Slow Leaf-Rusting Resistance in Triticale

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ABSTRACT

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Six triticales were evaluated as possible sources of resistance to *Puccinia recondita* for wheat. These lines were evaluated for resistance in the greenhouse and in the field. PIs 429120, 429215, 429121, and 429155 expressed hypersensitivity at all stages of growth, and the last two also had long latent periods in the adult stage. PIs 429220 and 434889 expressed a compatible infection type with a long latent period in the adult stage. Latent periods of these lines were significantly longer in young flag leaves than in old flag leaves. In the field, the final rust severities and areas under the disease progress curves of all the resistant cultivars were low and correlated with each other. Slow-rusting PIs 429220 and 434889 maintained leaf rust severities as low as the lines with hypersensitivity. The hypersensitive and slow-rusting resistances in these lines should be useful for development of wheat cultivars resistant to leaf rust.

Additional key words: alien germ plasm, durable resistance, general resistance, specific resistance, *Triticum aestivum*, ×*Tritiosecale*.

Plant breeders are encouraged to broaden the base of germ plasm in their breeding programs (2). Breeders of wheat (*Triticum aestivum* L. em Thell) are fortunate to have at their disposal a large and relatively untapped gene pool in ancestral and related species and genera (5). One of the most obviously desirable traits in alien germ plasm, and that which has been the most studied and exploited, is disease resistance (27).

Hexaploid triticale (× *Tritiosecale* Wittmack) offers wheat breeders a unique source of alien germ plasm because it possesses both rye (*Secale cereale* L.) and tetraploid wheat (*Triticum turgidum* L.) germ plasm. Genes from triticale may be crossed into common wheat through translocations between wheat and rye chromosomes (12) or by normal homologous recombination within the *Triticum* genomes.

Several triticales were selected from the spring wheat nursery of the Purdue small-grains breeding program in 1982 as possible sources of leaf rust resistance because of their very low levels of disease late in the season. This research was conducted to evaluate more thoroughly the resistance of these triticales in greenhouse and field inoculation tests.

MATERIALS AND METHODS

Greenhouse experiment. Seeds of the selected triticales and susceptible wheat controls were sown 1.5 cm deep in soil in flats, watered, and placed in a cold room at 2 C for 3 days to promote uniform germination and emergence. The plants were grown on greenhouse benches under natural daylight supplemented with 16 hr/day of about 20,000 ergs· cm^{-2}·sec^{-1} fluorescent lighting.

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Seedlings in the flats were inoculated at the two-leaf stage by brushing them with leaves of seedlings that bore uredinia of culture 7434-1-1T of *P. recondita*. Culture 7434-1-1T is avirulent toward *Lr* genes 1, 2a, 3b, 10, 11, 12, 13, 17, 18, 19, 24, and 25. It is virulent toward *Lr* genes 2b, 2c, 2d, 3a, 3bg, and 9. The flats of inoculated seedlings were misted with deionized water and placed in a moist chamber overnight (15 hr). Seedling infection types were recorded 9 days after inoculation on an infection type scale of 0–4 (29). After the infection types were determined, the seedlings were transplanted to soil in 10-cm-diameter plastic pots.

The plants were reinoculated when the flag leaf blade was fully emerged, when the head was half emerged, or at the end of anthesis. A total of 20 plants of each line were inoculated at each growth stage. The adaxial surfaces of the flag leaves were sprayed with an aqueous spore suspension consisting of 50 mg of urediniospores and three drops of Tween 20 per 100 ml. The plants were placed in a moist chamber overnight and were then returned to the greenhouse bench.

Infection types on adult plants were determined 10–20 days after inoculation, depending on the latent period. To measure latent period, the percentage of infection sites on the flag leaf with erupted uredinia was estimated at 1- to 2-day intervals, beginning 6 days after inoculation and continuing until eruption of uredinia ceased. If fewer than 100% of the infection sites on a particular plant developed uredinia, the final percent eruption was adjusted to 100 and the earlier estimates were adjusted accordingly. Probits of the daily proportion of uredinia erupted were regressed on time (days); the latent period was calculated from the regression equation as the time required for 50% of the uredinia to erupt (24). The latent period data for PIs 429121, 429155, 429220, and 434889 were analyzed by analysis of variance to determine if the latent period was affected by stage of growth at the time of infection. The sums of squares were partitioned into effects attributable to genotype, growth stage, genotype × growth stage, and experimental error.

