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Effect of leaf area on maize productivity

Robert J Lambert[1]*, Brian D Mansfield[2], Rita H Mumm[1]

[1]Department of Crop Sciences, University of Illinois, Urbana, Illinois, 61801, USA
[2]NW Illinois Agricultural Research Demonstration Center, University of Illinois, Monmouth, Illinois, 61462, USA
*Corresponding author: E-mail: rjlamber@illinois.edu

Abstract

Maize (*Zea mays* L) leaves provide energy for growth and development. Increases in plant densities the past 75 years have contributed to increased maize grain yields. No recorded change has been observed in leaf area per plant during this period, but some change may have occurred. Plant density increases are associated with increases in leaf area per-unit of land mass. Grain yield increases resulted from hybrids with improved tolerance to higher plant densities. Recently developed maize hybrids have upright leaves and smaller tassels allowing more light to penetrate the leaf canopy. Tolerance to increased plant density is directly related to intra and inter-plant shading plus changes in leaf area per plant may change leaf canopy structure. To evaluate the concept, maize leaf area affects grain yield, we developed high- and low leaf area hybrids. Objectives were to evaluate productivity of high and low leaf area maize hybrids at three high plant densities for two years. Averaged over three plant densities low leaf area hybrids produced significantly more grain than high leaf area hybrids. Low leaf area hybrids tolerated higher plant density better than high leaf area hybrids. Results indicate low leaf area hybrids are superior in several maize productivity traits.

Keywords: leaf area per plant, grain yield, plant density, leaf canopy

Introduction

Increases in maize grain yields (GY) the past 75 years are the result of maize breeding 50% and improved production practices 50% (Duvick, 2005a). USA maize GY from 1930 to 1950 averaged 63 kg ha^{-1} and from 1960 to 2000 110 kg ha^{-1}, a 43% increase, (Troyer, 2000). Duvick (2005b), estimated an increase of 1,000 plants per ha per year in plant densities during this period, a 40% increase. Following are factors contributing to maize breeding progress: i) a better understanding how a maize plant functions to produce GY; ii) introduction of single cross hybrids in the 1960's; iii) selection for improved male and female parents necessary for single cross hybrid seed production; iv) recycling elite inbred lines for breeding purposes and use of molecular markers for hybrid improvement; v) application of quantitative genetics to breeding problems; vi) development of inoculation procedures for disease and insect resistance plus the addition of GMO's for insect resistance; vii) improved mechanical equipment for planting and harvesting small plots resulting in evaluating larger amounts of maize breeding materials; viii) winter nurseries allowing for faster improvement of inbred lines and hybrids; ix) maize breeders with increased knowledge of basic genetic principles; x) wide area performance trials resulting in hybrids with improved stable GY over larger geographical areas.

Maize leaf canopy structure is a function of several plant variables. A mature maize leaf canopy is established when total plant height is determined. Plant height is determined by the number of internodes and their elongation. Leaf blade area, number, angle, orientation and functional period, all contribute to leaf canopy structure and function. Several leaf traits may change resulting from canopy development, such as leaf angle number plus internode growth. A mature leaf canopy is established at tassel maturity (VT). Several reports describe maize leaf canopy, structure and function, (Maddonni et al, 2001; Stewart et al 2003; Valentinuz et al, 2006). Maize leaf area (LA) development is affected by growing degree days and available moisture, (Dwyer et al, 1986). A reduction in light intensity in the leaf canopy at high plant density can result in lower GY. Higher GY of recently developed maize hybrids were associated with higher photosynthetic rates compared to older developed hybrids at high plant density (Dwyer et al, 1991). The ability to maintain adequate photosynthetic rates at higher plant densities, should allow light to penetrate into the ear leaf area resulting in higher GY. A maize defoliation study, with normal maize hybrids, found ear leaf defoliation plus all leaves above the ear leaf, at pollen-shed, educed GY 75% in some hybrids (Subdi et al, 2003).

