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Crop Rotations and Residual Effects of Non-Host Plants**

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INFLUENCE OF PLANT INTERACTIONS ON VESICULAR-ARBUSCULAR MYCORRHIZAL INFECTIONS.

II. CROP ROTATIONS AND RESIDUAL EFFECTS OF NON-HOST PLANTS

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SUMMARY

The effects of crop rotation on mycorrhizal development were examined in pot experiments, using sterilized soil inoculated with *Glomus fasciculatus* 'E3' or *Gigaspora margarita* or unsterile soil containing mainly a type of *Glomus macrocarpus* var. *geosporus*. In four crop pairs tested, the amount of VA mycorrhizal infection in a host plant was not depressed in soil previously cropped with a 'non-host' plant, even where roots of the preceding 'non-host' plant were retained intact in the soil. Indeed the early establishment of VA infection in barley, lettuce and maize inoculated in sterilized soil was stimulated by the 'non-hosts' oilseed rape, cabbage and sugar beet, respectively. VA hyphae were sometimes observed growing in moribund 'non-host' roots. Effects of crop rotation in unsterile soil were similar but less marked. *G. margarita* in sterilized soil infected lettuce considerably less than other crops.

INTRODUCTION

Populations of vesicular-arbuscular (VA) mycorrhizal fungi vary with different cropping regimes in the same soil (Hayman, Johnson and Ruddlesdin, 1975; Kruckelmann, 1975; Strzemska, 1975). This is generally supposed to be because the fungi develop most around those plant species which are most susceptible to mycorrhizal infection (Hayman, 1978). A logical inference is that in crop rotations which include non-host plants or plants which develop little mycorrhiza infection may be less after them than after a strongly mycorrhizal crop. Field observations, however, are not consistent. Kruckelmann (1975) found about nine times as many VA chlamydospores in soil growing oats (a host plant) than sugar beet (a 'non-host' plant) where these crops were grown 16 years in monoculture, but more spores in fields growing sugar beet after oats following potato (host) than in oats after rye (host) following potato. Strzemska (1975) reported that the relative amounts of mycorrhizal infection in different crops grown 5 years in monoculture varied with fertilizer levels. Hayman *et al.* (1975) found that although swedes were not infected by VA fungi in the field, there were as many spores associated with them as with barley and potato in soil given low or high dosages of phosphate fertilizer; at intermediate phosphate levels, however, spore numbers increased with barley and potatoes but not with swedes. Not surprisingly, Black and Tinker (1977) found fewer spores in soil kept fallow than in adjacent soil cropped with barley.

The direct effects of fallow (no plant) and 'non-host' plants on the infectivity of VA fungal propagules in soil can be more readily examined experimentally

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under controlled conditions in pot experiments than in the field. We did this using conditions and plant combinations similar to those in previous experiments (Ocampo, Martin and Hayman, 1980).

MATERIALS AND METHODS

Four mycorrhizal hosts, viz. barley (*Hordeum vulgare* L. 'Julia'), lettuce (*Lactuca sativa* L. 'Fortune'), maize (*Zea mays* L. 'Cargill Primeur 170') and potato (*Solanum tuberosum* L. 'King Edward') and four plant species believed to be non-mycorrhizal ('non-hosts'), viz. oilseed rape (*Brassica napus* L. 'Victor'), cabbage (*Brassica oleracea* L. 'Ormskirk'), sugar beet (*Beta vulgaris* L. var. *rapa* 'Kleine') and kale *Brassica oleracea* L. 'Maris Kestrel'), were tested in six experiments.

The same two soils were used as before (see Ocampo *et al.* 1980, for full details), one from a fallow area at Woburn and the other from a maize field at Rothamsted (Long Hoos). The Woburn soil (Tables 1, 4, 5 and 6) was sterilized with γ -irradiation (1 Mrad), mixed 1:1 with sterilized sand, and inoculated with soil from stock plant cultures of either *Glomus fasciculatus* 'E3' or *Gigaspora margarita* which contained spores, mycelium and infected root fragments, at the rate of 5 g soil inoculum mixed with 5 g sand per 75 mm pot. The Long Hoos soil (Tables 2, 3, 7 and 8) was mixed 1:1 with sand and used unsterile to allow infection by the indigenous VA endophytes, predominantly spore types resembling *Glomus macrocarpus* var. *geosporus*.

