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EFFECT OF LEAF ORIENTATION AND DENSITY ON YIELD OF CORN

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ABSTRACT

Genetic selection for adaptation to different environments has significantly contributed to yield improvements in corn. The mechanism of tolerance to high densities, however, is not fully understood. Six corn hybrids, each two known to have upright, semi-upright and horizontal leaves were grown at 3 densities in 1987 and 1988. Several morphological and physiological traits as well as yield performance of the hybrids were investigated. Grain Yield in 1988 was greater than 1987. Growing degree days (GDD) and precipitation were greater in 1988. Rate of photosynthesis in ear leaves was not significantly different among the hybrids. Highly significant differences in the rate of photosynthesis and concentration of chlorophyll were shown between the high and low densities in all hybrids. In 1987, no significant difference in the grain yield of hybrids was found. However, in 1988 upright and semi-upright hybrids out-yielded hybrids with horizontal leaves. The results indicated that the advantage to grain yield of upright leaf hybrids would prevail only in favorable climatological conditions and high densities. The number of productive ears per plant was the component of yield most sensitive to increased density where an average of 36% reduction was observed. Kernel number per row and weight per kernel were less affected by density than ears per plant.

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تاثیر آرایش برگ و تراکم بوته بر روی عملکرد ذرت

ابوالحسن هاشمی دزفولی و استفن هربرت
به ترتیب دانشجوی دوره دکترا (اکنون استادیار مجتمع عالی آموزشی و پژوهشی کشاورزی رامین دانشگاه شهید چمران اهواز، ایران) و استاد بخش علوم گیاهی و خاکشناسی دانشگاه ماساچوست آمریکا.

چکیده

انتخاب ژنتیکی به منظور تطابق با شرایط محیطی مختلف سهم عمده‌ای در افزایش عملکرد ذرت داشته است، اما مکانیسم مقاومت ذرت نسبت به تراکم زیاد کاملاً شناخته شده نیست. شش هیبرید ذرت که دو به دو دارای برگهای قائم، نیمه‌قائم و افقی بودند در سه تراکم مختلف در سالهای ۱۹۸۷ و ۱۹۸۸ کاشت گردیدند. چندین خصوصیت مورفولوژیکی و فیزیولوژیکی و نیز عملکرد این هیبریدها مورد بررسی قرار گرفت. عملکرد در سال ۱۹۸۸ به دلیل بالا بودن حرارت تجمعی رشد و میزان بارندگی بیشتر از سال ۱۹۸۷ بود. میزان فتوسنتز در برگهای بلال هیبریدها تفاوت معنی‌دار نشان نداد. این امر می‌تواند به این علت بوده باشد که هیبریدها از لحاظ فنولوژیکی و ارتفاع بلال از سطح زمین متفاوت بودند. میزان فتوسنتز و همچنین میزان کلروفیل در تمام هیبریدها در تراکم‌های مختلف بگونه‌ای معنی‌دار متفاوت بودند. در سال ۱۹۸۷ از لحاظ عملکرد دانه اختلافی میان هیبریدها مشاهده نشد، اما در سال ۱۹۸۸ هیبریدهای با برگهای قائم و نیمه‌قائم پر محصول‌تر از هیبریدها با برگهای افقی بودند. نتایج بدست آمده نشان می‌دهد که برتری عملکرد دانه در برگهای عمودی تنها در شرایط آب و هوایی مناسب و در تراکم زیاد دیده می‌شود. در میان اجزاء عملکرد، تعداد بلال در گیاه با ۳۶ درصد کاهش حساس‌ترین مؤلفه نسبت به افزایش تراکم بود. تعداد دانه در هر ردیف و وزن متوسط تک‌دانه کمتر از تعداد بلال در گیاه نسبت به تراکم حساسیت نشان دادند.

INTRODUCTION

Within a given environment, the productivity of a crop canopy depends on the level of available resources and on the genetic potential of the crop to exploit that environment. The productivity of a crop canopy is ultimately determined by the quantity of intercepted photosynthetically active radiation (PAR), when other environmental factors are favorable. A common practice for maximizing interception of PAR is increasing the plant density. However, not all corn genotypes respond positively to density increases. The response of grain yield to increasing density is parabolic. It declines when optimum plant density is exceeded. Reduction in yield is primarily due to reduction in kernel number (12, 18) and barrenness (4). This is primarily due to inter-plant competition for incoming solar energy. Hashemi-Dezfouli and Herbert (10) found that shading caused a dramatic increase in barrenness. A 50% light reduction at high density resulted in 50% barren stalks. Buren *et al.* (4) concluded that the high density tolerant cultivars could be characterized by rapid silking, shorter pollen shed-silking intervals, prolificacy and reduced tassel size.

