Genotypes and Plant Densities for Narrow-Row Cotton Systems. II. Leaf Area and Dry-Matter Partitioning

T. A. Kerby,* K. G. Cassman, and M. Keeley

ABSTRACT

Interest in production of narrow-row cotton (Gossypium hirsutum L.) is increasing. Plant characteristics considered important for cultivars grown in 1-m row spacings may not be the same for plants grown in 0.76-m spacings. This field study was conducted to determine the influence of genotype and plant density on accumulation and allocation of dry matter in a narrow-row production system. Five genotypes representing a wide range in size and growth habit were grown in factorial tests at 5, 10, and 15 plants m⁻² at the U.S. Cotton Research Station in Shafter, CA, in 1984 and 1985, Growth measurements were made four times during each season. Increasing plant density increased mean leaf area index (LAI) and total dry matter of genotypes at all sample dates but decreased harvest index (HI) from 0.58 to 0.53 at maturity. Genotypic differences in LAI and total above-ground dry matter became apparent only after anthesis. Mean season-end dry matter ranged from 9.78 Mg ha-1 for the short determinate genotype 2086 to 10.88 Mg ha-1 for 'Acala SJ-2'. Final mean HI ranged from 0.66 for 2086 to 0.47 for Acala SJ-2. Height and vegetative growth rates (HGR and VGR) per 100 heat units (HU) were closely negatively associated with fruit growth rates (FGR) between the June and August sample dates. Including leaf area growth rate (LAGR) with FGR as a FGR/LAGR ratio as the independent variable improved r^2 from 0.59 to 0.81 for HGR and from 0.69 to 0.90 for VGR. Node growth rate (NGR) was only minimally sensitive to the FGR/LAGR ratio. These results show that vegetative development during early fruiting is related to size and earliness of the reproductive sink and growth rate of the source. Cultural practices that are presently used for cultivars with a low FGR/LAGR ratio may not be ideally suited for more determinate cultivars with a high ratio.

UNDOMESTICATED cotton plants growing in the wild have a HI that ranges from 0.08 to 0.20 (3). Evaluations of historical germplasm have shown that

T.A. Kerby and M. Keeley, Univ. of California Cooperative Extension, 17053 Shafter Ave., Shafter, CA 93263; and K.G. Cassman, Dep. of Agronomy and Range Science, Univ. of California-Davis, Davis, CA 95616. This research was supported by a grant from the California Dep. of Food and Agric. Cotton Pest Control Board. Received 22 May 1989. *Corresponding author.

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modern cultivars have a higher HI and that increases in HI are associated with yield improvements (13,14). Similar conclusions have been drawn for other field crops (4). Increasing HI alone does not always result in higher yield. For example, genotypes with superokra leaf morphology had a greater fraction of dry matter partitioning to fruit but no yield improvement, due to decreased total dry matter production (8,12).

Under field conditions, dry-matter accumulation during early growth of cotton is limited by insufficient leaf area until a minimum LAI of 3.0 is achieved (11). Increasing plant density in narrow-row plantings has been proposed as a means to reduce the time required to obtain a closed leaf canopy (2). The optimal LAI associated with maximum yield of cotton, however, appears to vary. Ashley et al. (1) estimated an LAI of 5.0 was necessary to sustain growth of late maturing fruit and achieve maximum yield in an irrigated system. More recent work, however, suggests the LAI of many cultivars exceeds the requirement for total light interception, maximum dry-matter production, and yield (13,14).

Cotton leaf-area development is also influenced by moisture regime. In California, irrigation scheduling is used to control vegetative growth, since highest yields are obtained when the first postplanting irrigation is withheld until leaf water potential reaches —1.9 MPa (5,6). This applies a mild level of water stress, sufficient to reduce plant height and the rate of leaf expansion. One of the genotypes we used, Acala SJ-2, was selected in a production system using plant densities of 5 to 10 plants m⁻² with standard interrow spacings of 1 m. It is not clear if these same management strategies would optimize yield of earlier-fruiting plant types, which have shorter fruiting branches and may be better adapted for narrow-row production using higher plant densities.