Interest in maize LA started in 1975, with the finding of a recessive gene for reduced LA. The gene was backcrossed into several inbred lines. Phenotypic variation in ear leaf area (ELA) of normal maize inbred lines indicated modifiers genes were present in normal maize genotypes. To determine if modifier genes were present in maize populations, a divergent half-sib recurrent selection program for high and low ELA

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in two maize synthetics was started in 1985. Eight cycles of selection for low ELA per plant, reduced ELA in RSSSC synthetic by 29% and RBS20 synthetic 26%. Eight cycles of selection for high ELA per plant increased ELA by 22% in RSSSC and 17% in RBS20. Crosses between cycles of low ELA of RSSSC and RBS20 had a 25% reduction in ELA per plant. Eight cycles of selection for low ELA was associated with an increase in GY of 2.1 t ha^{-1} *per se* for RSSSC and no significant response for RBS20. Evaluation of crosses of low leaf area cycles resulted in a 4% increase in GY (Lambert, 2010). Results found selection for low ELA genotypes resulted in greater tolerance to higher plant densities *vs* high ELA genotypes. Objectives of the study were to evaluate leaf and kernel traits of high and low LA single cross maize hybrids developed from RSSSC and RBS20 ELA genotypes for possible tolerance to high plant density.

Materials and Methods

High and low ELA maize inbred lines were developed from cycle 8 of four selected versions of high and low ELA of RSSSC and RBS20. RBS20 was developed from BS20 (S) C2, the latter released in 1976 by Iowa State University (Russell et al, 1976). BS20 (S) C2 was developed from 12 inbred lines with six related to BSSS, resulting in a genetic relationship between RBS20 and RSSSC. RSSSC was developed by Kaufmann and Dudley (1979), from four strains of BSSS. The Pedigree Method, with ear-to-row selection for ELA, was used to develop four sets of maize inbred lines. The four sets were: i) RSSSC low ELA; ii) RSSSC high ELA; iii) RBS20 low ELA; iv) RBS20 high ELA. In each inbreeding generation, plants in a row with lowest or highest ELA were selected depending phenotype. The selection intensity based on rows was one out of 15 plants. Ten inbred lines were developed for each ELA group. Ear leaf area means for 10 RBS20 low ELA inbred lines ranged from 286 to 474 cm^2 and RSSSC low ELA from 336 to 478 cm^2 per plant. Ten RBS20 high ELA inbred lines ranged from 484 to 604 cm^2 and RSSSC high ELA from 552 to 749 cm^2 per plant. Hybrids were produced by crossing RSSSC low ELA inbred lines with RBS20 Llow ELA inbred lines to produce 12 low leaf area hybrids (LLAH) plus three LLAH using backcross-5 inbred lines, RB73, RB84, and ROH43, each with the recessive gene for reduced ELA. These three inbred lines were crossed to RBS20 inbred lines. This resulted in 15 low leaf area hybrids (LLAH). Fifteen high leaf area hybrids (HLAH) were produced by crossing high ELA RSSSC inbred lines with high ELA RBS20 inbred lines. Thirty maize hybrids, 15 LLAH and 15 HLAH were evaluated for two years, 2010 and 2011, at 80,000, 90,000 and 100,000 plants per ha.

To estimate ELA of maize hybrids ear leaf length and width at the widest point were measured on four internal random plants per plot, both years. Montgomery's, (1909), formula: (length x width) x 0.75, was used to estimate ELA of individual leaves. Pearce et al (1975), procedure was used to estimate LA above ear leaf (ULA). To estimate ULA regression analysis we used ELA as independent and ULA as dependent variable. Regression analysis used b values to estimate ULA. The values were b = 3.17** for LLAH and b = 3.92** for HLAH. To estimate the amount of ULA required to produce a gram of grain per plant, (Lag.), ULA per plant was divided by grams of grain per plant. All individual plant data was averaged for each plot and the ANOVA used plot means.

The experiment was conducted for two years, 2010-2011, using the same procedures both years. Row spacing was 76.2 cm. All plots were over planted and thinned to proper plant density. Previous crop both years was Soybean, (*Glycine max* L, Merr). Plant height was measured from soil surface to the tassel central spike apex, on five internal random plants and plot means used in the analyses. Days-to-pollen-shed was estimated when 50% of plants in a plot shed pollen. All kernel traits except GY were based on sample dry weight. Grain samples from each plot were dried for 10 d at 48°C. Kernel size estimates were obtained by placing a bulk sample of

Table 1 - Comparison of two year averages for 11 agronomic traits for 30 leaf type maize hybrids, 15 low leaf area and 15 high leaf area average for three plant densities and two years.

