)
2004	–	MI (211), MN (225), ND (363), ON (596), WI (157)	CO (348), DE (150), GA (150), IA (895), IL (767), IN (585), MO (809), NE (706), QC (217), TN (335), WI (236)	NE (392), OH (300), PA (191)
2005	ON (97)	IA (250), ND (357), NE (476), OH (334), ON (72), QC (190)	CO (196), DE (94), IA (929), IL (733), IN (420), KS (469), MI (300), MN (672), MO (298), NE (911), OH (218), ON (368), PA (139), SD (333), TN (226), WI (448)	NE (491)
2006	–	MN (141),MO (300), ND (172), NE (569), OH (58), SD (269)	CO (303), IA (1455), IL (958), IN (662), MI (156), MN (509), MO (450), ND (172), NE (568), OH (671), ON (227), QC (189), SD (144), TN (255), WI (446)	DE (117), NE (491)
2007	MN (145), SD (295)	IA (168), MN (177), ND (134), NE (755), ON (170), WI (135)	CO (474), DE (186), IA (937), IL (815), IN (730), MI (219), MN (612), MO (820), ND (104), NE (499), OH (391), QC (86), SD (163), TN (162), WI (404)	GA (164), NE (268), OH (219), PA (266)
2008	–	KS (345), MI (247), ND (213), NE (404), ON (141), PA (10), WI (180)	AR (221), CO (448), IA (948), IL (293), IN (453), KS (338), MN (1010), MO (952), NE (439), OH (448), ON (210), QC (176), SD (522),TN (235), WI (498)	IA (234), IL (227), IN (300), KS (340), NE (536), PA (211)
2009	WI (157)	MN (889), ND (167), ON (292), SD (434)	AR (188), CO (264), GA (169), IA (1244), IL (551), IN (1181), KS (653), MI (315), MN (785), MO (594), NE (1337), PA (279), QC (168), SD (518), TN(192), WI (584)	IA (387), OH (552)
2010	IA (257), KS(105)	IA (484), MI (118), MN (282), ND (86), ON (90)	CO (254), IA (441), IL (1413), IN (119), KS (723), MN (505), MO (151), ND (90), NE (692), OH (31), ON (287), PA (149), QC (102), SD (391), TN(89), WI (331)	KS (225), OH (27)

CRM hybrids was in relatively lower plant density as compared with the medium CRM groups. Perhaps due to low per-plant potential and reduced leaf area, greater density was required for short CRM to yield comparable to long CRM hybrids. Hybrids with very short maturity (CRM <78 d) did not yield >13 Mg ha^{-1} even when plant density reached 100 thousand plants ha^{-1}. Thus, short CRM hybrids are not present in the VHY environment (Fig. 7d).

DISCUSSION

This synthesis-analysis confirmed that corn yield response to plant density is a function of the complex G × E interaction. Comparable yield distribution for the entire meta-database herein analyzed was previously documented (Just and Weninger, 1999; Claassen and Just, 2011; Assefa et al., 2014). However, there are studies which argued that crop yields (at county scale) were not normally distributed, but instead were negatively or positively skewed (Harri et al., 2009; Hennessay, 2009). A small skewness to the negative on both the 2000–2010 ('training data') and the 2011–2014 ('validation data') datasets were evident but not highly deviated from the normal distribution (Fig. 1), with similar mean and median parameters. Strength of the yield–density relationship increased from LY (R^2 = 0.56 or 0.80) to VHY (R^2 = 0.98 or 0.99) environments (Fig. 5, 6; Table 2), indicating a large proportion of unaccounted variation under most limiting productivity environments, with many other factors blocking potential yield.

For the yield–density meta-database, a quadratic model resulted in the best fit regardless of the hybrid, location, and other factors. Previous research documented comparable quadratic yield–density models (Stanger and Lauer, 2006; Coulter et al., 2010; Van Roekel and Coulter,

