

Influence of Nonhosts, Crucifers, and Fungal Parasites on Field Populations of *Heterodera schachtii*

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Abstract: *Heterodera schachtii* egg number decline under nonhosts was surveyed for 3–4 years at soil depths of 0–30 cm and 30–60 cm in three fields in the Imperial Valley, California. In the two fields continuously cropped to alfalfa, annual decline rates were 49 and 63%, respectively, and did not differ ($P = 0.05$) between depths. In the third field, cropped to annual nonhosts and fallowed, decline rates of 56 and 80% at 0–30-cm and 30–60-cm depths, respectively, were significantly different ($P = 0.05$). Egg hatch is the major cause of decline. Soil moisture in relation to type of cropping sequence apparently influenced egg hatch and activity of fungal parasites. An interaction matrix is used to assess the importance of biological, environmental, and management factors affecting decline of *H. schachtii* egg numbers. The required rotation length to nonhosts for various egg densities can be predicted. In coastal California, inclusion of a winter crucifer crop in the rotation increased *H. schachtii* egg density up to threefold. **Key words:** sugarbeet cyst nematode, *Acremonium strictum*, *Fusarium oxysporum*, crop rotation, population dynamics, biological control.

The sugarbeet cyst nematode (*Heterodera schachtii* Schmidt) is an important pest of sugarbeets (*Beta vulgaris* L.) in most sugarbeet growing areas in the world, although yield losses can be minimized by cultural practices and nematicides (1,3,6). Minimal yield loss, however, does not result in maximum net return. The high cost of treatment in relation to sugar prices often restricts nematicide use. Therefore, rotations with 3–5 years of nonhosts and/or fallow between sugarbeet crops is widely used for control of *H. schachtii* on infested land (1,17).

Decisions on the nonhost interval required to reduce nematode density below the damage or economic threshold can be based on the initial population density at rotation commencement and the rate of population decline under a nonhost rotation. Dump-sampling surveys (1,17) are useful for detecting infested fields, which can then be individually sampled (4) to determine the initial population densities.

Damage threshold levels vary with soil temperature, type, and moisture (14) and are characteristic for different sugarbeet growing areas. The damage threshold in the Imperial Valley, California, is attained with 1–2 eggs/g soil (3), but 3–8 eggs/g are required in the Netherlands (7) and 10 eggs/g in England (9).

Annual decline rates in European soils were estimated at 40–50% (9), but estimates are not available for other climatic regions

such as the Imperial Valley. Decline is determined by intrinsic and environmental factors that influence juvenile hatch and egg survival. *H. schachtii* eggs survive where the soil freezes and in dry fallow soils above 40 C (18), but the effects of the soil temperature, moisture, and type on long-term survival of egg populations are unknown. Biological antagonists of cyst nematodes occur, especially fungi (19), and these can influence nematode population dynamics (10). Fungal parasites of *H. schachtii* eggs are present in most California sugarbeet fields infested with *H. schachtii* (12).

This paper reports on long-term surveys of *H. schachtii* field population levels under nonhost crop rotations and fallow in California. The objectives were to identify major factors influencing population decline so that rational management decision can be made on the selection and duration of rotation crops.

MATERIALS AND METHODS

Fields previously cropped to sugarbeets and with known infestations of *H. schachtii* were selected from the Imperial Valley and Oxnard coastal plain, California. The sand:silt:clay ratios for the Imperial Valley soils were for Martin field, Brawley, 14:35:51; Brinkman field, El Centro, 20.0:21.4:58.6; Doel field, El Centro, 10.0:34.5:55.5; and Gould field at Oxnard, Ventura county, 50.3:26.1:23.6.

Cropping history and treatment before sampling: Brinkman field was planted with sugarbeets in September 1974 and 1975, and

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each planting harvested the following June. The field was fallowed between June and November. In November 1976 the field was planted with alfalfa. Soil in alternate strips (7.3 m × 15.2 m) was fumigated on 29 September 1976 with Telone (1,3-dichloropropene, 1,2-dichloropropane) at 374L/ha, shanks on 30-cm centers and 23 cm deep. Martin field was planted with sugarbeets in 1975-76, fallowed during summer 1976, and planted with alfalfa in November 1976. Doel field was planted with sugarbeets in September 1971 and 1972, then planted with a series of annual nonhost crops, mostly winter cereals, and fallowed prior to commencement of sampling. Gould field was planted with sugarbeets in January 1975, harvested in October 1975, and fallowed until March 1976 when tomatoes were planted. Cropping sequences in the Doel and Gould fields during the sampling period are listed in Table 1 and Figure 3, respectively.