Years	ELA	ULA	Lag	g pp	Pht	Ds
	cm^2	cm^2	cm^2	g	cm	d
2010	677	2,352	24	102	234	67
2011	646	2,073	69	73	214	62
	***	***	***	***	***	***
	Swt	Knv	Kwt	Kpp	GY	
	g	no	mg	no	kg ha^{-1}	
2010	173	598	290	355	10,830	
2011	165	620	269	274	8,435	
	***	***	***	***	***	

*** significant at 0.0001 P level. ELA = ear leaf area $plant^{-1}$; ULA = upper leaf area $plant^{-1}$; Lag = amount of leaf area required to produce a gram of grain $plant^{-1}$; g pp = grams of grain $plant^{-1}$; Pht = plant height cm $plant^{-1}$; Ds = days to silk; Swt = sample weight of 200 cc of kernels; Knv = number of kernels in 200 cc; Kwt = kernel weight; Kpp = kernel number $plant^{-1}$; GY = kilograms of grain ha^{-1}.

kernels from a plot into a 200cc beaker, weighing the sample and counting kernel number. Kernel weight was obtained by dividing sample weight (200cc) by kernel number. The assumption was these two variables estimated kernel size. A smaller kernel number per volume indicated larger kernel size, larger kernel number indicated reduced kernel size. Grain weight per plant was obtained by dividing number of plants per plot by grain weight per plot. Kernel number per plant was obtained, dividing grain weight per plant by kernel weight per plant. Grain yields used standard procedures to estimate kilograms per ha at 155 grams kg^{-1} moisture.

A spilt-spilt-split plot experiment arranged in a randomized complete block design with three replications, was used both years. Plant densities were randomized in main plots, (80,000, 90,000, 100,000 plants per ha). Sub-plots were high and low leaf types randomized within plant densities. Sub-sub-plots were hybrids or genotypes. Plant densities were randomized within replications, leaf types within plant density and genotypes within leaf types. Statistical inferences for years, plant density, leaf types and hybrids were fixed effects, because of the non-random selection of materials. In addition, soil type, nutrient levels, weed control, and planting date were non-random.

Data analysis used Proc.GLM (SAS Institute, 2003). Single year analysis allowed for estimates of main plot effects (i.e. plant densities), sub-plots (i.e. leaf types) and sub-sub-plots (hybrids plus their interactions). Interactions for single year analysis were plant densities x leaf types, plant densities x hybrids, leaf types x hybrids and plant densities x leaf types x hybrids. Data for each year was analyzed separately and a combined analysis with years as an additional factor and their interactions. The 0.01, 0.001, and 0.0001 probability levels were used for all statistical comparisons.

Significant GY variation among the 15 LLAH was present both years. To evaluate this GY variation among the 15 LLAH, a separate analysis using only these 15 LLAH was used. This analysis used three plant densities, three replications and two years. To determine if certain hybrids had consistent performance over years and plant densities, two hybrids were selected to compare with the other 13 LLAH. The two highest GY LLAH at a plant density of 80,000 in 2010 were hybrids 4 and 13 and their performance at the other two plant densities in 2010 plus their performance in 2011 were selected. A separate analysis for each year, using only these 15 LLAH, was used to compare hybrids 4 and 13 with the average of 13LLAH to determine if significant variation was present among these 15LLAH.

Results and Discussion

Comparison of grand means for 2010 vs. 2011 for 11 traits is presented in Table1. Grand means for traits between 2010 *vs* 2011 were significant plus their interactions. Years were very different in 2010 *vs* 2011 relative to rainfall, temperatures, length of growing season and GY. Planting date in 2011 was 21 days later than 2010, due to wet soil. Rainfall during May thru September and temperature in addition to planting date all contributed to differences between 2010 *vs* 2011. Rainfall in 2010 was 52.3 cm and 31.2 cm in 2011. Average temperature was 26°C in 2010 and 28°C in 2011 with an average high temperature of 30°C in 2011. Upper leaf area in 2011 was reduced 279 cm^2 per plant compared to 2010. Estimated reduction in ULA in 2011 on an area basis was 2,224,000 cm^2 per ha at 80,000 plants. The leaf area reduction in 2011 may have contributed to lower GY. In 2011, greater LA per plant was needed to produce a gram of grain per plant compared to 2010. In 2011, kernel weight decreased 21 g per plant compared to 2010 and kernels were smaller. Plant height was 20 cm taller in 2010. Taller plants may have resulted from longer internodes thus reducing intra-plant shading. Total GY was 2,395 kg ha^{-1} lower in 2011 compared to 2010, Comparing grand averages for 11 productivity traits between 2010 and 2011 indicated