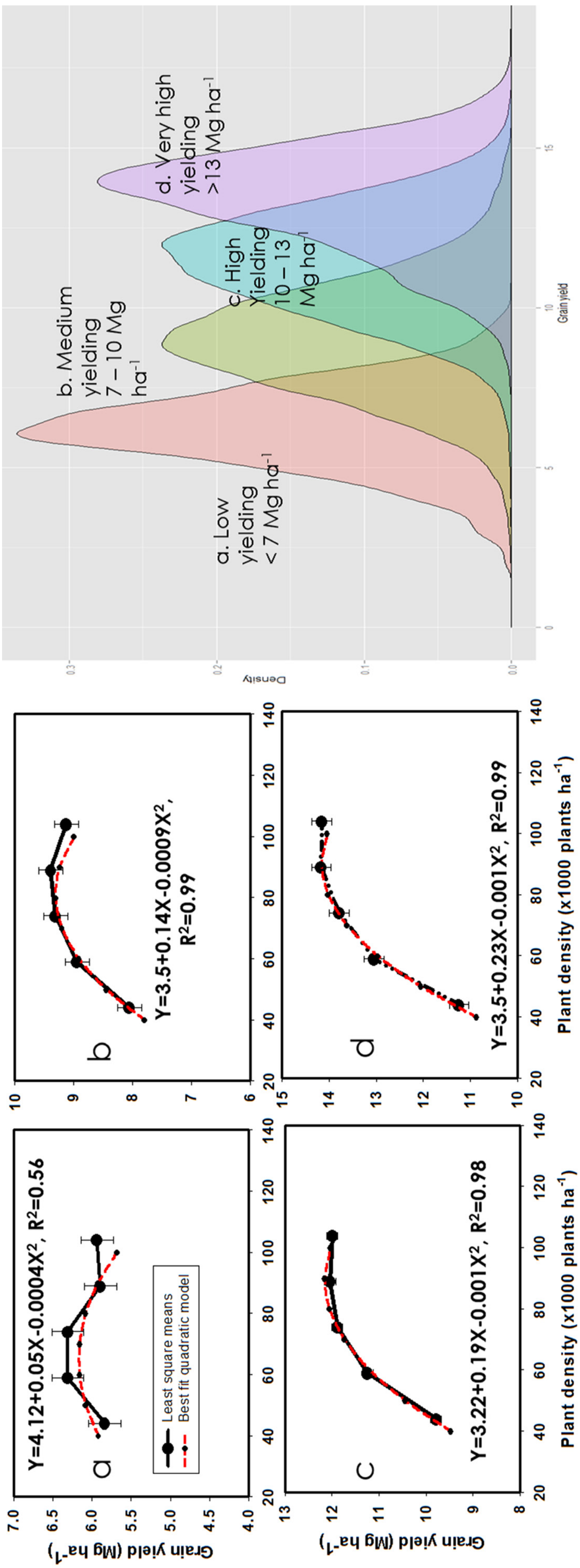


Fig. 6. Models for grain yield response to plant density in four productivity environments, i.e., (a) low yielding, (b) medium yielding, (c) high yielding, and (d) very high yielding. The frequency distribution plot on the right indicates the yield boundaries of each environment and grain yield frequency. Productivity environments are delineated by average of site yield approach. Average grain yield approach uses a site average grain yield to determine environment for all grain yield measurements at that site for that given year. Vertical bars in the graph are the standard error.

2011). An important consideration is whether the quadratic model is biologically meaningful. Looking at the least square mean estimate connected by line side by side with quadratic curves (Fig. 2, 3, 6), it can be generalized that a quadratic curve constitutes four major regions, i.e., (i) relatively rapid growth, (ii) slow growth, (iii) no (zero) growth, and (iv) declining growth as density progresses from low to high (Fig. 8a). The rapid yield growth region is represented by an area where the addition of more plants increases yield more rapidly than in any other region of the curve (or plant density level). Theoretically, starting from a very low density where there is a sufficient supply of resources and no plant-to-plant competition, it might be expected that each additional plant will increase yield with a magnitude to the product of yield components: additional ears, number of kernels, and weight of each kernel. Following this rationale, yield at very low density increases with increasing density with slope that is equal to ears by kernels per ear by kernel weight. The first region in the yield–density relationship, described as a positive and rapid increase area, can be understood as purely a linear ratio of yield improvement as density increases under no other limiting factors. The theoretical framework depicted in Fig. 8 demonstrates the departure from the rapid increasing zone as plant density increases.

As density increases, resource allocation at the plant scale decreases and plant-to-plant competition increases consequently limiting per-plant yield potential. The impact of crowding stress on corn yields was previously reported by several researchers (Downey, 1971; Duncan, 1984; Weiner, 1993; Averbeke and Marais, 1992). A slow growth yield–density response region is a region where yield per area increases slowly even though yield per plant is less than the maximum potential. In this slow growth region, individual plants produce less than expected due to competition that reduces either number of ears, kernels per ear, or kernel weight. Resource competition constrains yield proportionally as the number of plants increases per unit area (and moisture stress deficit), consequently reducing yield per plant (and its components). However, in the slow yield response to plant density region, the reduction in yield per plant is smaller than the yield gain from the additional plant. Therefore, yield gain in the slow growth region is less than that of the rapid growth yield–density response region. As plant density increases, a decrease in yield per

Table 5. Cumulative precipitation by location (state or province) from April 1 to October 1, 2000–2014.