As a first step to developing improved management systems that optimize yield in a narrow-row, high plant-density system, our studies were designed to evaluate the relationship between vegetative growth and development of the reproductive sink. The influence of environment (years), genotypic variation in determinacy, and plant density on growth, development, and dry-matter partitioning was examined in a two-year study.

MATERIALS AND METHODS

Identical experiments were planted in 1984 and 1985 at the USDA-ARS Cotton Research Station in Shafter, CA. The soil is a Hesperia sandy loam (coarse-loamy, mixed, nonacid, thermic Xeric Torriorthent). The experimental design had five genotypes (Acala SJ-2, 'Acala SJC-1', and three Shafter germplasm lines 2218, 2280, and 2086) grown in factorial combination with 5, 10, and 15 plants m⁻² in rows 0.76 m apart. Years was a subplot, with four sampling dates as sub-subplots. The factorial treatments were replicated four times in each year. The experimental unit was six rows, 18 m long, with Rows 2 and 3 used for mechanical harvest and Row 5 for destructive plant sampling. Sample dates and heat units after planting (HUAP) were 12 June (315), 9 July (614), 6 Aug. (931), and 4 Sep. (1246) 1984 and 10 June (288), 10 July (611), 7 Aug. (893), and 3 Sep. (1109) 1985. The four sample dates correspond to early square, early bloom, near-peak bloom, and early open-boll growth stages.

Plots were seeded on 12 Apr. 1984 and 8 Apr. 1985 at high rates, then hand thinned to the three treatment densities soon after the first true leaves developed. Cultural practices have been described in a companion study conducted within the same field experiment (9).

All sampled plants were cut at the cotyledonary node. Sample size was 2.4, 2.1, 1.8, and 1.5 m of row for the first through last sampling date, respectively. Plants were partitioned into stem, leaves, and fruits. Petioles were separated from blades and the weight of petioles and blades and the area of blades were determined from a 50-leaf subsample taken from each plot sample. Area was determined by a LI-COR LI-3000 leaf area machine. All remaining leaves (blades and petioles) were dried, and the area-to-mass ratio of the subsample was used to determine the LAI. Large bolls were mechanically cracked open to facilitate drying. Dry weight of all plant parts was determined after drying with forced air at 50 °C to constant weight.

Analysis of variance (ANOVA) was used to determine differences due to genotypes, densities, or years between sample dates. In addition, ANOVA was used to separate differences in growth rates for plant height, nodes, leaf area, and vegetative and reproductive organs. Growth rates were determined for the three intervals between adjacent sample dates as well as all other possible combinations of three or more sample dates. The HGR, NGR, and LAGR were expressed as rates per 100 HU, using a lower threshold of 15.6 °C (15). The FGR and VGR were expressed as g m⁻² 100 HU⁻¹ between the sample periods. Vegetative growth included leaves and stems, while fruit included squares and bolls. Either the FGR or the FGR/LAGR ratio was used as the independent variable in regression analysis, with HGR, NGR, or VGR as the dependent variables.

RESULTS AND DISCUSSION

Leaf Area Index

Increasing plant density resulted in higher LAI at all four sample dates for all genotypes. Averaged across genotypes, LAI at 15 plants m⁻² was 67, 27, 14, and 30% greater than the LAI of plants grown at 5 plants m⁻², on the June, July, August, and September sample dates, respectively.

Table 1. Leaf area index of five cotton genotypes (G) as influenced by sample date (SD) and year (Y).

		Genotype								
Sampling date	HUAP†	SJ-2	SJ-2 SJC-1 2218		2280	2086				
				– LAI –						
		19	984							
12 June	315	0.67	0.71	0.65	0.62	0.66				
9 July	614	2.97	2.78	2.83	2.24	2.23				
6 August	931	5.14	4.31	4.21	3.39	3.16				
4 Sep.	1246	3.78	3.25	2.85	2.80	1.78				
		19	985							
10 June	288	0.50	0.49	0.46	0.58	0.49				
10 July	611	4,26	3.16	3.91	3.63	3.14				
7 August	893	4.38	3.88	4.03	3.63	3.32				
3 Sep.	1109	3.41	3.22	3.16	3.03	2.88				
$G \times SD \times Y$	interaction I	SD (0.05) = 0.38							

† HUAP represents cumulated heat units after plantings.