Table 2 - Comparison of means for 15low leaf area hybrids vs, 15high leaf area hybrids for three leaf, four kernel traits plus grain yield averaged for three plant densities and two years grown at the Crop Sciences Research and Educational Center, University of Illinois, Urbana, Illinois.

Leaf Type	ELA cm^2	ULA cm^2	Lag cm^2	g.pp g	Swt g	Knv no	Kwt mg	Kpp no	GY kg ha^{-1}
					2010				
Low LA	592	1878	19	102	171	607	285	362	11330
High LA	761	2976	30	100	172	588	295	346	10329
Lvs H	***	***	***	ns	ns	***	***	***	***
					2011				
Low LA	570	1810	22	91	167	652	258	311	8784
High LA	741	2875	47	72	163	578	280	235	8065
Lvs H	***	***	ns	***	***	***	***	***	***

***, Significant at 0.0001 P level, ELA = ear leaf area $plant^{-1}$, ULA = upper leaf area $plant^{-1}$, Lag = amount of leaf area required to produced a gram of grain $plant^{-1}$, g.pp = grams of grain $plant^{-1}$, Swt = sample weight of 200 cc of kernels, Knv = kernel number in 200cc, Kwt= kernel weight , Kpp = kernel number $plant^{-1}$, GY = Grain yield in kilograms ha^{-1}.

Table 3 - Comparison of averages for 15 low leaf area maize hybrids vs. 15 high leaf area hybrids at three leaf and four kernel traits plus grain yields grown at three plant densities for two years at Crop Sciences Research and Educational Center, University of Illinois, Urbana, IL.

Plant Density	ELA cm²	ULA cm²	Lag. cm²	g.pp g	Knv no	Kwt mg	Kpp no	GY kg ha⁻¹
				2010				
80000								
Low LA	606	1918	17	113	608	288	395	11368
High LA	731	2862	26	112	589	299	350	10122
90000								
Low LA	598	1896	19	104	607	285	362	11263
High LA	752	2940	27	102	589	299	350	10766
100000								
Low LA	574	1818	20	92	608	282	332	11360
High LA	719	2820	34	86	591	293	305	10098
PDxLT	*	**	***	ns	*	ns	*	***
				2011				
80000								
Low LA	574	1821	18	119	642	101	397	9443
High LA	737	2881	35	100	575	100	380	8655
90000								
Low La	576	1816	20	90	645	80	305	9043
High La	758	2971	48	65	579	59	217	8056
100000								
Low La	563	1785	29	64	669	62	249	7865
High LA	726	2941	59	52	595	51	191	7483
PDxLT	*	**	***	ns	*	ns	***	**

*, **, ***, Significant at the 0.01, 0.001, 0.0001 P levels, respectively, ELA = ear leaf area plant^{-1}, ULA = upper leaf area plant^{-1}, Lag = amount of leaf area required to produce a gram of grain, Kn = number of kernels in 200 cc, Kwt = kernel weight, Kpp = Kernel number plant^{-1}, GY = grain yield in kilograms ha^{-1} .

LLAH were more productive both years.

To develop low and high ELA inbred lines, selection was only for ELA during inbreeding in RSSSC and RBS20. Genetic principles dictate all traits other than ELA should be similar between hybrids sets. Thus means for grain weight per plant, kernels per plant, kernel weight, kernel size, plant height and other traits not linked or affected by ELA should have similar values between LLAH *vs* HLAH.

