Effect of Age, Size, and Weight of Witchweed Seeds on Host/Parasite Relations

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ABSTRACT

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An inherent problem of work with parasitic weeds is variability of seed germination. This study was conducted to develop a procedure for segregating seeds of witchweed (*Striga asiatica*) by age, size, and weight to eliminate part of this variability. Seeds were classified into seven age groups (1, 2, 3, 4, 6, 7, and 8 yr old) and five size and weight groups for testing. The latter were large (>149 μm in diameter) and heavy (specific gravity >1.0) (LH), large and light (specific gravity <1.0) (LL), small (<125 μm in diameter) and heavy (SH), small and light (SL), and random (mixture of seed sizes) (R). Significant reductions in seed viability were manifested with seeds >2 yr old and in seed germination with seeds >4 yr old. Average viability rate of seeds >4 yr old was 20%. Witchweed total infestation and emergence significantly increased with 1-, 2-, and 3-yr-old seeds but significantly decreased with seeds >4 yr old. Shoots of corn (*Zea mays*) plants grown in soil infested with 1-, 2-, 3-, and 4-yr-old seeds were significantly lighter than those grown in soil infested with seeds >6 yr old, whereas roots of corn plants grown in soil infested with 1-, 2-, 3-, and 4-yr-old witchweed seeds were significantly heavier than those grown in soil infested with seeds >6 yr old. Maximum seed viability and germination occurred in LH seed. Seed viability and germination diminished with age faster with LL, R, SH, and SL than with LH. Maximum witchweed infestations and emergence in corn was obtained with LH seed. Shoots of corn plants grown in soil infested with LH, R, and LL seed were significantly lighter than those grown in soil infested with SH and SL seed, whereas roots of corn plants grown in soil infested with LH, R, and LL were significantly heavier than those grown in soil infested with SH, SL, and the control. Witchweed seed viability and germination responses were less variable with uniform seed size (eg, LH, LL, SH, and SL) than with mixed seed (eg, R).

Witchweed [*Striga asiatica* (L.) Kuntze] is a parasitic weed of corn (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], millet [*Pennisetum americanum* (L.) K. Schum], rice (*Oryza sativa* L.), and sugarcane (*Saccharum officinarum* L.). Witchweed infests more than 100,000 ha of land in North and South Carolina. Damage to corn in the United States could range up to 90% reduction of yield (16). The Department of Agriculture and United States farmers now spend more than $4 million per year to eradicate this pest from infested areas. Witchweed seedlings are relatively easy to kill after germination of the seed. However, dormant seeds are very difficult to exterminate. Witchweed seeds do not normally germinate unless they are in close proximity of the roots of host and false host plants that exude a stimulant that induces germination (6). Present control programs are largely restricted to application of herbicides to the emerged plants (16), induction of seed germination in absence of a host by soil fumigation with a germination stimulant, ethylene gas (7), and breeding host cultivars resistant to witchweed (5).

Several conditions influence longevity of seed of nonparasitic plants in the soil. Increasing soil depth favors greater seed longevity (4). Acid and water-logged soils also favor maintenance of dormancy and seed survival (3). Cultivation reduces seed longevity and seed survival (21).

Storage temperature and relative humidity (RH) were reported to affect witchweed seed viability (13). Temperatures <24 C accompanied by low RH promoted longer seed viability of witchweed. Robinson and Kust (19) showed that witchweed seed viability increased with burial depth. However, several workers (1,4,11,13) working with parasitic and nonparasitic plants reported considerable variation in the germination results of replicate samples of seed even if all experimental conditions were identical.

In a screening program for host resistance to witchweed, any reduction in variability between results of replicate samples could produce more reliable information about any host cultivar being tested. Different strains of witchweed seed were reported to differ significantly in weight, total phenolic content, and electrophoretic protein patterns (14). Differences in seed size and weight may account for the observed variabilities in results derived from replicate samples (1,4,11,13). Relatively little information has been reported about seed characters of parasitic plants, especially witchweed.

This study was conducted to investigate the effects of age, size, and weight of witchweed seeds on host/parasite relations under both laboratory and greenhouse conditions.