The pots were maintained on sand trays and given nutrient solution (Hewitt's) when required; the soil was kept moist by capillary watering from below. In the first experiments (Tables 1 and 2) the pots with inoculum were either kept with no plants (fallow), or planted with seedlings of a 'non-host' plant, three seedlings per pot. After 10 weeks the tops of these 'non-host' plants were cut off and the roots either left undisturbed in the soil or the soil was tipped out and the roots removed before replacing the soil. Seedlings of host plants were then planted in these pots, with three replicate pots per treatment, in the following pair combinations: barley after oilseed rape, lettuce after cabbage, maize after sugar beet and potato after kale. The host plants were harvested after 10 weeks and the roots examined in detail for infection. These same three treatments were repeated for maize-sugar beet (Table 3) together with two more, one where fresh soil was used and the other where a host species, viz. maize, was the first crop - after 10 weeks the large roots were removed and the small roots retained. In the next experiment (Table 4), soil in which 'non-hosts' (cabbage and swede) inoculated with *Gigaspora margarita* had grown was diluted with sand (1:9, 3:7 and 6:4 parts soil:sand) before replanting with host species (lettuce and onion, respectively). Later experiments included the original three treatments (Tables 1 and 2) plus a treatment with fresh soil either amended with the same 'E3' inoculum that had been stored at 2 °C for 10 weeks, (sterilized soil, Tables 5 and 6) or unamended (unsterile soil, Tables 7 and 8) and a treatment where host plants that were already 10 weeks old were grown for a further 12 weeks to assess the constancy of infection with time. Plants in these experiments were harvested after 3, 6 and 12 weeks to monitor early effects on infection in the three pair combinations barley-rape, lettuce-cabbage and maize-sugar beet.

After harvesting each experiment, the whole root systems were cleared and stained, and infection recorded on 20 random 1 cm root segments per replicate at $\times 160$ magnification as before. (Ocampo *et al.* 1980).

RESULTS

In all four plant combinations tested (Table 1), VA infection in a host species was not depressed when grown in sterilized soil containing 'E3' inoculum and which had previously grown a 'non-host' compared to when grown in the same inoculated soil which had been kept 10 weeks with no plants (fallow). This was so even when the roots of the 'non-host' plant were retained in the soil in contact with the roots of the newly transplanted host seedlings. In fact there was significantly more mycorrhizal infection (both percentage root length and percentage cortex) in barley after oilseed rape than after fallow. With maize the proportion of root cortex infected was greater in soil containing sugar beet roots than after fallow. Other differences in the amounts of infection between treatments were not statistically significant. Arbuscule development appeared greater after 'non-hosts' than after fallow, but this was significant only for barley after oilseed rape where the roots were retained in the soil and for lettuce after cabbage.

In unsterile soil infection by the indigenous VA endophytes showed similar results (Table 2) to the sterilized soil with 'E3', namely no inhibitory effect of the 'non-host' roots and, with barley following oilseed rape, a slight stimulatory effect which was significant in terms of percentage root cortex infected. More entry points were formed on roots of maize than on roots of the other three host plants in all three treatments. Less VA infection developed in the unsterile Long Hoos soil than in the sterilized E3-inoculated Woburn soil, especially in barley and potato.

Pre-cropping with a host plant was next compared to a 'non-host':host rotation. Table 3 shows that this led to differences in infection levels which were still evident when the plants were harvested after 15 weeks. Infection in maize was highest in soil that had previously grown a maize crop and lowest in maize planted in soil kept fallow or disturbed by the removal of the pre-crop sugar beet roots. As before in this soil, there was a trend towards more infection in the presence of intact sugar beet roots than in the fallow soil.

To examine further the possibility of residual inhibitory substances remaining in the soil after a 'non-host', despite evidence above to the contrary, soil in which cabbages or swedes had grown was mixed with increasing amounts of sand before replanting with lettuce or onion, respectively. It was considered that adding sand would dilute any toxic residues without decreasing the number of infection propagules enough to markedly slow down infection since the inoculum density was relatively high. Table 4 shows no significant effect of diluting the infective soil with sand on the amount of VA mycorrhiza that developed in lettuce and onion in all but one instance (cortical infection in onions in 1:9 soil:sand). This is further evidence against any negative chemical effect of 'non-hosts' on hosts.