Location	County latitude	Cumulative precipitation April 1 to October 1, 2000–2010										
		2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
	°N	mm										
GA	30–35	521	551	548	846	791	726	481	433	403	692	512
AR	35–40	523	470	487	595	573	455	534	557	870	812	508
DE	35–40	724	607	540	729	707	507	673	489	558	361	525
KS	35–40	347	461	358	484	504	481	381	495	533	525	494
MO	35–40	520	552	554	544	543	475	414	534	792	652	729
TN	35–40	586	583	619	897	730	619	612	271	490	772	613
IN	35–45	634	551	595	724	578	533	529	424	552	559	490
OH	35–45	611	529	537	723	647	519	605	465	521	476	468
PA	35–45	582	467	532	755	865	434	652	473	508	600	528
CO	40–45	196	208	143	206	271	211	197	239	208	270	224
IA	40–45	498	515	509	452	541	513	489	503	717	560	743
IL	40–45	621	492	597	565	514	390	520	456	673	585	610
MI	40–45	352	463	442	436	451	369	466	386	392	415	483
NE	40–45	265	418	294	368	309	384	349	493	487	411	506
SD	40–45	275	364	279	307	402	414	320	287	396	336	466
MN	40–50	347	491	559	403	550	533	416	478	458	347	594
ON	40–50	589	461	520	522	561	606	603	542	588	589	461
WI	40–50	442	618	592	452	564	421	498	517	558	421	692
ND	45–50	255	327	301	310	330	374	249	355	320	274	411
QC	45–50	589	461	520	522	561	606	603	542	588	558	568

Location	County latitude	Cumulative precipitation April 1 to October 1, 2011–2014			
		2011	2012	2013	2014
	°N	mm			
GA	30–35	398	497	740	560
MS	30–35	637	741	722	738
TX	30–40	139	358	361	384
KS	35–40	335	295	494	469
MO	35–40	605	392	626	572
TN	35–40	712	556	770	576
IN	35–45	628	389	507	573
OH	35–45	698	414	524	543
MD	35–40	660	452	479	562
NC	35–40	555	601	676	653
IL	35–45	582	357	525	589
CO	40–45	251	165	292	271
MI	40–45	516	341	463	488
NE	40–45	471	235	398	524
SD	40–45	375	243	373	403
MN	40–50	447	455	441	567
ON	40–50	558	568	669	513
WI	40–50	491	382	525	610
IA	40–45	488	344	548	697
PA	40–45	833	509	535	554
ND	45–50	355	233	364	361
QC	45–50	669	513	562	553