TABLE 1. Reactions of wheat and triticale to infection by *Puccinia recondita* culture 7434-1-1T in the greenhouse

Cultivar[a]	Origin	Infection type[b]		Latent period[c] at growth stage[d]		
		Seedling	Adult	40	55	70
Morocco (W)	Israel	4	4	6.3 ± 0.4	6.5 ± 0.5	6.4 ± 0.2
PI 447343 (W)	China	4	4	6.4 ± 0.5	6.4 ± 0.4	6.4 ± 0.3
PI 429007	India	4	4	6.4 ± 0.5	6.3 ± 0.4	6.5 ± 0.5
PI 429049	U.M., Canada	4	4	6.5 ± 0.4	6.5 ± 0.3	6.2 ± 0.4
PI 419120	CIMMYT	0;1c	0;n			
PI 429121	CIMMYT	0;1c	0;1n	19.4 ± 2.9	18.1 ± 5.5	18.7 ± 3.0
PI 429155	CIMMYT	0;1c	2c	15.0 ± 1.3	13.5 ± 1.8	13.5 ± 1.2
PI 429215	CIMMYT	0;1n	0;n			
PI 429220	California	3c	3	12.2 ± 1.4	11.0 ± 2.8	10.4 ± 2.3
PI 434889	Unknown	3c	3c	15.1 ± 3.8	14.5 ± 3.1	12.9 ± 1.5

[a] Cultivar names followed by W are wheat; all others are triticale.
[b] Infection type on a scale of 0–4 (29); c and n designate a distinct chlorotic or necrotic zone around the uredinium.
[c] The time in days required for 50% of the infection sites to erupt into uredinia (24). Each entry is the mean and standard deviation for 20 plants.
[d] 40 = Flag leaf fully emerged, 55 = spike half emerged, and 70 = anthesis complete (34).

Field experiment. The selected triticales and susceptible wheat controls were planted at the Purdue Agronomy Farm during the springs of 1983 and 1984. The experimental design was a randomized complete block with one replicate in each of three blocks. Each replicate was a 1-m row of 15–30 plants. Disease spreader rows were inoculated with urediniospores of culture 7434-1-1T of *P. recondita*. Heading date was recorded as the day when half of the spikes were half emerged from the boot. Standard diagrams were used to estimate leaf rust severity on the flag leaves on a scale of 0–100% (21). In the 1983 experiment, readings were taken at 3- to 5-day intervals and the severity was estimated for each entire plot. In the 1984 experiment, readings were taken every 2 days and severity was recorded for each of three plants per plot. These plants were tagged so that the same three plants were examined each time. The mean disease severity for the three plants was calculated to obtain a value for the plot. Notes were taken on an entry until the flag leaves were decimated by disease, heat and drought, or natural senescence.

The area under the disease progress curve (AUDPC) for lines with low disease severity was calcuated by AUDPC = $[(Y_{i+1} + Y_i)/2] \times [X_{i+1} - X_i]$, where Y_i = percent disease severity at time X_i. The disease progress curves were truncated 21 days after heading for the AUDPC calculations.

The AUDPCs of lines with final severities greater than 40% were calculated differently. The disease severity data (Y_i) of the three replicates were transformed into logits and regressed on time (days from heading) by means of a quadratic equation. The quadratic equation was then used to estimate transformed disease severities at 21 days after heading, by interpolation or extrapolation. The transformed disease severity data were converted back into proportions, and the AUDPC for each replicate was calculated by the above equation. In this manner, the disease progress curves for lines whose flag leaves senesced before 21 days after heading could be extrapolated to this time. The AUDPCs were calculated for a common time interval so that the resistance of the lines could be evaluated over a comparable period of host plant development.

The arc sine square root-transformed final severity and AUDPC values of each year for each line were analyzed with the analysis of variance with lines as treatments and one replicate per block. The final disease severities were transformed to reduce the heterogeneity of the variances of the treatment means (31). The transformed final severities and AUDPC values obtained in each year were compared by single degree-of-freedom linear contrasts (31). Orthogonal comparisons between and within susceptible and resistant cultivar groups were examined. The correlations of AUDPC means with final severity means were calculated for each year's data.

RESULTS

Greenhouse experiment. There were several reactions to infection by *P. recondita* among the lines (Table 1). The seedling and adult-plant infection types of each triticale line were similar.

TABLE 2. Effects of triticale genotype[a] and growth stage[b] at the time of inoculation[c] with *Puccinia recondita* on latent period of infection

Source	df	Mean square	*P*
Genotype (G)	3	581.592	<0.005
Growth stage (S)	2	51.899	<0.005
G × S	6	4.936	>0.100
Error	228	7.913	...