Sampling sites and procedures: Square 4.6-m sites were established for soil sampling, two each in the Doel and Martin fields and three in the Gould field. Five fumigated and five nonfumigated sites, each 7.3 m × 15.2 m, were established for soil sampling in the Brinkman field.

On each sampling date (Table 1), eight soil cores 0-60 cm deep were removed by Oakfield soil tube (2 cm i.d.) from each site. The cores were divided into 0-30-cm depth and 30-60-cm depth and composited for each depth to give 4, 4, 6, and 20 samples from the Doel, Martin, Gould, and Brinkman fields respectively. The samples were air dried, mechanically pulverized, and thoroughly mixed. One 600-g subsample was removed from each bulked sample, and cysts were extracted by Fenwick flotation (16). Cysts were separated from organic debris in ethanol:glycerine (9:1 v/v) (2), rinsed in water, and homogenized in water: Chlorox® (1:1 v/v) to release the eggs. The numbers of viable eggs were determined per gram of air-dried soil.

Data analysis: Regressions for estimations of *H. schachtii* egg decline rates were performed on data sets of egg numbers transformed to unity at the first sampling date and fractions thereof for subsequent samplings; a \log_e transformation of both

sides of the model $Y = e^{-\beta X}$ (where Y = transformed egg numbers and X = days after first sampling) was used to generate the fitted lines by linear regression. Slopes of curves representing the two soil depths in each field, and the fumigated and non-fumigated treatments in the Brinkman field were compared according to Draper and Smith (5).

RESULTS

H. schachtii population decline in the Imperial Valley: Egg numbers declined at both depths on all Imperial Valley sites under nonhost crops and fallow from 1975 to 1979 (Table 1). Egg numbers in the Doel field declined from 1.3-14.5 eggs/g soil to below the 1-2 eggs/g soil damage threshold in 2 yr and in most samplings to below the detection level during the third year under annual nonhosts and fallow. Eggs numbers in the Martin field sampled after the last sugarbeet crop ranged from 31.4 to 99.3 eggs/g soil, although greater numbers were generally found at 30-60 cm deep. Egg numbers declined to below the damage threshold on all sites at both depths during the fourth year under continuous alfalfa.

Numbers of eggs following sugarbeets ranged from 12.2 to 60.9 eggs/g soil on the Brinkman sites at both depths in the fumigated and nonfumigated areas and were generally, but not consistently, higher at 30-60 cm deep. Slopes of regression lines of *H. schachtii* egg decline were not significantly different ($P = 0.05$) between fumigated and nonfumigated Brinkman sites. Soil fumigation was ineffective in reducing numbers of *H. schachtii* viable eggs probably because of restricted movement of the fumigant in the fine-textured moist clay (11). In the regression analysis on the Brinkman field (Fig. 2 A), data from the fumigated and nonfumigated sites were considered together. The number of *H. schachtii* eggs throughout the 4-yr sampling period was below the damage threshold (1-2 eggs/g soil) during the last year under continuous alfalfa in the Brinkman field on six sites at 0-30 cm deep and on four sites at 30-60 cm deep.

Comparisons of initial and final egg population densities over yearly periods starting at November-December sampling

Table 1. Egg densities of *H. schachtii* field populations at two soil depths under nonhost crops and fallow in the Imperial Valley, 1975-79.