MATERIALS AND METHODS

Witchweed seed of seven age groups; 1-, 2-, 3-, 4-, 6-, 7-, and 8-yr-old seed that had been collected from plants parasitizing corn at the USDA Whiteville Methods Development Center Experimental Farm at Evergreen, NC, were used in both laboratory and greenhouse experiments. The seeds were stored in unsealed glass jars under room conditions.

Large and small seed size groups were obtained by sieving the seed successively through two copper screens of 149 and 125 μm mesh, respectively. The large size group constituted seeds that were retained by the 149-μm screen, whereas the small size group comprised seed that passed through the 125-μm screen. Seeds <149 μm and >125 μm were discarded.

Two seed weight groups, heavy and light, were obtained by separate flotation of the large and small seeds in a 250-ml glass separatory funnel filled with distilled water. Each size group was vigorously shaken for 20 min and then allowed to stand for an additional 20 min to allow seed separation into light seed (specific gravity <1.0) which remained floating at the surface of the water

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and heavy seed (specific gravity > 1.0) which sank to the bottom of the funnel. The heavy seeds were recovered by opening the bottom stopcock and collecting the material on a 116-μm mesh plastic screen. The floating seeds were subsequently recovered on a separate screen. All four seed types (large heavy [LH], large light [LL], small heavy [SH], and small light [SL]) were then left overnight in a drying cabinet at 30 C before use. In addition to the four seed types, a random (mixture) (R) seed type was included to represent the conventional seed type used in testing. Both laboratory and greenhouse experiments utilized a split-plot design with the seven age groups representing the main-treatments and the five seed types the subtreatments. The laboratory experiment was replicated six times while the greenhouse experiment had four replications. Both experiments were carried out at the USDA Whiteville Methods Development Center, Whiteville, NC.

Statistical evaluation for stability of results obtained from replicate samples of a seed size and weight treatment over all age groups of all parameters measured was performed by regression analysis, using the regression coefficient "b" in a Finlay and Wilkinson (9) style analysis, and regressing results of replicates on block totals. In such an analysis, $b = 1$ indicates average stability while $b > 1$ reveals low stability. Correlation analyses were also performed to test the strength of the relationship between witchweed emergence and total witchweed plants (emerged and submerged) and between total witchweed plants and root weight of corn.

Laboratory experiment. Seed germination was determined by using an aqueous solution containing 1 ppm of the experimental synthetic germination stimulant (GR-24) as the stimulant (12). Seeds were conditioned by placing 200–500 seeds in each of six 60 × 15-mm plastic petri dishes containing 5 ml of distilled water. Seeds were then stored in a seed germinator kept at 31 C and 100% relative humidity for 14 days. When the conditioning treatment was completed, ~4 ml of distilled water were drained from the petri dishes. Postconditioning treatment involved addition of about 4 ml of the stimulant solution and further incubation in a germination chamber at 31 C for 24 hr before running the viability test. The control treatment did not receive any stimulant.

Seed viability was determined by draining off the stimulant solution from the petri dishes and adding 5 ml of a solution containing 3,000 ppm of TTR (triphenyl tetrazolium chloride) to the germinated and ungerminated seed in the petri dishes. The seeds were then stored in a seed germinator for 8 days at 31 C. At that time the ungerminated viable seed varied from light red to brick red, but nonviable seed remained the usual light-brown. Counts of germinated, viable, and nonviable seed were then determined simultaneously. Seed viability was counted as percent germinated plus percent viable. Analysis of variance was performed on arc sine-transformed data.

Glasshouse experiment. This experiment determined the effects of age, size, and weight of seed on witchweed emergence and host parasitization. Effects of host parasitization on root and shoot weights of corn were also determined. The Lakeland loamy sand (thermic coated Typic quartzisamment) used as potting soil was sterilized by fumigation for 48 hr with methyl bromide and then received a "compound" fertilizer NPK (5-10-30) at the rate of 560 kg/ha. Witchweed-infested treatments were obtained by the addition of witchweed seed to plastic pots (21 cm in diameter) filled with 4,000 cm^3 of soil. The concentration of witchweed seed in the soil was 0.001 mg/cm^3 to a depth of 3 cm. Addition of witchweed seed to the soil involved the removal and placement of 1,000 cm^3 of soil from each pot in a small tumbler kept rotating at an angle of 45 degrees for 5 min to ensure thorough mixing. The control treatment was maintained free of witchweed seed. Seed-infested soil was then returned to each pot and leveled. Three seeds of corn cultivar Pioneer 3030 were sown 2 cm deep and later thinned to one seedling per pot. The experiment was terminated at witchweed flowering. Analysis of variance was performed on all data.