In densely planted corn, the upper one-half of the plant canopy intercepts almost all incoming solar radiation, while the lower leaves are shaded. Using fluorescent lamps, they showed that supplemental radiation at the lower part of the corn canopy resulted in a 45% increase in dry matter production. Light penetration to lower regions of the crop canopy, theoretically, might be increased by altering canopy architecture with the use of upright vs. horizontal leaves (6, 15). Upright leaves result in a more uniform distribution of light through the canopy area by intercepting less light at the top of the canopy and increasing light penetrating to lower leaves. Use of mechanically supported leaves above the ear in a vertical position as well as use of hybrids with upright leaves showed a substantial increase in grain yield which was attributed mainly to a decrease in barrenness (15, 16). The following experiment examines the interaction of plant density with corn hybrids having different leaf orientations.

MATERIALS AND METHODS

Cultural Practices

A 2-year field study was conducted in 1987 and 1988 at the University of Massachusetts Agricultural Experiment Station Farm. The soil type was a Hadley fine sandy loam (Typic Udifluvent, coarse-silty, mixed, nonacid, mesic). In 1987, the experimental site received 2200 kg ha^{-1} lime and a basal application of 66-30-23 kg ha^{-1} of N-P-K broadcast prior to planting and 100 kg N ha^{-1} as a side dressing four weeks after planting. In 1988, the experimental site tested high for P and K, thus only N supplied as NH_4NO_3 was added; 75 kg N ha^{-1} preplant plus 95 kg N ha^{-1} sidedress. In both years, weeds were controlled with 1.8 kg a.i. ha^{-1} cyanazine (2- { [4-chloro-6-(ethylamino)-S-triazine-2-yl] amino}-2-methylporpionitrile), and 2.2 kg a.i. ha^{-1} alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide) pre emergence. Irrigation was not needed in either year.

Six hybrids with 3 different leaf orientation habitats (upright, semi-upright and horizontal) were planted on 21 May 1987 and 5 May 1988. The selection of hybrids was based on their performance in earlier hybrid corn evaluation at this location. The six hybrids were:

H_1 = Agway 650X (upright)
H_2 = Hytest 650A (upright)
H_3 = Pioneer 3475 (semi-upright)
H_4 = Hytest 712 (semi-upright)
H_5 = Agway 584S (horizontal)
H_6 = Funks G4072 (horizontal)

The experiment was arranged in a randomized complete block design with 4 replications. Five-row plots were 6.6 m in length with a row spacing of 76 cm. Each hybrid was factorially combined with 3 densities. All plots were over-seeded and thinned to desired densities of 3, 7.5 and 12 plants

m^{-2}, 15 days after emergence (DAE).

Measurements and Sampling

Interception of PAR. Measurements of available PAR were taken above, within and below the canopy for all plant densities and hybrids in 2 replications. Measurements were obtained with a Li-Cor line quantum sensor (LI-188B), at 1045 to 1315 hr on days when clouds caused no interference. All readings were integrated over 1 min and 10 s. Inter-row light readings were taken with the light sensor placed across the inter-row space, at 0, 70, 120, 150 and 180 cm above the ground, and above the canopy. Readings from 3 adjacent plants in each plot were taken at completion of tasseling for the latest maturity hybrids i.e. hybrids 2 and 4. Percentage available light (PAL) was determined:

$$PAL = I_i \times 100/I_a$$

where I_i and I_a are the irradiance at a given level in canopy and above canopy, respectively.

Photosynthesis. Using a LI-COR 6000 portable photosynthetic system, the rate of photosynthesis was measured on August 5 and August 11 which coincided with the mid-silking stage of the latest hybrids (hybrids 2 and 4). For this measurement, ear leaves of 3 consecutive plants in a row adjacent to the final harvest were randomly selected. Measurements were replicated twice for the low and high densities and were made on a day when clouds caused no interference.

Chlorophyll. The concentration of chlorophyll in each ear leaf was determined immediately after photosynthetic measurements were taken, using the procedure reviewed by Bruinsma (3). Starting from the edge of the leaf blade, 1 cm^2 disks were cut from the middle of each ear leaf that had been used for the photosynthetic measurement. Disks were macerated with a mortar and pestle and extracted with 80% (v/v) acetone. Extracts were refrigerated at 5°C in dark until analysis. Total chlorophyll (a and b) content was determined using a Coleman model 124D double beam spectrophotometer (Coleman Instruments, Maywood, IL) with optical density at 663 and 645 nm (1).