[a] PIs 429121, 429155, 429220, and 434889.
[b] Latent periods measured on flag leaves inoculated at growth stage 40, 55, or 70, where 40 = flag leaf fully emerged, 55 = spike half emerged, and 70 = anthesis complete (34).
[c] Twenty plants of each cultivar were inoculated at each growth stage in a completely random, two-factor design.

As adults, some triticales and wheats exhibited both compatible infection types and short latent periods. Three types of reaction were observed among the resistant lines. A highly resistant response was exhibited by PIs 429120 and 429215. PIs 429121 and 429155 exhibited intermediate infection types and long latent periods. PIs 429220 and 434889 had compatible infection types but latent periods longer than those of the susceptible triticales and wheats.

The latent periods of the susceptible triticales and wheats were unaffected by the stage of plant growth at infection (Table 1). The latent periods of the other triticales were longest when the young flag leaf was inoculated and became shorter as the age of the flag leaf at the time of inoculation increased. The latent period differed significantly among PIs 429121, 429155, 429220, and 434889 and also among stages of growth at the time of inoculation (Table 2).

Field experiment. Leaf rust severity increased rapidly on susceptible wheat and triticales but slowly or negligibly on the resistant lines (Fig. 1). In 1983, the disease was first observed on the last disease rating before leaf senescence on PIs 429155, 429220, and 434889 and not at all on PIs 429120 and 429121, resulting in AUDPCs being equal to zero.

In both 1983 and 1984, the flag leaves of many of the susceptible lines were decimated before 21 days after heading; however, extrapolation of the disease progress curves to 21 days after heading by means of the quadratic equations was considered appropriate. The higher coefficients of determination and the random distribution of residuals about the regression lines suggested that quadratic regressions described disease progress curves more accurately than did linear regressions.

Analysis of variance revealed that final severities and AUDPCs did not differ significantly among replicates ($P = 0.05$) but did so among the lines. The results of the orthogonal comparisons of AUDPCs were more consistent among years than were the comparisons of the final disease severities (Table 3). There were fewer significant differences among the resistant cultivars than among the susceptible cultivars. The triticales with hypersensitive resistance were more resistant than the slow-rusting triticales only when the final disease severities of 1984 were compared. There was

a high correlation ($r \geqslant 0.91$) between AUDPC and the final disease severity each year.

DISCUSSION

Results from both greenhouse and field experiments indicated that PIs 429120, 429121, 429155, 429215, 429220, and 434889 may be useful sources of leaf rust resistance for *T. aestivum*. Collectively, these triticales could contribute both hypersensitivity and slow rusting.

Inoculations in the greenhouse demonstrated that PIs 429120, 429121, 429155, and 429215 possess the "seedling" type of hypersensitive resistance to *P. recondita*. That is, resistance is expressed throughout the life of the plant. Most of the described *Lr* genes in wheat confer this type of resistance to *P. recondita* (1). The results of preliminary experiments suggest that the infection type of some of these triticales is controlled by one or two genes (33), whose relationship to the *Lr* genes is presently unknown.

The latent period data suggest that PIs 429121 and 429155 possess factors for this component of slow rusting in addition to