Main effects of genotypes and years were also significant. Since the three-way interaction among genotypes, sample dates, and years was significant, main effects of these three variables will not be discussed. Averaged across plant densities, LAI reached peak values by early August and then declined, due to leaf senescence (Table 1). Genotypes had similar LAI at the first sample date both years, but LAI was greater at the July sample date in 1985 than in 1984, even though HUAP was nearly the same. In 1985, there were three postplanting irrigations before the July sample date, but only two in 1984. In addition, there were more early bolls set in 1984 than in 1985 (9). Both factors probably contributed to the high LAI noted at the July sample date in 1985 compared with 1984. The increase in LAI between July and August in 1984 was greatest for Acala SJ-2 and least for 2280 and 2086. In 1985, LAI developed earlier and only Acala SJC-1 had a significant increase in LAI between July and August. In both years, Acala SJ-2 had the highest LAI at the last sample date, while 2086 had the lowest LAI.

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There was a weak association between final total dry wt. and August LAI when LAI was less than $3.9 (r^2 = 0.21, n = 15; P = 0.07)$. Total dry wt. increased 0.12 Mg ha⁻¹ for each 0.1 increase in August LAI between 2.6 and 3.8. At LAI values greater than 3.8 (3.9 to 5.4), final dry matter was not related to LAI $(r^2 = 0.03, n = 16)$. Wells and Meredith (13,14) found that LAI between 3.9 and 6.3 does not limit net carbon assimilation rates. Our results support this conclusion. Although maximum dry-matter gain per day can be achieved at an LAI of 3.0 early in the season (11), an LAI near 3.9 was necessary for maximum dry-matter production, presumably due to senescence of lower leaves in all genotypes beginning in early August.

Dry-Matter Accumulation and Distribution

Averaged across genotypes, plant densities, and years, above-ground dry biomass was 0.63, 4.02, 8.39, and 10.40 Mg ha⁻¹ for the four sample dates. For each genotype, total dry matter accumulation was similar in both years at each of the four sample dates. To simplify presentation of data, results for genotypes, plant densities, and sample dates were pooled over years.

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Table 2. Total dry matter and dry-matter distribution in five cotton genotypes (G) averaged across years as influenced by plant density (D) and sample date (SD).†

	Dry matter partitioning															
	Total dry weight		Leaves			Stems			Fruit							
	Sample date		Sample date			Sample date			Sample date							
Genotype	T ₁	T ₂	T ₃	T ₄	T,	T ₂	T ₃		T,	T ₂	Т,	T ₄	Tı	T ₂	T ₃	T ₄
_	Mg ha-1					proportion of total dry weight										
Acala SJ-2	0.63	4.39	8.96	10.88	0.69	0.49	0.32	0.21	0.30	0.42	0.37	0.31	0.01	0.09	0.31	0.47
Acala SJC-1	0.65	3.91	8.53	10.90	0.68	0.50	0.32	0.22	0.31	0.40	0.32	0.26	0.01	0.11	0.36	0.53
2218	0.62	4.33	8.37	10.45	0.69	0.49	0.31	0.19	0.30	0.41	0.34	0.29	0.01	0.10	0.35	0.52
2280	0.61	3.64	7.82	9.97	0.71	0.50	0.32	0.22	0.27	0.33	0.22	0.18	0.02	0.18	0.46	0.60
2086	0.64 3.83 8.27 9.78			0.68 0.47 0.27 0.17			0.29			0.03 0.21 0.53 0.66						
G × SD Interaction LSD (0.05)	0.05) 0.43			0.01						0.02						
Plants m ⁻² 5 10 15 D × SD Interaction LSD (0.05)	0.49 0.67 0.74	3.65 4.06 4.35	8.22 8.33 8.61	10.00 10.43 10.76	0.70 0.69 0.69	0.49 0.49 0.49 0.	0.30 0.31 0.31 01	0.19 0.20 0.21	0.29 0.30 0.30	0.37 0.37 0.38	0.28 0.29 0.30	0.24 0.24 0.26	0.02 0.01 0.01	0.15 0.14 0.13 0.	0.42 0.40 0.39 01	0.58 0.56 0.53
Main effect LSD (0.05) Genotypes Plant densities Sample dates	0.23		0.01			0.01			0.01							
	0.18		0.01			0.01			0.01							
	0.19		0.01			0.01			0.01							

[†] Sample dates T₁, T₂, T₃, and T₄ refer to samples taken June 10 to 12 (early square); July 9 to 10 (early bloom); Aug. 6 to 7 (near peak bloom); and Sep. 3 to 4 (early open boll).