Final Harvest. Grain harvesting occurred after physiological maturity of the latest maturity hybrids, 125 and 135 DAE in 1987 and 1988 respectively. All ears were shelled, using a hand-sheller. Cobs and kernels were dried in a forced-air oven at 80°C for at least 72 hr and weighed separately. Weight per kernel was determined from 1000 kernel sub-samples.

Statistical analyses were performed using either GLM or REG procedures of .Statistical Analysis System (17). All differences reported are significant at P > 0.05 unless otherwise stated.

RESULTS AND DISCUSSION

Interception of PAR

Light readings at the bottom of the canopy as a percent of available light above the canopy at completion of tasseling averaged for hybrids 2 and 4, were 19, 5 and 3 percent ages for the 3, 7.5 and 12 plants m^{-2}, respectively. All hybrids intercepted 95% or more of incident light in medium and high densities. No significant difference was observed (p=43) between the amount of light available at the soil surface of hybrids with horizontal and upright leaves. However, available light readings at the ear position of hybrids 1, 2 and 3 were higher than other hybrids (Fig. 1). These hybrids could be characterized by having near upright or semi-upright leaves.

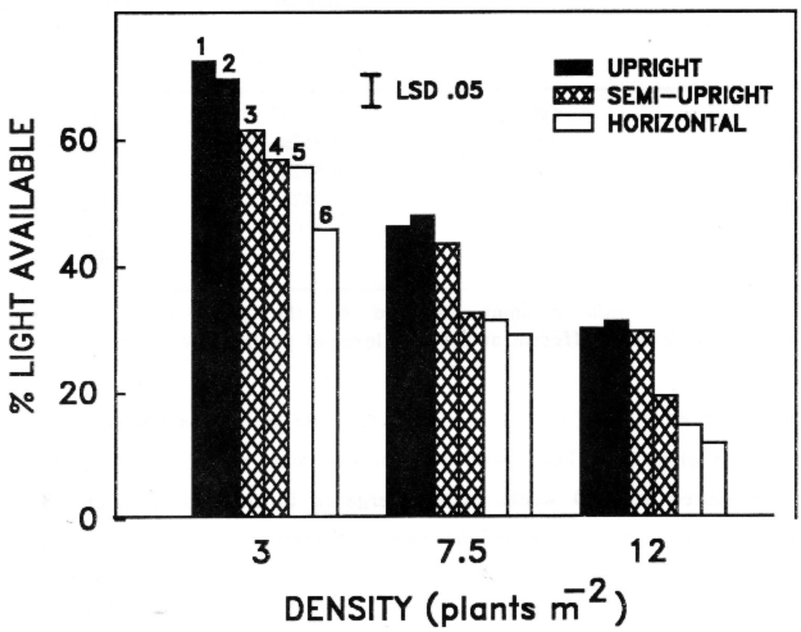

Fig. 1. Percent available light at ear position of 6 hybrids at 3 densities measured at completion of tasseling in the latest maturity hybrids i.e. hybrids 2 and 4.

Photosynthesis and Chlorophyll

Ear leaf photosynthetic rates measured near anthesis were reduced by 50%, as density increased from 3 to 12 plants m^{-2} (data not shown). Photosynthetic rates for hybrids are shown in Table 1.

Table 1. Photosynthetic rate and chlorophyll concentration of the ear leaf of the six corn hybrids averaged over densities.

Hybrid	Leaf orientation	Rate of photosynthesis $mg\ s^{-1}\ m^{-2}$	Chlorophyll concentration $\mu g\ cm^{-2}$
H_1	upright	0.853a†	7.18a
H_2	upright	0.917a	7.63a
H_3	semi-upright	0.982a	6.34b
H_4	semi-upright	0.742a	7.59a
H_5	horizontal	0.950a	7.01ab
H_6	horizontal	0.979a	7.04ab

† Means within columns followed by the same letter are not significantly different at the 0.05 level of probability.