RESULTS

Laboratory experiments. *Seed viability.* There were highly significant differences ($P = 0.01$) in seed viability among the age treatments and among the witchweed seed size and weight treatments (Table 1). The seed age × seed size and weight interaction also manifested significant differences. However, there were no significant differences ($P = 0.05$) in seed viability between the 2- and 3-yr-old seeds. Maximum seed viability was obtained by the 1-yr-old seeds and the minimum by the 8-yr-old seed. Seed viability of the 2-, 3-, 4-, 6-, 7-, and 8-yr-old seed was 7.6, 8.3, 19.2, 40.9, 46.2, and 62.6%, respectively, less than that of the 1-yr-old seed.

LH witchweed seed exhibited maximum seed viability whereas SL seed manifested minimum seed viability (Table 1). Seed viability of the LH seed exceeded that of the R by 10.6%. Viabilities of the LL, SH, and SL seeds were 1.5, 24.7, and 27.3%, respectively, below that of the R seeds.

Seed germination. Highly significant differences ($P = 0.01$) in witchweed seed germination were detected between the seed age treatments and between the seed size and weight treatments (Table 2). The seed age × seed size and weight interaction also exhibited significant differences ($P = 0.01$). No significant differences in seed germination were found between the 1- and 2-yr-old seeds. Maximum seed germination occurred in the 3-yr-old seeds. No germination was observed in the 8-yr-old seeds. Seed germination of the 3-yr-old seeds was 7.6% above that of the 1-yr-old seeds, whereas the 4-, 6-, and 7-yr-old seeds had 8.7, 34.8, and 41.9%, respectively, less germination than the 1-yr-old seeds.

Maximum seed germination occurred in the LH seeds and the minimum in the SL seeds. LH and LL seeds had 5.3 and 1.5%, respectively, greater germination than the R seeds. SH and SL seed germination was 21.7 and 24.1%, respectively, less than that of the

TABLE 1. Witchweed seed viability as affected by age, size, and weight of seed

Witchweed seed age (yr)	Viability (%) relative to seed size and weight[x]					
	R	LH	LL	SH	SL	Mean
1	77.9[y]	77.3	68.8	48.6	44.1	63.3 a[z]
2	78.1	78.1	70.9	27.8	23.6	55.7 b
3	63.8	57.2	66.1	45.4	42.6	55.0 b
4	45.6	75.2	51.6	24.4	23.7	44.1 c
6	41.1	43.2	26.5	0	1.3	22.4 d
7	16.1	30.3	31.7	7.5	0	17.1 e
8	3.8	0	0	0	0	0.7 f
Mean	46.6 b	51.6 a	45.1 b	21.9 c	19.3 c	36.9

[x] LH = large heavy, LL = large light, SH = small heavy, SL = small light, and R = random.

[y] Viability as determined with triphenyl tetrazolium chloride.

[z] Means followed by the same letter do not differ, $P = 0.05$, according to Duncan's multiple range test.

TABLE 2. Witchweed seed germination as affected by age, size, and weight of seed

Witchweed seed age (yr)	Germination (%) relative to seed size and weight[x]					
	R	LH	LL	SH	SL	Mean
1	61.2[y]	57.2	66.1	45.4	43.3	54.6 b[z]
2	76.4	77.8	72.6	27.7	23.6	55.6 b
3	76.7	75.0	67.7	47.8	43.8	62.2 a
4	45.2	73.7	58.9	26.1	25.5	45.9 c
6	34.3	36.2	26.5	0.9	0.9	19.8 d
7	11.7	22.5	23.7	5.6	0	12.7 e
8	0	0	0	0	0	0 f
Mean	43.6 b	48.9 a	45.1 b	21.9 c	19.5 d	35.8

[x] LH = large heavy, LL = large light, SH = small heavy, SL = small light, and R = random.

[y] Germination, percent of seed.

[z] Means followed by the same letter do not differ, $P = 0.05$, according to Duncan's multiple range test.

