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LEAF AREA DEVELOPMENT IN SOME CROP AND WEED SPECIES*

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ALM D. M., PIKE D. R., HESKETH J. D. and STOLLER E. W. *Leaf area development in some crop and weed species.* BIOTRONICS 17, 29-39, 1988. Leaf expansion is an important factor determining the competitive ability of a crop or weed. Crop models for leaf expansion have been under study and development for some time; we report here an exploratory effort to develop a similar information base for weed models. Such models summarise what is known about plant behavior; study of crop: weed competition models may lead to better methods for weed control and better predictions of crop yield. Crop and weed plants were grown in growth cabinets to determine the effect of temperature on leaf appearance rate; such information was used to develop species-specific degree day models for germination, seedling emergence to the first leaf, and the appearance of successive mainstem leaves. Total leaf area was measured on seedlings with a range of mainstem leaf numbers, in both controlled environment and field conditions. Area per plant vs. accumulated degree days could then be determined from the predicted mainstem leaf number, using the degree day models and derived, allometric relationships between leaf numbers and accumulated area. A method for estimating threshold temperatures for leaf expansion was also developed. Limitations to such a simple model for predicting seedling leaf area are discussed, with an indication of improvements needed.

Key words: phenology; degree-days; base temperature; crop systems modeling; *Zea mays* (L.); *Glycine max* (L.) Merr.; *Gossypium hirsutum* (L.); *Helianthus annuus* (L.); *Pisum sativum* (L.); *Chenopodium album* (L.); *Amaranthus hybridis*; *Abutilon theophrasti* Medic.; *Datura stramonium* (L.); *Digitaria sanguinalis* (L.); *Solanum ptycanthum* Dun; *Xanthium strumarium* (L.).

INTRODUCTION

Yield results from weed density studies are used to predict yield losses, with a correction for the timing of weed emergence (8). Further corrections are needed for other factors such as water, nitrogen, temperature or shading stresses. Spitters

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and Aerts (6) outlined logic for a crop-weed competition model, emphasizing the importance of leaf area expansion and display, but they offer little new information on how to quantify such logic. We have been developing a soybean-corn production system model for some time with emphasis on the research aspects of model construction, such as phenological information needed. Pests are a major limiting factor to yield in such systems, yet pest modeling has not kept up with the needs of model developers and farm managers.

Leaf expansion and duration are important factors controlling crop growth and yield; recently we and others (5) have been researching and modeling leaf behavior in soybean and corn (14, Hesketh *et al.*, unpublished). Here we describe preliminary results from an application of some of these same techniques for the prediction of leaf area development in weed species.

MATERIAL AND METHODS

Degree day model for leaf area development

The species we included in this study are listed in Table 1. Crop species were included in the growth cabinet experiments for reference, since more is known about their phenology. One encounters considerable variability in such research; comparisons with test species with known temperature responses growing under the same experimental conditions should offer some control.

In the Urbana growth cabinets, plants were grown in 8-liters of a 1:1:1 peat:perlite:sand potting mix irrigated with a solution of commercial (Rapid Grow* 32-7-7) soluble fertilizer at the recommended rate twice weekly and with water as needed. A sliding 1.2 × 2.4 m bank of General Electric Deluxe Cool White fluorescent lamps was positioned about 0.4 m above the plants, to give about 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR at the plant level. A 5°C temperature differential was maintained between the 14/10 h light/dark periods to give mean temperatures of 11.5, 15 and 22°C. Thermograph records were kept to determine the mean temperature. Leaf dimensions were measured twice weekly; dimensions were calibrated against areas obtained from dissected plants using a Lambda area meter. Plants were mapped for mainstem and branch nodes at various stages of growth. Leaf counts included leaf tips in the grasses and leaves greater than one cm in length in the dicots. The base temperature for growth and the reciprocal of the slope of the rate of leaf appearance vs. temperature, or degree days per leaf, were determined from plots of mainstem leaf numbers per day vs. the mean growing temperature.

In the DSIR growth cabinets (for a detailed description, see (12)) plants were grown in a 1.2-liter 1:1 fine pumice:peat potting mix with dolomite added and at temperatures comparable to those used at Urbana. This potting mix was irrigated periodically with a modified Hoaglands solution.