Another result from this experiment was the apparent host specificity of *Gigaspora margarita* in this soil. It consistently infected about three times more onion root than lettuce root, in contrast to 'E3' in this same soil which was equally highly infective to both onion and lettuce. Also, in the unsterile Long Hoos soil, the native endophytes infected lettuce as heavily as the other crops. These results confirm previous observations (Ocampo *et al.* 1980).

Because differences in the amounts of infection between treatments were usually fairly small in plants harvested after 10 weeks (Tables 1 and 2) or more (Tables 3 and 4), the possibility of larger differences in the early stages of infection was next examined by taking serial harvests. Table 5 shows the amounts of infection after 3, 6 and 12 weeks, and Table 6 gives concurrent details of entry points and

Table 1. *VA* infections in mycorrhizal host plants grown in sterilized soil previously inoculated with *E3* and cropped with 'non-hosts' or kept fallow

Plant	Pre-crop	Root infection		Entry points	Vesicles	Arbuscules*
		Percentage length	Percentage cortex			
Barley	Fallow	53	29	1.4	1.1	5
	Rape-rm†	81	51	4.2	2.1	15
	Rape-rt†	85	60	3.2	0	19
LSD 5%		9	18	2.4	3.5	12
Lettuce	Fallow	89	54	4.7	0	2
	Cabbage-rm	97	75	5.5	0.2	19
	Cabbage-rt	94	75	6.5	0.3	18
LSD 5%		14	25	4.4	0.5	14
Maize	Fallow	89	53	4.2	0	7
	Sugar beet-rm	80	59	5.3	0.6	15
	Sugar beet-rt	93	77	5.3	0.1	21
LSD 5%		34	20	6.2	0.8	19
Potato	Fallow	61	46	2.2	5.7	18
	Kale-rm	74	61	3.5	2.9	24
	Kale-rt	74	63	3.7	3.6	23
LSD 5%		34	38	2.9	3.6	14

* estimated in categories: 10 \approx 25% infection, 20 \approx 50%, 30 \approx 75%.

† rm = roots removed; rt = roots retained.

Number of entry points, vesicles and arbuscules are given per cm of root length.

Each figure is the mean for three pots and 60 cm root.

Table 2. VA infections in mycorrhizal host plants in unsterile soil previously cropped with 'non-hosts' or kept fallow

Plant	Pre-crop	Root infection		Entry points per cm root	Vesicles per cm root	Arbuscules
		Percentage length	Percentage cortex			
Barley	Fallow	36	20	1.3	0.7	5
	Rape-rm	46	32	1.6	3.1	11
	Rape-rt	50	33	1.7	0.6	11
LSD 5 %		17	9	0.8	5.5	3
Lettuce	Fallow	66	40	2.2	1.7	11
	Cabbage-rm	55	35	3.6	0.9	5
	Cabbage-rt	64	43	2.1	2.0	11
LSD 5 %		18	12	2.7	2.3	9
Maize	Fallow	65	47	5.2	0.9	12
	Sugar beet-rm	73	53	6.0	4.7	15
	Sugar beet-rt	83	60	6.3	1.5	10
LSD 5 %		77	58	6.8	4.7	14
Potato	Fallow	29	21	1.3	0.3	10
	Kale-rm	36	27	1.2	0.2	11
	Kale-rt	28	21	1.2	0.7	8
LSD 5 %		25	18	1.1	0.5	11

Explanations same as for Table 1.

Table 3. *VA infections in maize grown in unsterile soil previously cropped with sugar beet, maize or kept fallow*

Pre-crop	Root infection	
	Percentage length	Percentage cortex
Fallow	65	35
Sugar beet-rm	63	37
Sugar beet-rt	83	51
Maize	92	59
Fresh soil	74	44
LSD 5%	20	17

Explanation same as for Table 1.