R seeds. Reduction in both seed viability or seed germination in seeds >4 yr old compared with that of 3-yr-old seeds was at minimum for LH seeds (51.9 and 55.8%, respectively) and at maximum for SL seeds (98.6 and 84.9%, respectively).

Glasshouse experiment. *Emerged witchweed plants.* Data in Table 3 show highly significant differences ($P = 0.01$) in witchweed emergence among the age treatments, among the seed size and weight treatments, and at the age × seed size and weight interaction level. Maximum witchweed emergence was exhibited by the 3-yr-old seeds and no witchweed emergence was observed from 8-yr-old seeds. Witchweed emergence was faster and greater from LH seeds than from R seed (Fig. 1).

Host parasitization. As with the previous parameters, highly significant differences ($P = 0.01$) in total number of witchweed plants (emerged and submerged) were manifest among the seed age treatments and among the seed size and weight treatments (Table 4). Seed age × seed size and weight interaction also exhibited significant differences ($P = 0.01$). Maximum host parasitization was revealed by the 3-yr-old seed. Parasitization was very low for 6- and 7-yr-old seeds, and no host parasitization was obtained with 8-yr-old seeds. LH seed induced maximum host parasitization and SL seeds induced the minimum. Host parasitization induced by LH seed was 38% greater than that of R.

Corn shoot and root weights. Highly significant differences ($P = 0.01$) in host shoot and root weights were manifest among the seed age treatments and the seed size and weight treatments (Tables 5 and 6). Maximum effects on both shoot and root were induced by 3-yr-old seeds: host shoot weight was significantly reduced, and host root weight was significantly increased. LH seeds induced maximum reduction of host shoot weight and maximum increases of host root weight. LH, R, LL, SH, and SL seeds reduced host shoot weight by 36, 33, 32, 14, and 13%, respectively, below the control, and increased host root weight by 38, 30, 22, 13, and 9%, respectively, above the control. There were significant differences between the control and all seed size and weight treatments of both host shoot and root weights.

Regression analysis. The regression coefficient value "b" of all seed types characterized by a uniform seed size and weight of all

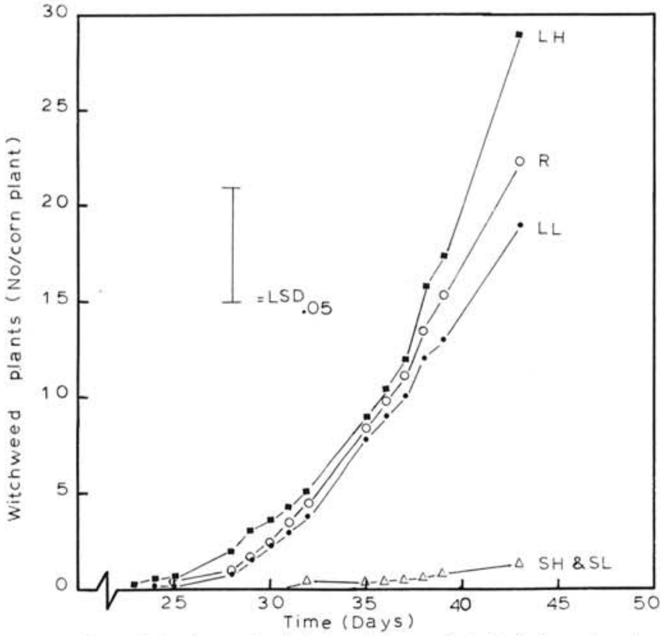

Fig. 1. Effects of the size and weight (specific gravity) of witchweed seed on the time required for witchweed plants to emerge. LH = large heavy, LL = large light, SH = small heavy, SL = small light, and R = random.

TABLE 3. Number of emerged witchweed plants as affected by age, size, and weight of seed

Witchweed seed age (yr)	Plant emergence (no.) relative to seed size and weight[x]					
	R	LH	LL	SH	SL	Mean
1	38.7[y]	42.0	24.7	4.2	2.2	18.6 b[z]
2	41.5	45.7	31.0	1.0	0.2	19.9 b
3	62.2	65.5	53.5	5.5	5.0	31.9 a
4	34.2	39.2	28.2	3.2	4.2	18.1 b
6	3.2	8.7	2.7	0	0	2.4 c
7	0	2.7	3.7	0	0	1.0 c
8	0	0	0	0	0	0 c
Mean	25.7 a	29.1 a	20.5 a	2.0 b	1.6 b	13.1

[x] LH = large heavy, LL = large light; SH = small heavy, SL = small light, and R = random.