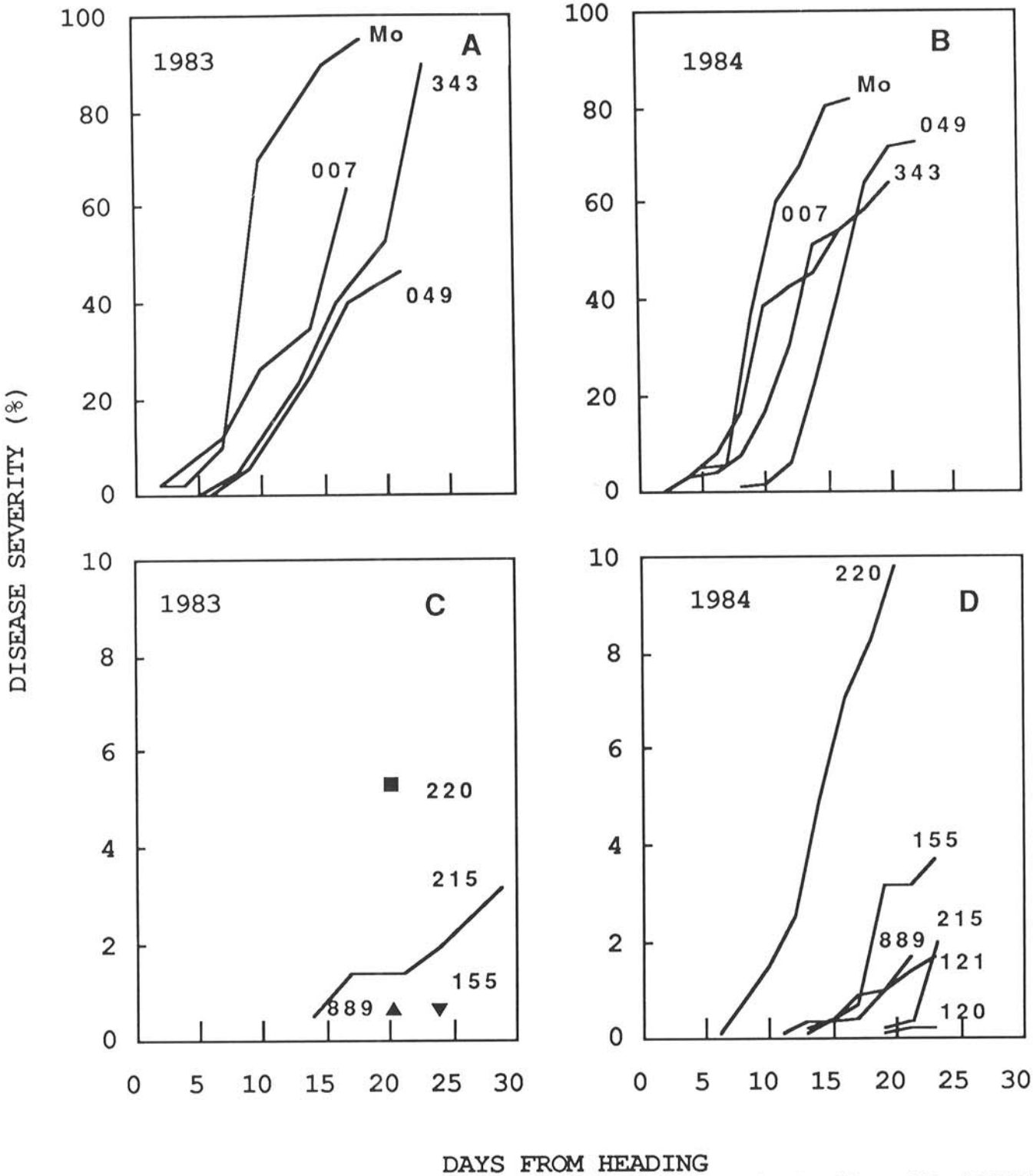

Fig. 1. Leaf rust increase on wheats and triticales at the Purdue Agronomy Farm, 1983 and 1984. **A and B,** Susceptible wheats Morocco (Mo) and PI 447343 (343) and triticales PI 429007 (007) and PI 429049 (049); **C and D,** resistant triticales PI 429120 (120), PI 429121 (121), PI 429155 (155), PI 429215 (215), PI 429220 (220), and PI 434889 (889). Data points are the mean severities of three replicates.

the factors they carry for hypersensitivity. Both of these types of resistance have been identified in barley (*Hordeum vulgare* L.) (19). These two types of resistance react independently against *Puccinia hordei* Otth (15). The existence of slow-rusting resistance (e.g., long latent period) in a hypersensitive line can only be detected when the hypersensitivity is less than complete. If the hypersensitive response entirely prevents sporulation, then the latent period cannot be measured. However, if the hypersensitive resistance permits a restricted uredinium to form (e.g., infection type 1 or 2, Table 1), then the latent period can be measured.

PIs 429220 and 434889 exhibited a susceptible infection type and a long latent period. This is the "slow rusting" type of resistance as commonly defined for cereals (3,32). Some octoploid triticales have previously been suggested to be slow rusting (22); however, the resistance described more closely resembles an "adult plant" type of resistance, in which the seedling shows a fully compatible reaction with the pathogen, whereas the adult plant exhibits a hypersensitive response. Our results are the only report of classical slow rusting in triticale that we know of.

The expression of slow rusting in triticale as a function of leaf age is similar to what has been observed in other cereals. Infections on young flag leaves tend to have a longer latent period than infections on older flag leaves in both wheat (16) and barley (17).

Triticales that possessed any combination of hypersensitivity and slow rusting also had low AUDPCs and final disease severities in the field. Although there were high correlations between the AUDPC values and final disease severites, the AUDPC was a more consistent statistic for comparing resistance among lines, as indicated by the orthogonal comparisons. This is possibly because the AUDPCs were calculated over a common time interval, whereas the final disease severities were greatly influenced by date of senescence.