Table 4. *VA infections in host plants in sterilized soil inoculated with Gigaspora margarita, pre-cropped with 'non-hosts', and diluted with sand*

Plant	Pre-crop	Percentage soil in mixture with sand	Root infection	
			Percentage length	Percentage cortex
Lettuce	Cabbage	10	16	7
		30	15	7
		60	21	9
		LSD 5%	—	15
Onion	Swede	10	52	20
		30	58	29
		60	61	29
		LSD 5%	—	14

vesicle and arbuscule development. The two most striking results for barley, lettuce and maize, (see especially figures for the 3-week harvest) were: (1) inoculum left in moist soil in pots with no plants in the glasshouse for 10 weeks produced a much more rapid build-up of infection than the same inoculum preserved at 2 °C; and (2) VA infection was fastest from the intact roots of 'non-hosts' left in the soil. Three weeks after transplanting to the sterilized Woburn soil, infection in barley was 7.5 times greater in inoculated soil kept moist in pots than in fresh soil with preserved inoculum and 17.5 times greater in soil containing inoculated rape roots. Similar results were obtained with lettuce and maize. However, after 6 weeks, differences in the amounts of infection between treatments were no longer evident for lettuce and maize, although with barley infection from the preserved inoculum had not yet caught up and was still behind after 12 weeks. Infection in plants already 10 weeks old at the beginning of the experiment remained constant over the subsequent 12 weeks and did not differ significantly from infection in the 12-week-old plants. This suggests a maximum level of infection for a particular crop under these conditions. The rate of infection was not related to the growth of the host plant.

Table 6 shows a peak of activity at 6 weeks, at which time infection had virtually reached its maximum level and there were generally most entry points and vesicles. Arbuscular development also peaked at this time or even earlier in barley and

Table 5. Amounts of VA infection in mycorrhizal host plants grown in sterilized soil inoculated with 'E3' and given different pre-cropping treatments

Plant	Pre-crop treatment	Percentage root length infected after (weeks)			Percentage root cortex infected after (weeks)		
		3	6	12	3	6	12
Barley	Fallow	30	69	66	18	38	40
	Rape-rm*	8	70	80	4	47	50
	Rape-rt*	70	79	84	50	54	60
	Fresh†	4	33	37	1	16	24
	Original‡	57	54	59	33	31	34
LSD 5%		14	21	17	16	22	15
Lettuce	Fallow	52	85	55	33	62	39
	Cabbage-rm*	33	89	73	22	68	52
	Cabbage-rt*	70	88	83	53	63	68
	Fresh†	5	68	62	1	47	40
	Original‡	71	73	73	48	53	57
LSD 5%		21	14	15	15	13	14
Maize	Fallow	22	87	84	12	63	58
	Sugar beet-rm*	23	85	83	12	60	55
	Sugar beet-rt*	40	82	74	25	58	49
	Fresh†	4	70	80	1	52	56
	Original‡	76	93	90	49	71	63
LSD 5%		17	16	17	16	15	13

* rm = roots removed; rt = roots retained.

† Fresh soil given inoculum stored at 2 °C.

‡ Original host plant continued.

Each figure is the mean for three pots and 60 cm root.

lettuce, especially where non-host roots were retained. A subsequent decline in arbuscule numbers per unit of root often occurred. This was more pronounced than for vesicles and entry points and most noticeable in the oldest (22 weeks) plants.

Table 7 records infection by native endophytes in unsterile soil from Long Hoos. It developed more slowly in barley and lettuce in this soil than in the sterilized soil (Table 5) but the rate of infection of maize was more similar in both soils. At the 6-week harvest maize was much more infected than either barley or lettuce. Differences between treatments were small for maize, whereas for barley and lettuce differences at the 6-week stage resembled those at the 3-week stage in the sterilized soil. Thus infection was slowest in fresh soil and appeared to be stimulated by the presence of intact rape and cabbage roots. By 12 weeks infection levels had become fairly constant for all three crops. As before, rate of infection was not related to growth.

Numbers of entry points in plants growing in unsterile soil reached a maximum at 12 weeks (Table 8), later than in the sterilized soil. Arbuscule development was also greatest at this time in barley and lettuce, but with maize a peak in arbuscule formation was already evident at 6 weeks. There was no apparent decline in arbuscule numbers. Vesicle numbers were highest at 22 weeks. Data from the 6-week harvest show that entry points formed faster on maize roots than on lettuce and onion roots.