Mainstem leaves including leaf tips in the grasses and mainstem leaves greater than 1 cm in length in the dicots were counted on labeled crop and volunteer weed plants in the field. Degree day values were calculated from local weather station records, using base temperatures for growth estimated from the controlled environment studies or, in the case of corn and soybean, from values commonly used in the

literature. The soil at the University of Illinois Agronomy-Plant Pathology South Farm in Urbana was a highly productive Flanagan (fine, montmorillonitic, mesic Aquic Argiudoll) silt loam soil. That at the DSIR Division of Plant Physiology experimental plots in Palmerston North was a Karapoti brown sandy loam.

The base temperature for leaf expansion

During the growth cabinet studies, an economical alternative to calculating the base temperatures for leaf expansion was explored. This new method required only two temperature treatments and four leaf area determinations (three time intervals). The four leaf area determinations were A_1 and A_2 at different times in the warm treatment, A_3 just before the cold treatment and A_4 at the end of the cold treatment; the time intervals between all determinations were approximately 60 h. The equations for calculating the base temperature are as follows:

$$(dA/dt)_1 = (A_2 - A_1)/\Delta t \quad (1)$$

$$(dA/dt)_2 = (A_3 - A_2)/\Delta t \quad (2)$$

and the acceleration is

$$d^2A/dt^2 = [(dA/dt)_2 - (dA/dt)_1]/dt. \quad (3)$$

Assuming the time step is short enough to consider the acceleration as linear with time, the rate that would have occurred in the third time interval (at the initial temperature) can be extrapolated as

$$(dA/dt)_E = (dA/dt)_2 + (d^2A/dt^2) dt \quad (4)$$

Renaming $(dA/dt)_E$ as R_E , the proportionality described is

$$(R_E - R_C)/(T_I - T_C) = R_E/(T_I - T_B) \quad (5)$$

where

$R_C = (dA/dt)_3$ = expansion rate after cold transfer,

T_I = initial temperature,

T_C = cold temperature, and

T_B = base temperature.

Setting $dT = T_I - T_C$ and $dR = R_E - R_C$ and solving for the base temperature yields

$$T_B = T_I - R_E(dT/dR). \quad (6)$$

Preliminary results using this method are presented.

RESULTS AND DISCUSSION

Mainstem leaf number

Plots of mainstem leaves per day vs. mean temperature for growth are given in Fig. 1. The reciprocals of the slopes of such plots gives the degree days required

to produce a new leaf, Table 1. When the response to temperature was non-linear, the points at the lowest two temperatures were used to determine the slope. Thermal requirements for a new leaf were lower (32 vs. 55 degree days per leaf) than reported earlier; we did maintain the light bank close to the plants to get as much light as

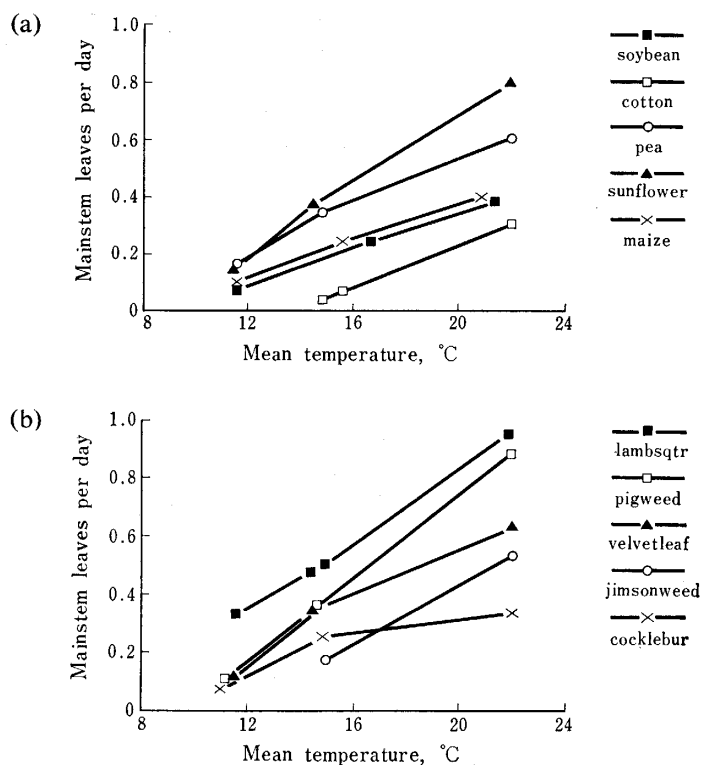


Fig. 1. Mainstem leaf appearance rates vs. mean growth cabinet temperature of (a) five crop and (b) five weed species. Plants were grown under a 16 h day with warm day/cool night temperatures to give daily means of 11.5, 15 and 22°C.