Martin field				Brinkman field				Doel field			
Sampling date	Cropping	Mean eggs/g soil		Sampling date	Cropping	Mean eggs/g soil		Sampling date	Cropping	Mean eggs/g soil	
		0-30 cm	30-60 cm			0-30 cm	30-60 cm			0-30 cm	30-60 cm
18/12/73	Fallow	32.7	77.0	23/1/76	Hay alfalfa	22.3	33.6	—	—	—	—
20/6/76	Seed alfalfa	12.6	32.3	—	" "	—	—	—	—	—	—
23/11/76	" "	11.2	26.7	23/11/76	" "	36.4	29.9	11/11/76	Barley	1.8	9.1
8/3/77	" "	16.6	13.7	8/3/77	" "	14.4	13.7	8/3/77	Cotton	3.3	1.9
28/7/77	" "	8.7	14.5	28/7/77	" "	8.9	17.1	8/8/77	Cotton	2.0	3.6
21/12/77	" "	5.2	25.2	21/12/77	" "	7.4	14.4	21/12/77	Cotton	0.5	0.2
14/3/78	" "	9.0	18.7	14/3/78	" "	6.1	12.0	14/3/78	Fallow	1.3	1.8
12/6/78	" "	14.3	22.1	12/6/78	" "	3.3	6.1	12/6/78	Barley	0.4	0.7
14/9/78	" "	6.0	13.2	14/9/78	" "	5.0	6.9	14/9/78	Barley	1.2	0.6
21/12/78	" "	1.4	4.1	21/12/78	" "	4.5	7.0	21/12/78	Fallow	0.2	0.2
3/4/79	" "	2.0	1.3	3/4/79	" "	2.4	7.9	3/4/79	Fallow	0.2	0.3
29/8/79	" "	0.4	0.4	29/8/79	" "	1.6	3.4	29/8/79	Sudan grass	0.2	0

Mean counts are from replicate sampling sites in each field.

dates for a range of egg densities (0.2–77.0 eggs/g soil) indicate that egg decline is largely independent of the initial population level at both depths (Fig. 1).

Regression lines in Figure 2 A, B, and C enable comparisons of annual percentage decline rates of *H. schachtii* eggs in different fields at two depths. In the Brinkman and Martin fields, the decline rates are the same at both depths. Egg decline rate is slower at 0–30 cm deep than at 30–60 cm deep in the Doel field. Difference in egg decline rate due to depth in the three fields is significant ($P = 0.05$) only for the Doel field (Fig. 2). Decline values for the two depths in the Brinkman field (50% at 0–30 cm and 48% at 30–60 cm) and in the Martin field (61% at 0–30 cm and 65% at 30–60 cm) are the same, so the values were averaged to give annual percentage rates of 49 and 63, respectively. In the Doel field, a rate of 56% at 0–30 cm deep is between these values, while the rate of 80% at 30–60 cm deep is higher than these other values.

Effect of crucifer and nonhost crops on H. schachtii populations: Numbers of *H. schachtii* eggs in the Gould field from 1976 to 1979 were similar at 0–30-cm and 30–60-cm depths (Fig. 3). After the 1975 sugarbeet crop, eggs/gram of soil declined under summer tomato and winter lettuce crops from an average of 8.4 in 1976 to 3.7 in 1977 (~

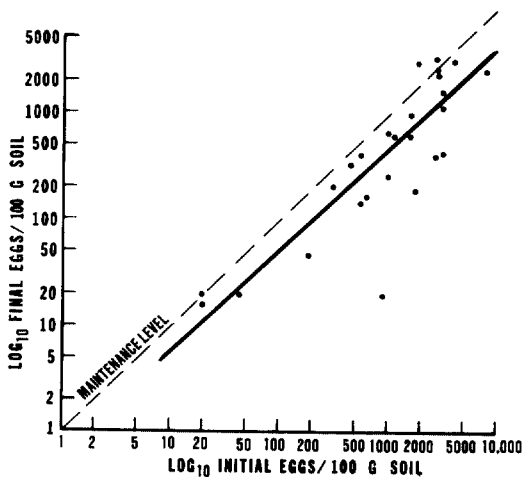


Fig. 1. Linear regression of the annual decline of *H. schachtii* egg numbers in Imperial Valley fields for a range of initial egg population densities. Correlation coefficient, $r = 0.8679$. Final egg numbers = initial egg numbers at the maintenance level.