Data comparing averages for 15LLAH *vs* 15HLAH, for two years, relative to leaf and kernel traits are presented in Table 2. LLAH were 24% lower in ELA per plant in 2010 and 23% in 2011 compared to the average of 15HLAH. LLAH were 37% lower in ULA in 2010 and 35% in 2011 compared to 15HLAH. Leaf area required to produce a gram of grain per plant was lower for 15LLAH compared to 15HLAH. Kernel number per volume for LLAH was higher, indicating smaller kernels for 15LLAH *vs* 15HLAH. Kernel number per plant was higher, indicating a GY advantage for 15LLAH *vs* 15HLAH. Average GY for 15LLAH was 10% greater than 15HLAH in 2010 and 9% in 2011. Leaf area required to produce a gram of grain suggests a GY advantage for the 15LLAH *vs* 15HLAH averages.

Data comparing 15LLAH *vs* 15HLAH at three plant densities are in Table 3. In 2010, GY for 15LLAH was 12% higher at 80,000, 5% at 90,000 and 12% at 100,000 compared to 15HLAH. In 2011, GY between 15LLAH *vs* 15HLAH was 9% at 80,000, 12% at 90,000 and 5% at 100,000. A significant amount of ULA was required to produce a gram of grain per plant both years. In 2010, 15LLAH required 35% less ULA, at a plant density of 80,000, 30% at 90,000 and 32% at 100,000 compared to 15HLAH. In 2011, ULA required to produce a gram of grain per plant for 15LLAH was 49% less at 80,000, 58% less at 90,000 and 58% less at 100,000 compared to 15HLAH. LLAH were more efficient producing grain weight per plant than 15HLAH. The 2011 environment resulted in a reduction of ULA during vegetative growth, aggravated by higher temperatures, which may have affected photosynthesis.

Illustration of the non-crossover GY interactions between 2010 and 2011 are in Figure 1. Grain yield response in 2010 for 15LLAH was on the average 11,250 kg ha^{-1} at the three plant densities than in 2011. Grain yields for 15HLAH varied from 10,200 to 10,700 and to 10,200 kg ha^{-1} at the three plant densities. Grain yields of 15LLAH were higher than 15HLAH at the three plant densities in 2010, however, GY in 2011 were reduced but still higher than 15HLAH at the three plant densities. The non-cross over interaction data show 15LLAH had higher GY compared to 15HLAH both years and at the three plant densities.

To evaluate variation within the 15 LLAH two hybrids were selected; Hybrids 4 and 13 for their higher

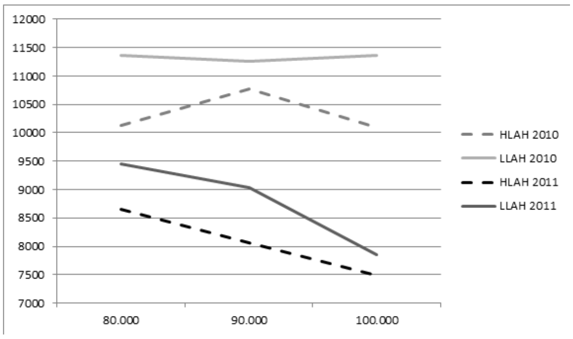

Figure 1 - Grain yield (kg ha^{-1}). Interaction of plant densities X leaf type for 15 low leaf area hybrids (LLAH) and 15 high leaf area hybrids (HLAH) at three plant densities and two years, 2010 and 2011.

GY in 2010 and 2011 at the three plant densities. Data comparing Hybrids 4 and 13 with the average of the other 13LLAH are in Table 4. Upper LA per plant for Hybrid 4 declined 245 cm^2 per plant at 100,000 in 2010. Hybrid 13 ULA did not vary with plant densities. The ULA required to produce a gram of grain for Hybrids 4 and 13 was lower at all plant densities, both years compared to the average of 13LLAH, indicating Hybrids 4 and 13 were more efficient in converting solar energy into GY. In addition grain weight per plant for Hybrids 4 and 13 were 26% higher at 80,000, 16% at 90,000 and 11% at 100,000, *vs* 13LLAH in 2010. Grain weight per plant in 2011 for Hybrids 4 and 13 increased 33% at 80,000, 23% at 90,000 and 29% at 100,000, because of lower grain weight per plant compared to the average of 13LLAH. In 2010, Hybrid 13 produced 27% more kernels at 80,000, 38% at 90,000 and 18% at 100,000 compared to the average of 13LLAH. In 2011, Hybrid 13 produced 18%, 32%, and 40% more kernels per plant than the average of 13LLAH at the three plant densities. Hybrid13 produced more kernels per plant at the higher plant densities both years. Grain yield for Hybrid4 compared to average of 13LLAH was 45% higher at 80,000, 35% at 90,000 and 7% at 100,000 in 2010. In 2011, Hybrid 4 was 19% higher at 80,000, 6% at 90,000 and 18% at 100,000. Results indicate Hybrids 4 and 13 had