Table 1. The thermal requirement for mainstem leaf production in some weed and crop species

Species	Notes	Base temperature (°C)		Degree days per leaf
		A*	B**	
<i>D. stramonium</i> (Jimsonweed)	U.G.C.		10	22.5
	U.F.	10		25
<i>A. theophrasti</i> (Velvetleaf)	U.G.C.		10	13-17
	U.F.	10		23.2
<i>C. album</i> (Lambsquarters)	U.G.C.		6.5	17
	U.F.	6.5		18
	N.Z.F.	6.5		13
<i>A. hybridis</i> (Pigweed)	U.G.C.		9.5	26
	U.F.	9.5		22
	N.Z.F.	9.5		9
		8		11

(continued)

Table 1 (continued)

Species	Notes	Base temperature (°C)		Degree days per leaf
		A*	B**	
<i>S. ptycanthum</i> (Black Nightshade)	N.Z.G.C. N.Z.F.		6	39-47 30
<i>X. strumarium</i> (Cocklebur)	U.G.C. U.F.		9.5	22 26
<i>D. sanguinalis</i> (Crabgrass)	N.Z.G.C.		7	35
<i>Z. mays</i> (corn)				
A) Leaf tips	U.G.C.		8	33
	U.F. 1985	10		38
	U.F. 1986	10		40
	U.F. 1987	10		34-39
	N.Z.F.	8		32
		8		34
		7		37.5
	N.Z.G.C.		8	30
	Tollenaar <i>et al.</i> (9)		9	35
	Hofstra <i>et al.</i> (1)		6	35
B) Leaf collars	Warrington and Kanemasu (12)		a. 8.4*** b. 10 c. 0.4	54 45 126
	N.Z.F.		7	46
	U.F.		10	45
<i>G. max</i> (Soybean)	U.G.C.		9	32
	U.F. 1985	10		48
	U.F. 1986	10		48
	U.F. 1987	10		43
	Sato (3)		9	55
	Thomas and Raper (10)		9	55
	Sinclair (5)		8-11	55
	Hofstra <i>et al.</i> (1)		7	54
		10		47
	Wang <i>et al.</i> (11)	10		40-50
<i>G. hirsutum</i> (Cotton)	U.G.C. Hofstra <i>et al.</i> (1)		13	35 42
<i>P. sativum</i> (English peas)	U.G.C. N.Z.G.C.		9 7.5	38 27
<i>H. annuus</i> (Sunflower)	U.G.C. N.Z.F.		9 9	29 11

* A=Assumed base temperature for calculation of degree days per leaf.

** B=Experimentally estimated base temperature.

*** a. experimental data, 11-30°C mean temperatures.

b. derived data within the 16-28°C temperature range.

c. derived data within the 6-16°C temperature range.

G.C.=growth cabinet results (23°C); U.F.=Urbana field results (~=23°C); N.Z.F.=field results, Palmerston North, New Zealand (~=17°C);

Full species names are *Datura stramonium* (L.), *Abutilon theophrasti* Medic., *Chenopodium album* (L.), *Amaranthus hybridis*, *Solanum ptycanthum* Dun., *Xanthium strumarium* (L.), *Digitaria sanguinalis* (L.), *Zea mays* (L.), *Glycine max* (L.) merr., *Gossypium hirsutum* (L.), *Pisum sativum* (L.), and *Helianthus annuus* (L.).

possible, probably enhancing the growing point temperature. Values for corn were similar to those reported earlier, Table 1, probably because the corn growing point was close to the potting mix at the base of the plant during the course of these experiments. Consequently we determined such values for the same group of species growing under field conditions, Table 1, using the base temperature estimated from Fig. 1 or that commonly used in the literature.