Dwyer *et al.* (7) found a parabolic response of photosynthesis rate in corn with plant age. They observed that maximum rate of photosynthesis was measured at 8-10 weeks after emergence in six corn hybrids. They concluded that comparisons among hybrids differing in development rates should be made at comparable phenological stages. In our study, the 3 highest photosynthetic rates were found among the hybrids which had the earliest tasseling and silking dates. It is also notable that the lowest photosynthetic rates were found among the hybrids with upright or semi-upright leaves (H_1, H_2 and H_4). This agrees with the statement of Gardner *et al.* (8) that since the photosynthetic response to radiation is curvilinear and radiation efficiency is greatest at low radiation levels, the vertical leaves are more efficient per unit of radiation intercepted. A small reduction in upper leaf photosynthesis because of vertical leaf inclination allows more radiation to penetrate to lower leaves. A reduction of 45% in photosynthetic rate averaged over hybrids was found as density increased from 3 to 12 plants m^{-2}

Chlorophyll content was significantly different among the hybrids (Table 1). The hybrids that showed the highest rate of photosynthesis had lower concentrations of chlorophyll. Since the ear height varied among the hybrids, a part of the variation in chlorophyll content of different hybrids could be related to the different levels of light received by ear leaves (2). In a shading study (10), a 50% reduction in radiant energy caused a substantial decrease in chlorophyll concentration especially at high densities. Fig. 1 also shows that ear leaves in upright and semi-upright leaf hybrids received higher levels of light compared to more horizontally oriented leaf hybrids. However, this suggests that the level of chlorophyll in all hybrids in this study was above the level needed for photosynthesis. Brougham (2) suggested that the chlorophyll in species with horizontally displayed leaves could be more efficient in converting CO_2 than that in species with more upright leaves. Our results also confirm this suggestion. However, this conclusion is based on the results of studies with a relatively limited germplasm and may not, therefore, be representative of other genotypes or other environments.

Plant and Ear Height

Positive relationship between plant height and final grain yield has been reported (5). It has been suggested that density tolerant hybrids might have increased ear height which may result in increased interception of solar radiant by the ear leaf (4). The results of our experiment showed that plant and ear height generally increased then decreased with increasing density (Table 2). However, the largest difference averaged over hybrids in both traits did not exceed 8 cm. It is notable that the shortest hybrids also

Table 2. Effect of hybrid and density on morphological characteristics measured in 1988.

Hybrid	Leaf orientation	Plant height	Ear height	Tassel size	Mid-silking (week of)
		---------- cm	---------		
H_1	upright	318	165	35	25 July
H_2	upright	332	165	51	1 Aug.
H_3	semi-upright	295	145	36	18 July
H_4	semi-upright	365	172	49	1 Aug.
H_5	horizontal	320	156	36	25 July
H_6	horizontal	267	126	42	4 July
F-test significance					
Hybrid	(H)	0.001†	0.001	0.001	
Density (Hybrid)					
H_1	(L)§	0.299	0.074	0.211	
H_1	(Q)	0.001	0.001	0.031	
H_2	(L)	0.001	0.009	0.795	
H_2	(Q)	0.001	0.001	0.177	
H_3	(L)	0.154	0.289	0.029	
H_3	(Q)	0.315	0.705	0.714	
H_4	(L)	0.002	0.002	0.184	
H_4	(Q)	0.034	0.038	0.338	
H_5	(L)	0.136	0.334	0.982	
H_5	(Q)	0.804	0.208	0.100	
H_6	(L)	0.157	0.135	0.002	
H_6	(Q)	0.129	0.004	0.006	
CV	%	4.4	7.5	6.6	

† Probability of a greater F value by chance.

§ L = linear and Q = quadratic trends, respectively.

had horizontal leaves, while the tallest hybrids showed either upright or semi-upright leaf orientation. There was a tendency to have more upright leaves especially at the upper part of the plant, as density increased. This coincided with an increase in the height of ear (Table 2). In all but one hybrid (H_4), the tassel size showed a significant linear decrease as density increased.

Grain Yield

Grain yields in almost all hybrids at all densities were higher in 1988 than in 1987 (Table 3). This could partly be due to 16 days earlier planting in 1988 compared to 1987 but also could be attributed to the differences in climatic conditions between the 2 years. In 1988, accumulated GDD were higher than in 1987 and were above the norm for this location. Average precipitation, especially during the months of July and August, was much higher than that reported for 1987. This coincided with reproductive stages of growth and grain filling period. Studies have also shown that the reproductive stage, especially mid-silking, is the most sensitive stage to drought (9, 11).

In both years, superiority of hybrids with more upright leaves was found at higher densities (Table 3). With the exception of hybrid 4, upright and semi-upright leaf hybrids showed linear or asymptotic responses to density increase, while the response of horizontal leaf hybrids was parabolic. The exception of hybrid 4 might partly be due to its high degree of lodging at high density compared to the other hybrids.