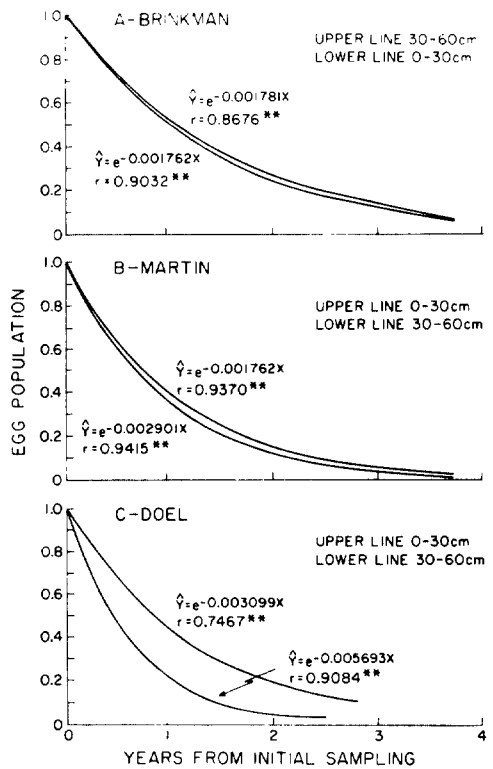


Fig. 2. Regressions fitted by the nonlinear function $Y = e^{-\beta X}$ of *H. schachtii* egg population decline with time from the first sampling date for three Imperial Valley fields: A) Brinkman, B) Martin, and C) Doel. Egg numbers were converted to fractions of egg numbers at the first sampling date (time 0).

the estimated damage threshold). Reproduction of *H. schachtii* on cabbage in winter 1977–78 (harvested in March 1978) increased the egg population to 11.2 eggs/g soil. The egg population declined under

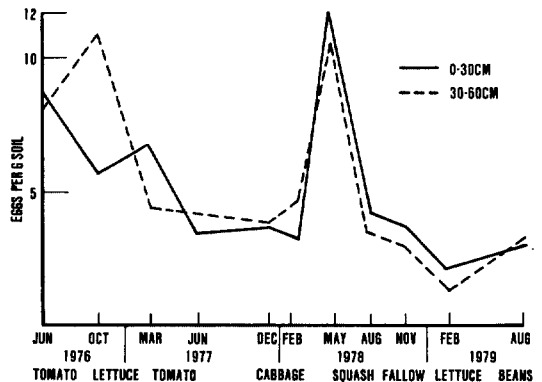


Fig. 3. Egg population levels of *H. schachtii* related to cropping sequence during 1976–79. Each value is a mean estimate from three sites.

squash, fallow, lettuce, and lima beans in the following year.

Decline rates of egg numbers for yearly periods from June 1976 and from May 1978 in the Gould field are approximately 54 and 79%, respectively, comparable with decline in the Martin and Doel fields in the Imperial Valley.

DISCUSSION

Because *H. schachtii* infestations occur in diverse climatic and agricultural areas where sugarbeets are grown, damage and economic thresholds and rates of population increase and decline must be evaluated under the conditions common for each area in order to maximize the effectiveness of management strategies. Population studies in Europe (7,8,14), particularly the field and microplot tests of Jones (9), have determined these variables for *H. schachtii* in northern European conditions. In California, damage and economic thresholds and rates of population increase have been assessed for the Imperial Valley (3,18), but knowledge of population decline, and its application, has been largely empirical.

Although variation occurs among sampling dates (Table 1) due to sampling error, long-term trends in *H. schachtii* egg numbers can be followed. Numbers of eggs decline under both annual and perennial non-host croppings and, as found in Europe (9), the decline rate is independent of initial population density. In the Imperial Valley fields, rates of egg decline at 0–30 cm deep are the same or slower than those at 30–60 cm; the 0–30 cm depth can be regarded as the "rate determining zone" in estimating population decline. Although there is some indication of higher *H. schachtii* populations at the lower depth, it appears that management estimates of rotation length can be based reliably on population levels assessed by surface soil sampling after soil cultivation (4).

Decline of *H. schachtii* egg populations is due to death of eggs and to hatching of second-stage juveniles. *In vitro* water hatch of *H. schachtii* ranges from 10 to 40% of total cyst contents (15); hatch in field soil under nonhosts or fallow where stimulatory root diffusates are absent (15) should be comparable (although more variable).

Hatch of *H. schachtii* is restricted to temperatures between 10 and 35 C (20). Imperial Valley soils are rarely temperature limiting, and spring and autumn temperatures are near the optimum (18).