We report collar production rates for corn because collar numbers are a commonly used phenological indicator for vegetative growth. The mainstem node number of the leaf with the youngest visible leaf tip increased in a much more linear manner than collars under constant temperatures; however, degree day models have been developed for collar production, taking into account the increased rate of appearance prior to tasseling (7, 14).

There is fair agreement among measurements of degree-days required per leaf; occasionally values don't agree, such as for *Amaranthus* and *Chenopodium*, Table 1. The mean temperature at the DSIR experimental field in Palmerston North was frequently lower than at Urbana (e.g., 16.5 vs. 22.5 °C during the main 20 day experimental periods at the two sites). We assumed a simple linear relationship between appearance rate and temperature above the temperature threshold; there is considerable evidence in the literature that this relationship is curvilinear with growth occurring below the estimated threshold. Differences in soil and air temperature can also affect field measurements, if not accounted for.

Degree day values from planting to the first leaf are given in Table 2, as derived from growth cabinet studies. Field measurements should be based upon soil tem-

Table 2. Specific leaf areas, the base temperature for leaf expansion, and the thermal requirement for emergence in some weed and crop species

Species	SLA _L	SLA _P	T _B	DD _E
<i>D. stramonium</i> (L.) (Jimsonweed)	238	1,191	11.3	203
<i>A. theophrasti</i> Medic. (Velvetleaf)	225	648	9	154
<i>C. album</i> (L.) (Lambsquarters)	240	—	6.5	120
<i>A. hybridis</i> (Pigweed)	223	—	10	104
<i>S. ptycanthum</i> Dun. (Black Nightshade)	248	—	—	—
<i>X. strumarium</i> (L.) (Cocklebur)	—	—	9.5	140
<i>D. sanguinalis</i> (L.) (Crabgrass)	252	—	—	—
<i>Z. mays</i> (L.) (Corn)	166	—	8	75
<i>G. max</i> (L.) (Soybean)	271	—	9	154

SLA_L=specific leaf area of the lamina (cm² g⁻¹); SLA_P=specific leaf area of the petiole (cm² g⁻¹); DD_E=degree days to first leaf in growth cabinets; T_B=experimentally determined base temperature (°C).

peratures; we have measured 147 ± 3.7 degree days from planting to the first leaf in soybean based upon air temperature. We have also measured 103 and 96 degree days to the second corn leaf tip for mean air and soil temperatures respectively, base 8°C . Better data are needed, although there are many reported models for seed germination and emergence.

Leaf area expansion rate

The threshold temperature for leaf expansion, as determined by the method outlined above, did not differ much from that for leaf production, Table 3 vs. Table 1. Warrington and Kanemasu (12) reported a curvilinear response for corn leaf collar (fully expanded leaves) production to temperature; whereas that for leaf primordia was fairly linear. Such relationships were derived from data taken under various combinations of day and night temperatures. Their threshold temperature for primordia development was much higher than that for collar production, indicating that the base temperature for area expansion is lower. Plants commonly grow faster than most degree day models predict at the lower temperatures, supporting the Warrington-Kanemasu derived response curve. Corn seedlings have a higher daylight temperature threshold for chlorophyll synthesis than for growth; fluctuating day/night temperature regimes with a mean temperature below this threshold can result in green plants with good growth. The Hofstra *et al.* (1) soybean plants produced leaves faster with each additional leaf in the lowest temperature regime used ($17/11^{\circ}\text{C}$ 16/8 h day/night temperature), giving a lower base temperature than that reported by others from measurements over a shorter growth period. For a climate with cold spells lasting only a few days, a base temperature of 10°C and 55 degree days per leaf may work better. However, lower values for degree days per leaf have been measured frequently in the field, suggesting that plants acclimate to cold over time or that growth responds to temperature in a non-linear manner near the base temperature. Zur *et al.* (14) lowered the base temperature for the lower mean temperatures in their corn degree day model.