Table 6. *Formation of entry points, vesicles and arbuscules in mycorrhizal host plants grown in sterilized soil inoculated with 'E3' and given different pre-cropping treatments*

Plant	Pre-crop treatment	Entry points per cm root after (weeks)			Vesicles per cm root after (weeks)			Arbuscules* after (weeks)		
		3	6	12	3	6	12	3	6	12
Barley	Fallow	0.6	1.3	1.0	5.2	12.5	17.6	7	10	1
	Rape-rm	0.2	0.9	1.4	0.8	25.8	13.1	2	13	9
	Rape-rt	1.0	1.5	2.1	11.8	19.3	8.4	21	19	15
	Fresh	0.2	0.7	1.6	0.3	6.5	6.2	1	3	1
LSD 5 % Lettuce	Original	1.3	1.1	1.2	10.5	16.4	11.8	10	3	3
	Fallow	0.8	0.9	1.7	4.0	16.0	9.8	6	11	8
	Cabbage-rm	0.8	2.6	1.1	26.6	50.6	24.5	9	6	0
	Cabbage-rt	0.4	3.0	1.5	13.5	56.2	36.9	7	5	4
LSD 5 % Maize	Fresh	0.8	3.9	2.9	24.5	37.3	30.1	19	15	4
	Original	1.9	2.6	1.5	0.3	20.4	40.0	1	2	0
	Fallow	1.1	1.4	1.7	17.4	25.1	26.3	7	10	4
	Sugar beet-rm	0.8	3.1	2.5	5.4	50.5	19.6	3	10	5
LSD 5 %	Sugar beet-rt	2.1	4.1	2.5	11.9	34.2	26.0	2	16	2
	Fresh	0.5	3.4	2.8	0.5	22.0	16.8	5	12	0
	Original	2.8	3.7	3.2	20.4	44.8	28.5	9	16	6
	LSD 5 %	1.6	2.7	1.0	14.5	20.8	14.5	2	8	7

* Estimated in categories: 10 ≈ 25 % infection; 20 ≈ 50 %; 30 ≈ 75 %.
Rest of legend same as for Table 5.

Table 7. Amount of VA infection in mycorrhizal host plants grown in unsterile soil with different pre-cropping treatments

	Pre-crop plant treatment	Percentage root length infected after (weeks)			Percentage root cortex infected after (weeks)		
		3	6	12	3	6	12
Barley	Fallow	2	6	85	1	2	63
	Rape-rm	1	3	65	<1	1	43
	Rape-rt	2	16	80	1	5	60
	Fresh	1	3	85	<1	1	59
	Original	36	22	99	21	11	83
LSD 5%		16	15	19	9	7	11
Lettuce	Fallow	6	17	72	2	10	50
	Cabbage-rm	<1	12	88	<1	8	67
	Cabbage-rt	1	25	83	<1	15	62
	Fresh	2	5	81	1	2	57
	Original	48	72	79	30	53	59
LSD 5%		27	15	19	17	13	17
Maize	Fallow	7	71	71	3	47	50
	Sugar beet-rm	5	47	50	2	31	33
	Sugar beet-rt	5	48	63	1	33	45
	Fresh	8	59	82	4	41	59
	Original	58	80	75	40	56	56
LSD 5%		13	48	17	9	33	16

Legend same as for Table 5.

DISCUSSION

These experiments show that, contrary to certain speculation (Hayman *et al.* 1975), pre-cropping with so-called 'non-host' species does not inhibit the development of VA mycorrhiza in a subsequent host plant. This was so with several host-'non-host' combinations. In some instances (e.g. Table 5) there was evidence of 'non-host' roots increasing the rate of infection in host plants. In addition, it seems that prior cropping with a strongly mycorrhizal plant (maize, Table 3) can increase soil infectivity even further. The effects of 'non-hosts' in these pot studies may help explain the field observation that VA mycorrhizal populations did not drop during a season with a 'non-host' (Hayman *et al.* 1975; Kruckelmann, 1975).