The resistance of slow-rusting PIs 429220 and 434889 in the field was comparable to that of the hypersensitive lines, even when these lines were evaluated in small plots where there was movement of spores among plots. Slow-rusting cultivars generally do not perform as well in small plots as would be expected in large fields where exogenous inoculum is a minor factor (20,25). However, the resistance of slow-rusting barley cultivars, as indicated by final severity or AUDPC, is correlated with their latent period (14,20). Latent periods of the lengths exhibited by these triticales should be sufficient to provide as much suppression of leaf rust as hypersensitive resistance. Although similar latent periods are not often found in wheat, they have been obtained by intercrossing slow-rusting lines from diverse sources (11).

Hypersensitivity has been the primary form of resistance used to control wheat leaf rust. However, the use of hypersensitive resistance places strong selection pressure on the pathogen and this resistance has been overcome repeatedly through the evolution of new virulent races (7,9,26). Slow-rusting resistance may provide more durable control of leaf rust. Although there is evidence that some isolates of *P. recondita* (10,13), *P. coronata* (6), and *P. hordei* (4,18) differ in their ability to overcome the various components of slow-rusting resistance (infection efficiency, latent period, and spore production) in their respective hosts, no complete "breakdown" of slow rusting has been reported. Moreover, the fact that the extant pathogen population is able to reproduce on slow-rusting cultivars means that the selection pressure exerted by slow rusting should be less than that exerted by a hypersensitive resistance.

Slow-rusting wheats grown extensively may nonetheless select for more aggressive strains of the pathogen. Whether the change in aggressiveness would render slow rusting ineffective can only be determined when slow-rusting cultivars have been grown extensively for several years (8). To reduce the chance that slow rusting would succumb to more aggressive races of the pathogen, it would be desirable to use several different sources of this resistance from the outset. Some of the triticales evaluated in this study may be unique sources of slow rusting for wheat.

Minor gene resistance and field resistance to rust fungi have recently been transferred to wheat (23) and oats (*Avena sativa* L.) (28) from alien species. The identification of slow-rusting tetraploid wheats (30) and this report of slow rusting in triticale suggest that alien species, especially those with chromosomes homologous to some of those in hexaploid wheat, could be useful sources of slow rusting. This resistance may be more valuable than hypersensitivity transferred from alien species, which has provided protection no more durable than that afforded by hypersensitivity found originally in hexaploid wheat.

TABLE 3. Development of leaf rust on wheat and on triticale in the field[a] and single degree-of-freedom linear contrasts between resistance groups

	Value or mean square			
	Final disease severity (%)[d]		AUDPC[e]	
Cultivar[b] or contrast[c]	1983	1984	1983	1984
1. Morocco (W)	93.3	81.7	1,090.9	919.0
2. PI 447343 (W)	90.0	64.5	425.0	579.9
3. PI 429007	63.3	54.4	665.2	633.8
4. PI 429049	46.7	76.1	355.7	422.7
5. PI 429120	0.0	0.2	0.0	0.3
6. PI 429121	0.0	1.4	0.0	5.5
7. PI 429155	0.7	3.7	0.0	11.3
8. PI 429215	2.7	0.8	7.3	0.4
9. PI 429220	5.3	9.8	0.0	69.7
10. PI 434889	0.7	1.7	0.0	6.1
(1,2,3,4) vs. (5,6,7,8,9,10)	23,517**[f]	17,111**	284,622**	2,796,991**
1 vs. 2	74	194*	665,227**	172,497**
3 vs. 4	152	296**	143,716**	66,845**
(1,2) vs. (3,4)	2,054**	65	183,774**	385,911**
5 vs. 8	84	7	81	0
6 vs. 7	11	30	0	49
(5,8) vs. (6,7)	17	114	40	194
9 vs. 10	100	168*	0	6,067
(5,6,7,8) vs. (9,10)	72	188*	13	4,494

[a] Experiments were conducted at the Purdue University Agronomy Farm. Each value is the mean of three replicates.
[b] Cultivar names followed by W are wheat; all others are triticale.
[c] Numbers in the contrast refer to the listed cultivars.
[d] Data were transformed to arc sine square roots before statistical analysis and mean separation. Untransformed values are presented here.
[e] Area under the disease progress curve, calculated from time of first appearance of rust until 21 days after heading.
[f] * And ** indicate significant differences at $P = 0.05$ and 0.01, respectively.

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