Rate of dry-matter accumulation differed among the genotypes (Table 2). All had similar dry matter at the June sample date, but growth rates began to differ in July. At the end of the season, Acala SJ-2 and Acala SJC-1 had accumulated slightly more dry matter than 2218, while 2280 and 2086 had only 91% of the dry matter of the Acala cultivars.

Dry-matter accumulation increased with high plant density at all sample dates (Table 2). At the end of the season, dry-matter production at the high plant density was 8% greater than at the lowest plant density.

Partitioning of dry matter differed among the five genotypes, and these differences became more apparent at late stages of development (Table 2). Acala SJ-2 and 2086 represent the extreme cases. At the last sample date, HI of 2086 was 0.67, compared with 0.47 for Acala SJ-2 (Table 2). When compared with Acala SJ-2, higher HI of Acala SJC-1 and 2280 resulted entirely from decreased dry matter in stems. The HI of 2218 was similar to Acala SJC-1, but the two differed in partitioning between stems and leaves. The high HI of 2086 was the result of low dry-matter allocation to both leaves and stems.

Plant density influenced the proportion of dry matter partitioned to leaves, stems, and fruits (Table 2). High plant density resulted in more dry matter in leaves and stems relative to fruit.

Vegetative Growth Rates in Relation to Growth Rates of Fruit and Leaf Area

Dependent variables were HGR, NGR, and VGR, while two variables (FGR or FGR/LAGR ratio) were selected as independent variables that reflected the strength of reproductive sink with or without consideration of the growth of the source. Growth rates were computed per 100 HU, to subtract year differences due to sampling date. Correlation coefficients were computed for all combinations of these variables for the six growth intervals possible (Table 3). The growth

Table 3. Association between growth rates in cotton for plant height (HGR), main-stem nodes (NGR), vegetative dry weight (VGR), and leaf area (LAGR) as dependent variables and fruit dry weight growth rate (FGR) or the FGR/LAGR ratio as independent variables for all possible growth intervals from four sample dates (n = 30).

	Independent variables											
		F	GR	FGR/LAGR ratio								
Casuah	I	Depender	nt variab	Dependent variables								
Growth Interval†	HGR	NGR	VGR	HGR	NGR	VGR						
	correlation coefficient											
$T_{2}-T_{1}$	0.67	0.57	0.88	0.75	0.61	0.62	0.95					
T_3-T_2	0.80	0.64	0.67	0.68	0.22	0.12	0.01					
T_4-T_3	0.45	0.34	0.15	0.30	0.59	0.13	0.78					
T_3-T_1	0.77	0.62	0.83	0.76	0.90	0.61	0.95					
T_4-T_2	0.57	0.71	0.28	0.61	0.42	0.46	0.43					
T_4-T_1	0.76	0.49	0.60	0.51	0.72	0.63	0.94					

[†] Sample dates T₁, T₂, T₃, and T₄ refer to samples taken June 10 to 12 (early square); July 9 to 10 (early bloom); Aug. 6 to 7 (near peak bloom); and Sep. 3 to 4 (early open boll).

interval T₃ to T₁ consistently had high correlation coefficients with all dependent variables. This interval covers the period from early squaring, when dry-matter allocation to fruiting forms begins, to early August, when vegetative dry matter reached a peak value that averaged 5.01 Mg ha⁻¹ (Table 2). Mean vegetative dry wt. declined to 4.61 Mg ha⁻¹ at the last sample date (T_4) . Using the FGR/LAGR ratio significantly improved the degree of correlation with HGR and VGR (Table 3). Use of the FGR/LAGR ratio was not desirable for many time intervals, since change in LAI after the third sample date was negative and either small or negative after the second time interval (Table 1). When vegetative growth rate was highest, however, during the T_1 to T_3 period, the FGR/LAGR ratio appears to be closely related to the vegetative growth response.