The four fields in this report were included in a survey that assessed the percentage of *H. schachtii* eggs parasitized by *Fusarium oxysporum* Schlecht and *Acremonium strictum* Gams (12). Respective values for total percent of eggs infested, percent of eggs infested by *F. oxysporum*, and percent of eggs infested with *A. strictum* in the four fields were as follows: Brinkman field, 1:36:21; Martin field, 21:53:0; Doel field 12:68:0; Gould field, 9:22:0. Infection of eggs by other fungi was also observed (12). A comparison of *H. schachtii* egg decline rates with the numbers of parasitized eggs indicates that there is a relationship between the egg decline rate and the amount of egg parasitism. Even though the soil type, cropping, field management practices, and climate were generally the same in both fields, *H. schachtii* egg decline rate in the Brinkman field was 49% and 1% of the eggs were parasitized, while in the Martin field egg decline rate was 63% and 21% of the eggs were parasitized. *H. schachtii* egg decline rate in the Doel field was 56% at 0–30 cm deep and 80% at 30–60 cm deep; 12% of the eggs were parasitized and 39% more eggs were parasitized at 30–60 cm deep than at 0–30 cm deep (E. A. Nigh, personal communication).

F. oxysporum and *A. strictum* have an optimum temperature range of 20–30 C for parasitic activity, and these fungi are well adapted to Imperial Valley and other California conditions (13). The apparent relationship between *H. schachtii* egg decline rate and the numbers of eggs parasitized by these fungi, together with the widespread occurrence of the egg parasites in California (12), suggest that egg parasitism by these and other fungi may be a major cause of death of *H. schachtii* eggs and thereby contribute to the control of *H. schachtii* in the field. The *H. schachtii* eggs within the cyst may provide a long-lasting protected food source for *A. strictum*, *F. oxysporum*, and other egg-parasitic fungi (12). The relationship between parasitism of *H. schachtii* eggs and egg population densities

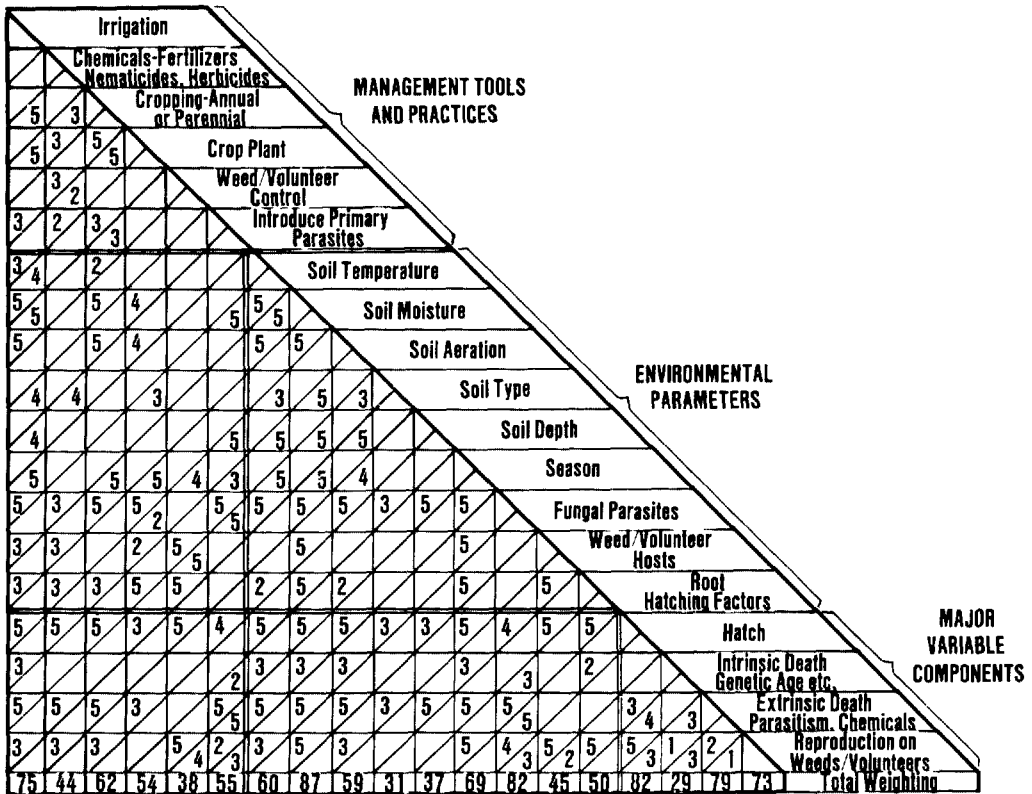


Fig. 4. Interaction matrix of the major components of *H. schachtii* population decline in southern California, their environmental parameters, and the management practices that can affect them. Interactions are weighted from 1 to 5; increasing with importance to decline. Each interaction has a double score; for example, soil temperature will affect fungal parasites (score = 5), fungal parasites will not affect soil temperature (no score).

in the soil needs to be fully assessed.