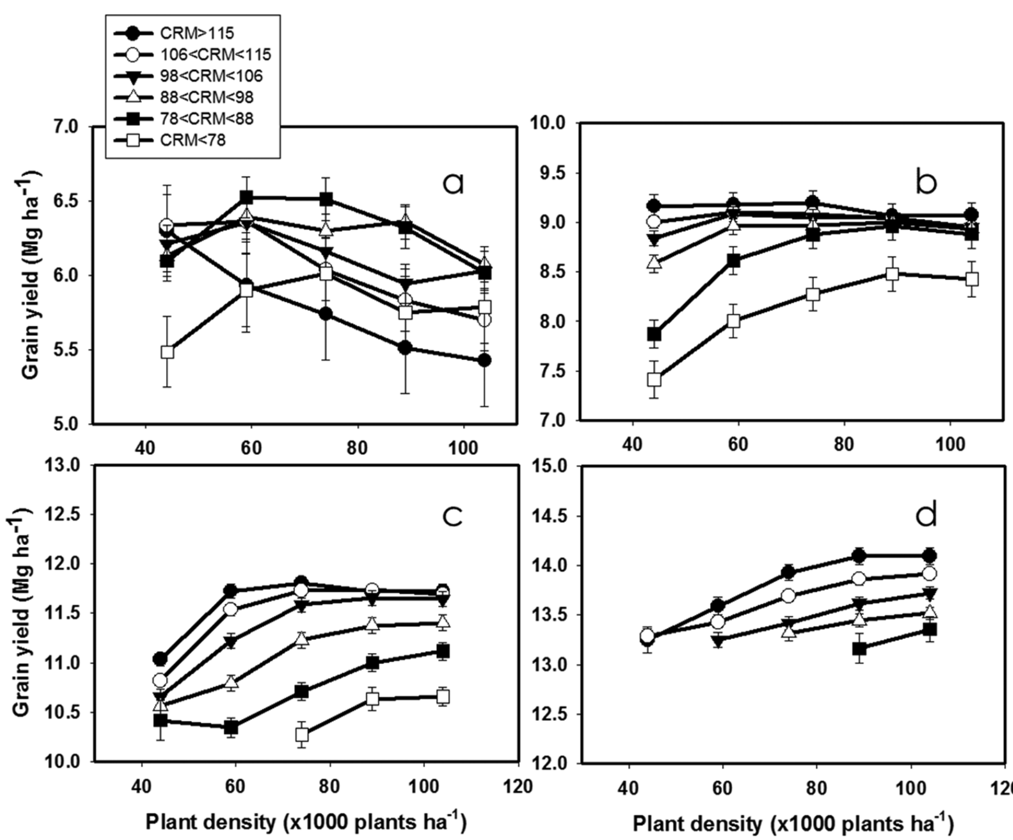


Fig. 7. Corn grain yield response to plant density in four productivity environments (low (a), medium (b), high (c), and very high (d) yielding) by hybrids maturity groups. Vertical bars in the graph are the standard error.

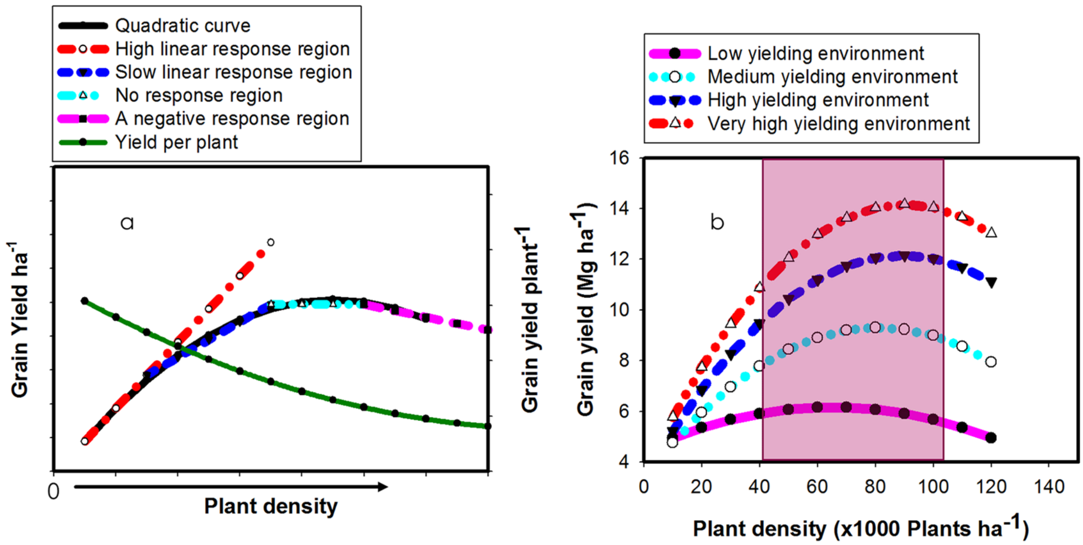


Fig. 8. Theoretical frameworks: typical corn grain yield–density and yield-per-plant–density relationship models at any productivity environment (a) and yield–density relationship for low, medium, high, and very high grain yielding environments (b). In (a) color-coded regions in the quadratic curve reflect variation in response due to increasing competition for resources and the continuation of the red high linear response region beyond quadratic curve reflects expected relationship between grain yield and plant density without resource limitation. In (b) the shaded region (~40 to 100 thousand plants ha^{-1}) represents the plant density ranges explored in this study. Extrapolation to other plant densities was conducted based on the quadratic models developed in the study.

plant and plant growth rate with increasing yield per unit-area basis until a plateau followed by a negative response region (Fig. 8a) is in agreement with previous research (Andrade et al., 1999; Echarte et al., 2004; Sarlangue et al., 2007; Li et al., 2015).

The third yield–density response zone is the 'zero growth' or 'no yield response to increasing density' zone. In this region, similar to the slow yield growth region, the yield contribution of additional plants (per-plant yield) is far less than expected compared with the rapid growth region. The 'zero growth' region is an extension of slow yield–density response region except that the yield from additional plants equals the reduction caused by the plant-to-plant competition process. Therefore, there is no relationship between yield and density in this region. A further increase in plant density leads to the fourth zone or negative yield–density response region. In this region, plant density increases cause a critical competition that exceeds the yield gain due to additional plants. Negative impact of increasing plant density from development of floral parts to final distribution of assimilates to seed was also described by several other researchers (Lemcoff and Loomis, 1994; Wilson and Allison, 1978; Borrás et al., 2003).