Leaf area vs. mainstem node number

Figure 2 shows area per plant vs. mainstem leaf number for growth cabinet

Table 3. Base temperature ($^{\circ}\text{C}$) for germination, leaf appearance and leaf expansion

Process:	Germination	Appearance	Expansion
Reference:	Wiese & Binning (13)	NA	NA
<i>X. Strumarium</i> (L.) (Cocklebur)	—	9.5	9.2
<i>G. max</i> (L.) (Soybean)	—	9.0	9.6
<i>C. album</i> (L.) (Lambsquarters)	6.0	6.5	6.3
<i>A. hybridis</i> (Pigweed)	10.0	10.0	11.0

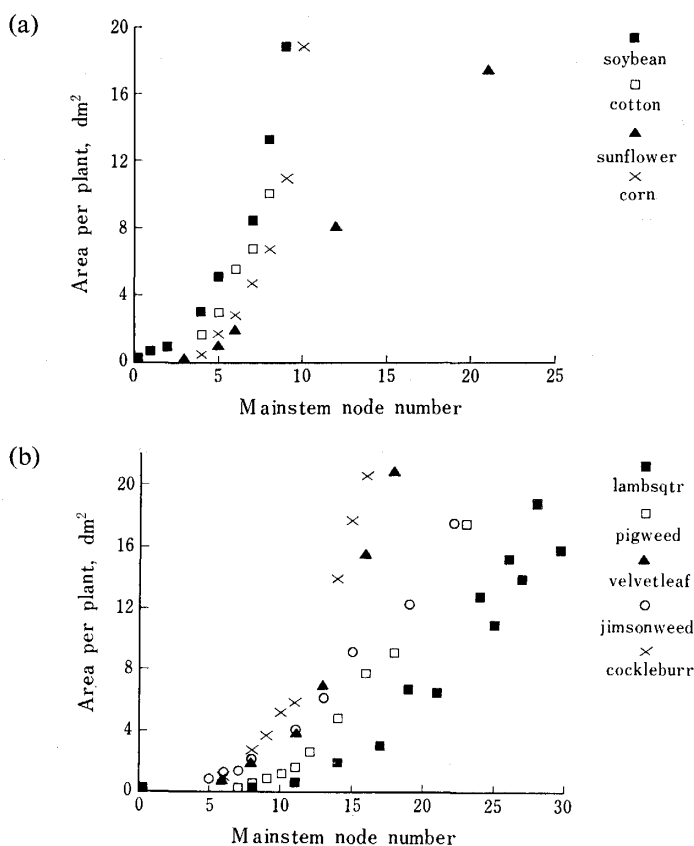


Fig. 2. Area per plant vs. total mainstem leaves: (a) four crop and (b) five weed species. The leaf area includes branch leaves. Equations are given in Table 4.

Table 4. Area per plant vs. total mainstem leaves: Data from crop and weed species fitted to the second order polynomial

$$\text{Area} = a + bN + cN^2$$

Species	Coefficient			
	<i>a</i>	<i>b</i>	<i>c</i>	<i>R</i> ²
<i>G. max</i> (L.) (Soybean)	.590	-.548	.273	.98
<i>G. hirsutum</i> (L.) (Cotton)	-.003	-.367	.199	.98
<i>H. annuus</i> (L.) (Sunflower)	-.674	.347	.025	.98
<i>Z. mays</i> (L.) (Corn)	.505	-1.527	.315	.94
<i>C. album</i> (L.) (Lambsquarters)	-.149	-.222	.028	.93
<i>A. hybridis</i> (Pigweed)	.027	-.325	.047	.99
<i>A. theophrasti</i> Medic. (Velvetleaf)	.487	-.720	.102	.98
<i>D. stramonium</i> (L.) (Jimsonweed)	-.115	.018	.035	.99
<i>X. strumarium</i> (L.) (Cocklebur)	.300	-.748	.125	.98

Plants were grown in cabinets under 14/10 h light/dark and 19/24°C temperature regimes. The mean values from which these coefficients were derived are shown in Fig. 2.