The similarity between egg decline rate at the 0–30-cm and the 30–60-cm soil depths in the Brinkman and Martin fields (Figs.

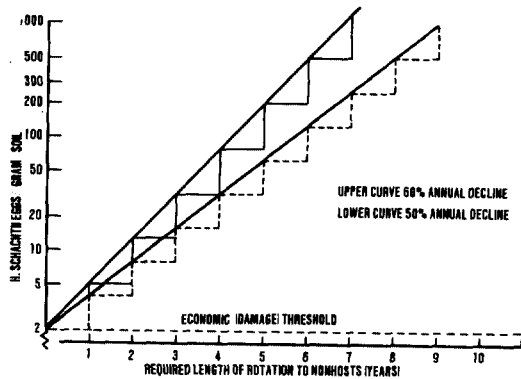


Fig. 5. A step scale for predicting the nonhost rotation length in years required to reduce the *H. schachtii* population in the Imperial Valley to the damage threshold or an economic threshold.

2 A and B) may reflect the relatively even vertical distribution of soil moisture under deep rooted perennial alfalfa in the 0–60 cm soil zone. The soil water potential apparently does not differentially affect the hatching of eggs and the activity of egg parasites at the two depths. In the Doel field during fallow intervals, the upper soil layer became very dry. Soil water potentials below the wilting point of plants may have decreased the hatching of eggs and the activity of egg parasites and depressed *H. schachtii* egg decline rate in the 0–30-cm soil depth; the higher soil water potentials at 30–60 cm deep would not restrict egg hatch and egg parasitism as indicated by the significantly ($P = 0.05$) higher egg decline rate at the 30–60 cm depth (Fig. 2 C).

When selecting nonhost crops for the rotation, consideration should be given to the option of perennial or annual croppings because of their associated differences in soil

Table 2. Major components, environmental parameters, and management tools and practices listed in order of importance to *H. schachtii* population decline, assessed by the interaction matrix in Figure 4.

Management tools and practices	Major components	Environmental parameters
1. Irrigation	1. Hatch	1. Soil moisture
2. Type of cropping	2. "Extrinsic" death— chemicals, parasites	2. Fungal parasites
3. Introduction primary parasites	3. Reproduction on weeds/ volunteers	3. Season
4. Crop plant (type of nonhost)	4. "Intrinsic" death— genetic, aging	4. Soil temperature
5. Chemical application		5. Soil aeration
6. Weed control		6. Root hatching factors
		7. Weed/volunteer hosts
		8. Soil depth
		9. Soil type

cultivations and movement, soil moisture, and soil aeration that can influence egg hatch and biological antagonism. Commercial plantings of several common non-host crops do not appear to differentially affect *H. schachtii* population decline, at least not during one growing season (6). The *H. schachtii* population increase on a winter crucifer in the Gould field (Fig. 3) emphasizes the importance of avoiding cruciferous crops during the rotation. The potential of winter crucifer hosts as trap crops is doubtful in view of the reproduction capacity of *H. schachtii* at normal winter soil temperatures in southern and coastal California.

The major factors and environmental parameters that can affect and determine *H. schachtii* egg decline, together with management tools and practices that could be manipulated to maximize rotation efficiency and improve sugarbeet production on infested land, are summarized in Figure 4. Interactions in the matrix have been weighted according to their known or potential influence on *H. schachtii* egg decline, and the total for each character gives an estimate of importance to egg decline within each category (Table 2). Scores were assessed according to our findings reported here and the cited literature, especially the reviews of Shepherd (15) and Wallace (21). Manipulation of soil moisture by irrigation and by selection of annual or perennial non-hosts to maximize hatch and parasite activity, and the potential of increasing fungal parasitism through introduction, are management controlled practices that appear to warrant critical investigation.

Based on a similar chart by Jones (9) for

European *H. schachtii* populations, Figure 5 provides a scale for estimating the rotation period required to reduce southern California *H. schachtii* populations to the damage threshold or an economic threshold, assuming that initial population levels are known. Decline rates are estimated at about 50–60%.

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