Previous observations (Ocampo *et al.* 1980) showed that VA fungal hyphae can make some growth around the roots of 'non-hosts'. The present study suggests that these hyphae are more active in infecting roots than is fresh inoculum added at the same rate as before. Therefore it is not surprising that removing 'non-host' roots, originally done on the assumption that this might remove inhibitory or toxic materials and so enhance infection, instead decreased the rate of infection compared to leaving these roots intact in soil. Probably some inoculum attached to the roots was removed, thereby decreasing the inoculum level, and that left in the soil was disrupted. The much faster build-up of VA infection in barley after oilseed rape (roots retained in the soil) than after fallow or the addition of fresh inoculum (Table 5) strongly suggests increased inoculum or increased vigour of the fungus, or both, after 10 weeks' close contact with the roots of supposedly non-mycorrhizal plants. Furthermore the faster build-up of infection in inoculated soil kept fallow in pots compared to infection from the same amount of inoculum

Table 8. *Formation of entry points, vesicles and arbuscules in mycorrhizal host plants grown in unsterile soil with different pre-cropping treatments*

Plant	Pre-crop treatment	Entry points per cm root after (weeks)			Vesicles per cm root after (weeks)			Arbuscules after (weeks)		
		3	6	12	3	6	12	3	6	12
Barley	Fallow	0.1	0.5	2.5	0	0	1.8	< 1	0	22
	Rape-rm	< 0.1	0.2	1.3	0	< 0.1	0.7	0	< 1	16
	Rape-rt	0.2	1.1	2.5	0	0	0	1	0	20
	Fresh	0.1	0.2	2.6	0	< 0.1	0.6	0	< 1	18
	Original	2.1	1.1	3.1	0.1	0.1	37.7	5	3	24
LSD 5%		1.3	0.9	1.2	0.1	0.2	24.0	2	3	7
Lettuce	Fallow	0.8	0.9	3.4	0	0.1	5.8	1	< 1	7
	Cabbage-rm	< 0.1	0.8	4.5	0	0.4	6.4	0	0	11
	Cabbage-rt	0.1	0.8	4.8	0	0.1	1.6	0	5	6
	Fresh	0.2	0.4	3.4	0	0	1.4	0	0	12
	Original	2.3	3.9	3.2	0.8	3.5	26.9	4	2	10
LSD 5%		1.4	0.6	1.3	0.6	1.0	19.1	3	1	11
Maize	Fallow	0.8	3.4	4.8	0	< 0.1	4.2	1	12	9
	Sugar beet-rm	0.5	2.2	3.9	0	0.4	0.9	1	4	1
	Sugar beet-rt	0.3	2.5	3.5	0.2	0.5	5.2	0	8	9
	Fresh	1.1	3.5	4.9	0	0.5	3.0	2	8	9
	Original	4.6	3.6	4.0	0.4	4.0	7.1	8	7	13
LSD 5%		1.1	2.4	3.2	0.4	1.2	7.2	3	13	7

Legend same as for Table 6.

stored at 2 °C for the same period suggests that the fungus remained or became more active in the potted soil, indicating the possibility of some saprophytic growth from the propagules (spores, hyphal clumps and infected root fragments). This possibility is supported by recent evidence from Warner and Mosse (1980). The alternative explanation, namely that the fungus lost much of its viability in storage at 2 °C, is not considered likely since such inoculum is routinely kept under these conditions and has not shown poor viability on other occasions. That differences in soil fertility after pre-cropping could account for the differences in mycorrhizal infection seems improbable because neither soil was P-deficient, the plants received nutrient solution, and dry wts were usually similar between treatments.

This study also produced evidence for host–endophyte specificity which is believed to be rarer than soil–endophyte specificity (see Mosse, 1973). Maize (Tables 7 and 8) became heavily mycorrhizal much faster from the endophytes native to Long Hoos soil (mainly *Glomus macrocarpus* var. *geosporus*) than barley or lettuce in this soil whereas with the E3 endophyte in Woburn soil (Tables 5 and 6) maize was more slowly infected than lettuce. This suggests that endophytes most infective to maize may have been preferentially increased in Long Hoos field which was growing maize at the time the soil was collected. *Gigaspora margarita* (Table 4) proved to be only about one-third as infective to lettuce as to onion in sterilized Woburn soil, confirming previous findings (Ocampo *et al.* 1980), whereas with the E3 endophyte in the same soil lettuce became much more infected, comparable to barley and maize in that soil and also to onion in a previous experiment (Ocampo *et al.* 1980).

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