Overall, corn yield was also observed to decline with increased latitude. This impact of location (in terms of latitude or distance from the equator) on yield reported here can be explained by solar radiation and length of growing season. As the distance from equator increases, both the amount of solar energy and the length of crop growing season (number of days above 5°C) decrease (Sacks et al., 2010; Peltonen-Sainio, 2012; Mueller et al., 2015).

The impact of environment on yield and plant density extends beyond physical location to annual and within field variations. Corn yield–density response at four productivity environments (LY, MY, HY, and VHY) resulted in four dominant response models within the range of plant densities in the study (shaded area in Fig. 8b). In the LY environment, the dominant response was that corn yield declined with increasing plant density. In the MY environment, yield response was constant across densities. In the HY environment, yield increased with increasing density (even though rate of increase varied) and reached a ceiling. In the VHY environment, yield continued increasing nearly to the highest density. A proposed explanation is that in the LY environment the yield–density relationship is limited by resources such as water and sunlight (since soil nutrient levels were maintained at high levels at all sites). Competition for resources between plants starts at a lower density than in other productivity environments and the three zones of the quadratic curve (sharp increase, slow increase, and constant) presented a short span in the yield–density response models. The dominant response in the LY environment, particularly at the densities evaluated (from 40 to 100 thousand plants ha^{-1}), is the negative response zone (yield decline with increasing plant density).

In the MY environment, yield did not reach the declining stage within the plant density range explored in this study. However, due to the factors that limited yield in the range between 7 and 10 Mg ha^{-1} for the MY environment, yields plateaued (from 40 to 100 thousand plants ha^{-1}). This suggested that in the MY environment the size of each zone is longer than in the LY environment and the 'no response zone' was dominant within the density range from 40 to 100 thousand plants ha^{-1}. With similar logic, in the HY environment, the length of the rapid yield increase and the slow yield increase zones are dominant within the 40 to 100 thousand plants ha^{-1} density range. In the VHY environment, the limiting factor to yield could be related to its genetic potential rather than to environmental factors. Therefore, yield may be expected to increase with increasing plant density. However, genetic potential of each hybrid in terms of the maximum number of ears (prolificacy), kernels per ear (ear size trait), and kernel weight may limit potential yield. Ear size or prolificacy were plant traits recently proposed to increase per-plant grain yield and in overall improve corn yield potential at the canopy scale (Ciampitti and Vyn, 2012; Egli, 2015).

In agreement with previous reports, strong yield–density response dependency on productivity environments were related to availability of resources such as soil water, sunlight, and other factors (Keating et al., 1988; Abbas et al., 2012; Sangoi, 2001; Sangakkara et al., 2004; Averbeke and Marais, 1992). However, these studies were focused on one factor at a time, i.e., impact of irrigation (Brown, 1986), soil class (Woli et al., 2014), nitrogen fertilizer (Blumenthal et al., 2003; Bruns and Abbas, 2005; Ciampitti and Vyn, 2011), or soil moisture deficit (Averbeke and Marais, 1992). Thus, bridging the unknown of what constitutes low, medium, high, and very high yielding environments and their relationship with crop limiting factors is still an unanswered critical research gap. Finally, this analysis also suggested that productivity environment categories and MYPD recommendations should consider corn hybrid CRM group. Greater MYPD but lower yield potential was documented for short CRM relative to the long CRM corn hybrids. The latter is in agreement with results documented by other researchers (Colville et al., 1964; Popp et al., 2006; Lindsey and Thomison, 2016).

CONCLUSIONS

Based on the current synthesis-analysis, the yield–plant density relationship, a quadratic model best fit the data when a large dataset with a wide range of plant density was employed. If the productivity environment is LY, the MYPD is lower than under HY or VHY environments. In the VHY environment, a higher plant density is needed to achieve MYPD. Although the data in the HY and VHY environments do not show a yield decline at the highest plant densities, a yield decline is expected with further increase in densities due to competition for light, reduced assimilate supply to developing cobs and, consequently, reduced kernel number or weight. The four dominant regions of a quadratic model, i.e., rapid increasing, slow increasing, constant, and decreasing yielding regions explain the theoretical framework between yield and its response with declining resource or increasing competition. Similarly, the four dominant yield responses in low, medium, high, and very high yielding environments fit into the same theoretical framework. Further research needs to be conducted to define what primarily constitutes the low, medium, high, and very high yielding environments in terms of more specific interactions among genotypes, soil–weather factors, and crop management practices.

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