[y] Emerged witchweed plants.

[z] Means followed by the same letter do not differ, $P = 0.05$, according to Duncan's multiple range test.

TABLE 4. Total number of witchweed plants (emerged and submerged) as affected by age, size, and weight of seed

Witchweed seed age (yr)	Total plants (no.) relative to seed size and weight[x]					
	R	LH	LL	SH	SL	Mean
1	55.0[y]	53.5	16.0	3.7	1.2	21.5 b[z]
2	33.5	70.5	29.7	0.2	0	22.3 b
3	102.2	115.0	55.7	9.2	4.5	47.7 a
4	27.7	55.0	32.7	5.5	1.5	20.4 b
6	1.5	7.0	0.7	0	0	1.5 c
7	0	3.2	0.7	0	0.2	0.7 c
8	0	0	0	0	0	0 c
Mean	31.4 a	43.4 a	19.3 b	2.6 c	1.0 c	16.3

[x] LH = large heavy, LL = large light, SH = small heavy, SL = small light, and R = random.

[y] Total witchweed plants (submerged + emerged).

[z] Means followed by the same letter do not differ, $P = 0.05$, according to Duncan's multiple range test.

TABLE 5. Corn shoot yields as affected by age, size, and weight of witchweed seed

Witchweed seed age (yr)	Corn shoot yields (g) relative to seed size and weight[x]						
	C	R	LH	LL	SH	SL	Mean
1	112.1[y]	51.4	62.9	87.0	125.5	127.5	94.4 c[z]
2	139.3	63.7	65.5	83.2	87.0	77.8	86.1 c
3	139.3	64.9	58.2	51.5	105.6	92.2	85.3 c
4	112.1	71.3	62.0	72.0	102.8	97.1	86.2 c
6	112.1	101.4	85.0	98.3	113.7	137.9	108.1 b
7	139.3	115.8	109.7	102.5	113.1	116.3	116.1 ab
8	139.3	127.5	122.2	106.1	114.7	122.0	122.0 a
Mean	127.6 a	85.1 c	80.8 c	85.8 c	108.9 b	110.1 b	99.7

[x] LH = large heavy, LL = large light, SH = small heavy, SL = small light, R = random, and C = witchweed-free control.

[y] Corn shoot fresh weight per plant.

[z] Means followed by the same letter do not differ at the 5% level according to Duncan's multiple range test.

TABLE 6. Corn root yields as affected by age, size and weight of witchweed seed

Witchweed seed age (yr)	Corn root production (g) relative to witchweed seed size and weight[x]						
	C	R	LH	LL	SH	SL	Mean
1	71.2[y]	127.0	151.3	100.5	89.9	89.3	104.9 a[z]
2	78.6	117.5	130.0	147.3	90.8	83.1	107.9 a
3	120.2	141.0	126.4	125.0	133.6	83.1	121.5 a
4	97.2	123.8	153.8	105.3	128.3	89.3	116.3 a
6	72.8	85.2	64.1	76.9	73.5	89.3	77.0 b
7	61.0	78.2	79.7	80.5	58.6	83.1	73.5 b
8	51.0	49.5	59.0	44.0	50.4	89.3	57.2 c
Mean	78.9 b	103.2 a	109.2 a	97.0 a	89.3 b	86.6 b	94.0

[x] LH = large heavy, LL = large light, SH = small heavy, SL = small light, R = random, and C = witchweed-free control.

[y] Corn root fresh weight per plant.

[z] Means followed by the same letter do not differ, $P = 0.05$, according to Duncan's multiple range test.