Analysis of variance was calculated for sample dates T_3 to T_1 for all variables used in regression analysis (Table 4). Mean growth rates during this interval were

Table 4. Influence of genotype, plant density, and year on growth rates per 100 heat units in cotton for plant height (HGR), mainstem nodes (NGR), leaf area (LAGR), vegetative dry weight (VGR), and fruit dry weight (FGR) between the first and third sample dates.

		Growth rate								
Genotype	Plants m ⁻²	HGR	NGR	LAGR	VGR	FGR	FGR:LAGR ratio			
		m	no.	LAI	— g ı	m ⁻²	(g m ⁻² LAI ⁻¹)			
			198	4			•			
'Acala SJ-2'	5	0.18	2.07	0.68	90	47	70			
	10	0.18	1.94	0.74	95	43	58			
	15	0.17	1.82	0.76	91	46	60			
'Acala SJC-1'	5	0.14	2.01	0.65	76	52	80			
	10	0.12	1.68	0.54	74	53	98			
	15	0.12	1.58	0.56	79	53	95			
2218	5	0.17	2.33	0.62	77	47	76			
	10	0.12	1.78	0.52	73	51	97			
	15	0.14	1.84	0.59	75	49	83			
2280	5	0.10	1.75	0.48	56	56	117			
	10	0.10	1.67	0.41	49	66	161			
	15	0.09	1.47	0.46	57	63	137			
2086	5	0.10	1.64	0.35	42	75	216			
2000	10	0.10	1.71	0.33	52	74	174			
	15	0.09	1.52	0.45	52	75	167			
			198	5						
(Apple CT 2)	•	0.15	2.10	- 0.61	06	40	70			
'Acala SJ-2'	5	0.15	2.10	0.61	86	48	79			
	10	0.14	2.10	0.54	79	40	75			
(A)- CTC 11	15	0.15	2.11	0.78	103	50	64			
'Acala SJC-1'	5	0.10	1.98	0.50	72	56	112			
	10	0.13	2.08	0.51	77	42	82			
2010	15	0.13	2.05	0.66	92	45	68			
2218	.5	0.15	2.44	0.60	88	53	89			
	10	0.14	2.13	0.63	92	45	72			
2000	15	0.14	2.24	0.55	74	39	72			
2280	.5	0.10	2.12	0.50	61	53	107			
	10	0.10	1.88	0.50	66	59	117			
2007	15	0.10	1.83	0.52	64	57	110			
2086	5	0.11	2.00	0.46	57	73	160			
	10 15	0.10 0.10	1.70 1.78	0.42 0.53	56 65	67 61	161 116			
LSD (0.05)						٧.				
Genotypes (G)	0.01	0.14	0.06	6	4	13			
Densities (D)	,	0.01	0.11	0.05	NS	NS	NS			
$G \times D$		NS	NS	NS	NS	NS	NS			
Years (Y)		NS	0.08	NS	3	4	10			
G × Y		0.02	NS	0.07	6	NS	23			
$\overrightarrow{\mathbf{D}} \times \overrightarrow{\mathbf{Y}}$		NS	NS	NS	NS	NS	NS			
$\overrightarrow{G} \times \overrightarrow{D} \times Y$		NS	NS	1.12	10	NS	NS NS			
3 7 5 7 1		מיי	140	1.12			110			

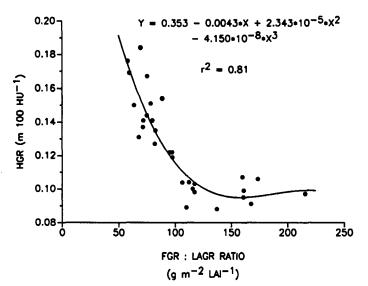


Fig. 1. Height growth rate (HGR) as related to fruit growth rate per leaf area growth rate (FGR/LAGR ratio) between 11 June and 6 Aug.

as follows: HGR, 0.13 m 100 HU⁻¹; NGR, 1.91 nodes 100 HU⁻¹; LAGR, 0.55 LAI 100 HU⁻¹; VGR, 72 g m⁻² 100 HU⁻¹; FGR, 55 g m⁻² 100 HU⁻¹; and FGR/LAGR ratio, 100 g m⁻². Averaged across densities and years, Acala SJ-2 and 2086 represented the extremes for each variable. Acala SJ-2 had high HGR, NGR, LAGR, and VGR but low FGR and FGR/LAGR ratio, while the opposite was true for 2086 (Table 4).