The comparison between yield components of hybrids averaged over densities indicated that all components responded similarly in both years (Table 4). The difference in the total kernel yield per plant in the 2 years is primarily due to weight per kernel which was substantially heavier in 1988 compared to 1987. This, as indicated before, is probably due to the amount of precipitation available during the critical months of

Table 3. Effect of hybrid and density on grain yield in 1987 and 1988.

Hybrid	Leaf orientation	Density (Plants m^{-2}) 3		7.5		12		Significant trend	
		87	88	87	88	87	88	87	88
		Mg ha^{-1}							
H_1	upright	7.1	7.0	9.0	10.6	9.7	10.7	$L^{\dagger **}$	Q^*
H_2	upright	7.2	7.1	8.7	11.3	10.2	12.4	L^{**}	Q^*
H_3	semi-upright	8.0	7.8	9.3	10.4	8.7	11.3	NS	L^{**}
H_4	semi-upright	7.3	6.6	9.1	11.4	6.4	10.0	Q^{**}	Q^{**}
H_5	horizontal	6.5	6.8	9.9	10.6	8.8	7.4	Q^*	Q^*
H_6	horizontal	6.6	7.0	9.2	9.3	7.1	8.8	Q^{**}	Q^*

† L = linear and Q = quadratic trends, respectively.

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

NS = Not significant.

Table 4. Effect of hybrid and density on yield components.

Hybrid	Leaf orientation	Ear $plant^{-1}$		Row ear^{-1}		Kernel row^{-1}		Weight $kernel^{-1}$	
		87	88	87	88	87	88	87	88
								----- mg -----	
H_1	upright	0.98b†	0.95b	14.9c	14.9c	40a	40a	240d	266c
H_2	upright	0.96b	0.99b	13.5e	13.9d	39ab	36b	279b	318a
H_3	semi-upright	1.30a	1.30a	15.3b	15.5b	31d	31cd	251cd	262c
H_4	semi-upright	0.96b	0.94b	15.7a	15.9a	36c	35b	256c	274c
H_5	horizontal	0.98b	0.96b	13.9d	14.1d	37bc	32c	290a	304b
H_6	horizontal	1.18a	1.21a	15.6b	15.1bc	30d	30d	241d	242d
Plants m^{-2}									
3.0		1.40	1.29	15.0	15.4	39.5	39.2	295	316
7.5		0.93	1.01	14.9	15.1	35.6	35.8	254	268
12.0		0.81	0.68	14.3	14.5	30.4	27.6	225	249
Responses§		LQ	L	L	L	L	LQ	L	LQ

† Means within columns followed by the same letter are not significantly different.

§ L = linear, LQ = linear and quadratic (significant at P = 0.05).

July and August. The total amount of precipitation during these 2 months was 139.2 and 286.8 mm in 1987 and 1988, respectively. Ouattar *et al.* (14) reported that water deficit at mid-silking and during early grain fill reduced the endosperm cell division and thus inhibited the establishment of kernel sink capacity.

The effect of density on yield components (Table 4) was generally similar in both years. The response to density was also similar among hybrids in most cases and was either linear or quadratic. Exceptions were variability in number of rows per ear in hybrids 2, 4 and 5 in 1987 which did not show a significant difference to increased density. The number of productive ears per plant was the component most affected as density increased except for hybrid 2 which in 1987 was unaffected by density. Reduction in ear number averaged over hybrids and the 2 years was 36% as density increased from 3 to 12 plants m^{-2}. None of the hybrids showed barrenness at either low or medium densities. However, at high density the percent of barren stalk showed a range of 3 to 24%. No relationship was found between leaf orientation and percent barren stalks. Hybrids 3 and 6, which showed prolific characteristics, also showed the least percentage of barren stalks. This is consistent with earlier reports that multiple ear hybrids are more density tolerant than single-eared genotypes (4, 18).

Number of kernels per row and weight per kernel averaged over 2 years and all hybrids were also reduced by 25 and 22%, respectively due to density increase. Number of rows per ear was the most stable component to density increase and showed only a 6% reduction.

In summary, the upright leaf hybrids showed some advantages in grain yield production over the horizontal leaf hybrids. The difference was higher in 1988 which was climatically more favorable than 1987. The superiority prevailed most in the densest populations. The data obtained in this study suggest that density should be one of the factors to be considered in hybrid evaluations.

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