TABLE 7. Regression coefficient values ("b") showing the functional relationship between seed size and weight treatments at all parameters measured

Plant characters	Regression coefficient "b" for seed size and weight classes[a]:				
	R	LH	LL	SH	SL
Viability	+1.27	+1.15	+1.10	+0.79	+0.75
Germination	+1.17	+1.03	+1.15	+0.87	+0.87
Emerged witchweed plants	+2.11	+1.89	+1.63	+0.17	+0.16
Total witchweed plants	+2.21	+2.14	+1.34	+0.12	+0.08
Corn shoot yield	+1.75	+1.60	+1.07	+0.40	+0.95
Corn root yield	+1.49	+1.30	+1.19	+1.22	−0.03

[a] LH = large heavy, LL = large light, SH = small heavy, SL = small light, and R = random.

parameters measured, was invariably less than that exhibited by the R seed type (Table 7).

DISCUSSION

Findings derived from the present study suggest that both seed age and seed size and weight significantly influenced witchweed seed viability, germination, witchweed emergence, host parasitization, and host shoot and root weights.

Seed viability progressively declined with age of seed, whereas germination, witchweed emergence, and host parasitization progressively increased to a maximum of 3 yr after harvest and progressively declined with seed >4 yr old. The decline in seed germination, witchweed emergence, and host parasitization appeared to be associated with seed viability.

Seed viability, germination, witchweed emergence, and host parasitization increased with increases in seed size and weight. Seed viability as calculated from viability data of 4-, 6-, 7-, and 8-yr-old seeds decreased with decreases in seed size; ie, LH<LL<R<SH<SL seeds. The viability study showed that SL seeds were viable for only 6 yr compared with 7 yr for the other seed types. This observation suggests that seed size and weight may affect witchweed seed longevity. Thus, the larger the seed the greater the life span. The virulence of large witchweed seed was reflected by both the early, fast emergence of witchweed plants and the greater number of total plants parasitizing the host plant.

Among nonparasitic plants, the germination of large alfalfa (*Medicago sativa*) seeds has been shown (8) to be superior to that of small seeds, but in turnip (*Brassica rapa*) (15) laboratory tests revealed little or no correlation between seed size and percentage germination. Several investigators, working with nonparasitic plants, have found no consistent relationship between seed size and field emergence. In studies of radish (*Raphanus sativus*) (20), alfalfa (2), and wheat (17) there was no evidence that seedlings from large seeds emerged sooner from greater depth or that planting depth and seed size affected the total emergence. However, Harper and Obeid (10) reported that seedlings from small seeds of cultivars of fiber flax (*Linum usitatissimum*) emerged more rapidly from shallow sowing than those from large seed sown more deeply, irrespective of cultivar.

Doggett (5) concluded that witchweed emergence under field conditions was not an indicator of the actual extent of parasitization. The present study under pot conditions confirms Doggett's (5) report but provided quantitative evidence of a positive and high correlation ($r = +0.96$) between witchweed emergence and total witchweed plants (emerged and submerged) parasitizing the host. On average, total witchweed infestation (emerged and submerged) may be 25% more in number than those counted for emergence.

The rationale of the regression analysis was to measure the degree of variability of responses between treatments. The regression analyses of all parameters measured suggest that using a uniform seed size and weight (LH, LL, SH, or SL) would yield relatively more stable, ie, more consistent results than using seeds of nonuniform mixture (R) as conventionally used in screening programs for host resistance to witchweed. The present study recommends using LH seed in the screening program to enable the host cultivar to be tested at maximum parasite pressure.

Host shoot weight was suppressed by witchweed infestation and the suppression effect increased with increases in extent of infestation. This finding agrees with that reported by Doggett (5). The present study showed that the suppressive effects were greatest from LH seeds; however, this appears to be a function of number of seeds rather than of seed size.

Host root weight responded differently from that of the shoot. Host root weight was stimulated by witchweed infestation. Host roots infested with witchweed plants were consistently heavier than those of the control (uninfested) host roots. Correlation analysis revealed a positive and high correlation ($r = +0.99$) between total witchweed plants (emerged and submerged) parasitizing the host root and host root weight. Thus, the greater the infestation, the greater the root weight. This phenomenon was also observed by Musselman (18). The synergistic effect of witchweed infestation on corn root weight may raise several physiological questions relating to the allocation of resources within the host system and possibly the balance of growth hormones within the infested host. We believe that the synergistic effect of the parasite upon the host root as manifested by the increased development of the root may be of survival value to the parasite because it would increase the probability for additional witchweed seeds to get attached to the host root; ie, it creates additional sites of infestation which would be translated into a greater progeny.

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