Table 4 - Comparison of the two highest grain yield low leaf area hybrids (hybrids 4 and 13) with the average for 13 low leaf area hybrids for two leaf and three kernel traits plus grain yield, grown at three plant densities for two years, at the Crop Sciences Research and Education Center, University of Illinois, Urban, Illinois, Urbana, IL.

	ULA	Lag.	g.pp	Kwt	Kpp	GY
	cm^2	no	mg	mg	no	kg ha^{-1}
			2010			
80000						
Hybrid4	1761	13	133	292	454	12132
Hybrid13	1946	14	141	297	476	12688
13Hybrids	1934	18	109	285	376	10708
90000						
Hybrid4	1765	16	115	293	391	12450
Hybrid13	1845	16	115	286	402	12307
13Hybrids	1881	19	99	283	338	10787
100000						
Hybrid4	1518	15	104	302	345	11712
Hybrid13	1724	18	95	300	345	11401
13Hybrids	1839	21	90	295	262	10673
Hybrids	***	***	***	***	***	ns
$LSD_{0.05}$	118	2	8	2	49	256
			2011			
80000						
Hybrid4	1764	13	132	253	422	9426
Hybrid13	1818	15	119	274	434	10251
13Hybrids	1792	19	97	263	369	9213
90000						
Hybrid4	1682	18	97	271	358	10598
Hybrid13	1869	20	94	243	387	10016
13Hybrids	1822	24	78	263	294	8557
100000						
Hybrid4	1817	22	81	264	306	9866
Hybrid13	1831	35	74	225	329	7617
13Hybrids	1787	31	59	251	235	6727
Hybrids ns	***	***	***	***	***	
LSD -	2	-	53	15	196	

*, **, ***, Significant at the 0.01, 0.001, 0.0001 P levels, respectively, ELA = ear leaf area plant^{-1}, ULA = upper leaf area plant^{-1}, Lag = amount of leaf area required to produce a gram of grain, Kn = number of kernels in 200 cc, Kwt = kernel weight, Kpp = Kernel number plant^{-1}, GY = grain yield in kilograms ha^{-1} .

increased tolerance to high plant densities both years compared to 13LLAH, however, grain yields were reduced in 2011 because of several environmental factors.

Brekke et al (2010), found different versions of Stiff-Stalk Synthetic (BSSS) selected only for GY tolerated an increase in plant densities by changes in plant morphology. Selection only for increased GY resulted in increases in leaf angle, lower tassel branch number, smaller tassels and reduced anthesis to silk interval. We also found maize genotypes selected only for ELA, produced plants able to adjust to *inter* and *intra* plant shading. In addition, low leaf area plants were able to tolerate higher plant densities. We were able to develop LLAH with a selective advantage for higher plant densities. The four inbred lines used in Hybrids 4 and 13 trace their origin to four different F_2 plants, two from RSSSC and two from RBS20 of low leaf area cycles, indicating these two synthetics contain favorable genes for tolerance to high plant densities.

Conclusions

This study, adds evidence to the concept that maize leaf types and leaf area contribute to genotypes able to tolerant higher plant densities, with an advantage for LLAH. Grain yield advantage from LLAH is determined by more kernels per plant. Grain yield potential of LLAH *vs.* HLAH should be similar based on genetic background of maize materials used and their development, we conclude LLAH confer a yield advantage due to their plant morphology. In addition, we infer a reduction in leaf area results in more light to penetrate the leaf canopy, enhancing light interception in the area of the ear. This allows for translocation of assimilates produced by photosynthesis to be deposited in the ear. Based on averages, LLAH yielded more than HLAH, however as plant densities increased under stressful environmental conditions grain yields of LLAH declined, suggesting LA is a factor in plant density tolerance but not entirely associated with higher grain yields. Results show maize leaf area is another trait associated with the complex of traits necessary for tolerance to high plant densities in maize.

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