Table 5. Leaf area per plant vs. mainstem node number in some weed and crop species

Species	Notes	Mainstem node number											
		2	4	6	8	10	12	14	16	18	20	24	28
<i>D. stramonium</i>	U.G.C.	—	—	1	2.6	3.7	5.6	7.6*					
	U.F.	—	—	0.5	1.5	5.3	20	47					
<i>A. theophrasti</i>	U.G.C.	—	—	1	2	3.8	8.2	12	18				
	U.F.	—	—	0.4	1	2	3.5	6	11	21			
<i>C. album</i>	U.G.C.	—	—	—	—	—	1	—	3.4	—	6.8		
	U.F., N.Z.F.	—	—	—	—	—	0.5	—	1.2	—	2.2	5.0	7.5
<i>A. hybridis</i>	U.G.C.	—	—	—	—	—	2.9	—	7.2	—	14		
	U.F.	—	—	—	—	—	1.1	—	3.5	—	12		
	N.Z.F.	—	—	—	—	—	0.5	—	2.3	—	3.2	4.8	14
<i>S. ptycanthum</i>	N.Z.F.	—	—	—	0.3	6.0	20						
<i>X. strumarium</i>	U.G.C.	—	1.2	—	3	—	8						
	U.F.	—	—	—	2	—	7						
<i>D. sanguinalis</i>	N.Z.F. (dry soil)	—	.03	.08	.45	.9							
<i>Z. mays</i> A) Leaf tips	U.G.C.	—	0.5	3	8.2	19							
	U.F.	—	—	—	—	—	9.5	18	38	60	78		
	N.Z.F.	—	—	2.5	4	8	15	31	49	71			
B) Col-ars	U.F.	—	2.6	6	26	51	63	70	75	76			
	N.Z.F.	3	9	25	46	66	79	83	85				
<i>G. max</i>	U.G.C.	1	3.2	7.7	15								
	U.F.	0.5	2.5	5.7	13								
<i>H. annuus</i>	Kenig <i>et al.</i> (2) (Field)	—	2.3	4.8	11	15	17	19	20				
	Sivakumar <i>et al.</i> (4)	—	2.1	4.8	9	13	16	18	21	25			
	Sinclair (5)	—	1.5	4.0	6.5	9	13	—	20				
<i>H. annuus</i>	N.Z.G.C.	0.2	0.6	2.0	3.5	5.3							

G.C.=growth cabinet results (23°C); U.F.=Urbana field results (~=23°C); N.Z.F.=field results, Palmerston North, New Zealand (~=17°C); (Field)=1985 results from Urbana and several other locations. *; $\times 10^2 \text{ cm}^2$.

studies; the respective second order polynomial equations are given in Table 4. Table 5 summarizes results from growth cabinet and field measurements. We anticipated that we would have to repeat these measurements on field grown plants; such values were often half of the growth cabinet ones, Table 5. The field data have been duplicated over years and locations, under fairly comparable row and plant spacings. Such values include the contribution from branches. The production of leaf area from branches (or tillers) can be very important in well spaced plants. We had to sample many weed plants to obtain a smooth curve through mean values.

The effects of spacing, fertility, moisture and the timing of seedling emergence were obvious throughout our experiments. Most of our measurements were on unfertilized plots such as in a soybean stand, as compared to corn stands heavily fertilized with nitrogen.

Weeds also flower early because of shorter days in areas with a mild winter.

This was evident at Palmerston North, where, because of the mild winter, crops are planted much earlier than in an area such as Urbana at the same latitude but with severe winters associated with a continental climate. Until such time as quantitative information becomes available about photoperiod effects on flowering in weeds, the weed models will have to be calibrated for every location.

We report some specific leaf area ($\text{cm}^2 \text{g}^{-1}$ dry mass) values for most species; associated values for petiole, stem and root are also needed, Table 2.

General discussion

Our logic needed to predict leaf area development in some crops and weeds, includes look-up tables for leaf area vs. mainstem node numbers. This approach was first used by Sinclair (5). He discussed the advantages and disadvantages developing more sophisticated models. The next level of sophistication would be to tie the expansion of each mainstem and branch leaf to the prediction for a mainstem node number; this has been done for corn and soybean, and we are making progress with weed species.

One of the largest, perhaps overwhelming, errors in any weed model is associated with predicting or measuring the spatial and age distribution of weeds in a field. Once weed numbers, ages, and distribution are established, one can proceed to predict how crop plants and such a population of weeds interact under different environmental conditions. At the minimum, we present a method for predicting seedling leaf area expansion rate before interplant competition sets in. This method will serve as a base for developing more sophisticated models for studying how weeds grow and how crop and weed plants compete. Possibly such models can someday be used to improve the population density—emergence date—yield reduction models in current use.

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