Averaged across genotypes and years, plants at low density had high HGR and NGR but low LAGR compared with high density (Table 4). Density did not influence VGR, FGR, or FGR/LAGR ratio. There was a higher NGR and VGR but lower FGR in 1985 compared with 1984 (Table 4).

The interaction between genotypes and years was significant for HGR, LAGR, VGR, and FGR/LAGR ratio (Table 4). All cultivars except Acala SJ-2 had similar NGR and LAGR in both years. Acala SJ-2 had higher NGR and LAGR in 1984 than in 1985. The two Acala cultivars had similar VGR in both years, while the three experimental lines had greater VGR in 1985 than in 1984. Acala SJ-2, Acala SJC-1, and 2218 had similar FGR/LAGR ratios in both years, but 2280 and 2086 had a greater FGR/LAGR ratio in 1984 than in 1985. Three-way interactions were significant for LAGR and VGR.

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In this factorial study, five genotypes were grown at three plant densities in two years that differed in timing of early irrigations and in early fruit load. All of these factors contributed to a considerable range in growth conditions. Genotypes included in these experiments had differences in growth patterns and yield (9), as well as in partitioning of dry matter among vegetative and reproductive organs (Table 2). It is our hypothesis, however, that across these environments and genotypes the rate of early fruit growth in relation to the rate of leaf area development governed vegetative growth after fruiting began. For a perennial crop grown as an annual, such as cotton, defining the mechanisms that control midseason vegetative growth is important for controlling the degree of determinacy and late season cut-out.

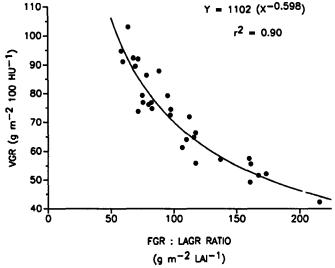


Fig. 2. Vegetative growth rate (VGR) as related to fruit growth rate per leaf area growth rate (FGR/LAGR ratio) between 11 June and 6 Aug.

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Only a weak relationship existed between NGR and FGR/LAGR ratio ($r^2 = 0.37$, n = 30). Across the range of FGR/LAGR ratio (70 to 216 g m⁻² 100 HU⁻¹), NGR varied only 0.92 nodes 100 HU-1. The relatively small range in node development and the low coefficient of determination indicate that change in main-stem node number is relatively insensitive to variation in the sink/source ratio. In a previous study, where up to 86% of the leaf area was removed until the time of first square, node development was less affected by source reduction than any other measure of vegetative growth (10).

Growth in plant height displayed a two-phase response to FGR/LAGR ratio. When the ratio was less than 100 g m⁻² 100 HU⁻¹, HGR declined linearly as the sink/source ratio increased (Fig. 1). A FGR/LAGR ratio above 100 g m⁻² 100 HU⁻¹ resulted in a nearly constant change in plant height of about 0.1 m 100 HU⁻¹ during the June-to-August sample periods across a wide range of FGR/LAGR ratio values. There was a close association between VGR and FGR/LAGR ratio across plant densities, genotypes, and years (Fig. 2).

Genotypic differences, insect damage to early fruiting forms, early irrigation scheduling, and plant density all contributed to large differences in early fruit load and leaf area to support further growth. Our results show that the sink/source ratio during early fruiting is an important factor controlling subsequent vegetative growth. Gutierrez et al. (7) suggested a large early-season boll load could limit yield, because of early cut-out in a long growing season. Yield in the present study was not significantly related to FGR/ LAGR ratio. This ratio impacts the amount of vegetative development between early squaring and maximum vegetative dry-matter accumulation. Yield is a function of HI and total biomass. Genotypes with a high FGR/LAGR ratio were high yielding (9) and had high HI but also had decreased total biomass. Cultural practices that are optimum for a low-HI genotype such as Acala SJ-2 (5,6) may limit the LAGR (and yield potential, due to early cut-out) of genotypes such as 2280 and 2086, which have high HI and high FGR/LAGR

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