

Organisms Impacting Waterhyacinth in the Panama Canal

DANA R. SANDERS, SR., RUSSELL F. THERIOT
AND EDWIN A. THERIOT

Plant Physiologist, Biologist, and Microbiologist
Environmental Laboratory
U.S. Army Engineer Waterways Experiment Station
Vicksburg, Mississippi 39180

ABSTRACT

Three arthropod species, *Neochetina eichhorniae* Warner, *Cornops aquaticum* Bruner, and *Orthogalumna terebrantis* Wallwork, fed substantially on floating waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) in the Panama Canal during 1978 through 1980. One plant pathogen, *Acremonium zonatum* (Saw.) Gams., was commonly found to infect floating waterhyacinth. The level of activity of these insects varied substantially with respect to location and time. *O. terebrantis* activity increased during the study period, while the level of activity of the other species declined. Spatial variation was attributed primarily to the predominance of robust plants in the mainstream Rio Chagres sites compared to the predominance of small, bulbous-petioled plants in the backwater sites. Regardless of the individual level of activity of these species on floating waterhyacinth in the Panama Canal, their combined activity was insufficient to produce the desired level of control.

INTRODUCTION

Waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) has been a noxious aquatic plant in the Panama Canal for nearly 60 years.¹ The problem has been of greatest concern in the many backwater areas of the Rio Chagres river (Figure 1), where the plants proliferate to form large mats. During periods of high rainfall, these mats are flushed out of the backwater areas into the main river channel, where they form large rafts of plants capable of blocking the river channel to navigation. Although these rafts initially moved directly into the ship channel and temporarily blocked the passage of ships, the Panama Canal Company (now the Panama Canal Commission) constructed a permanent boom across the Rio Chagres 0.8 km upstream from its confluence with the ship channel, which effectively prevents movement of waterhyacinths into shipping lanes. River currents now funnel the rafts of plants into a cove where they are removed by a large rake operated from a Sauerman slack-line cable (5). This mechanical system can remove a maximum of 650 tons of plant material per day at an approximate cost of \$3.75/ton.² Although very efficient at removing waterhyacinths from the river, the system must be operated approximately 75 days per year due to the continual proliferation of plants in backwater areas.

A cursory inspection of the waterhyacinth population in the Rio Chagres in 1977 revealed that two arthropod

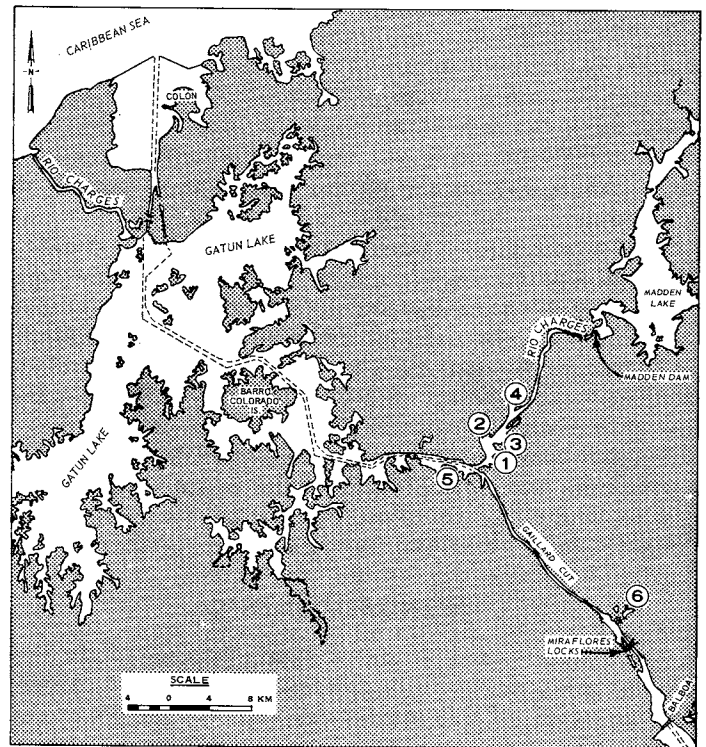


Figure 1. Area of Panama Canal in which the study was conducted. Study sites are numbered: 1—Manatee Lagoon, 2—Nevada, 3—Las Cruces, 4—Stump Lake, 5—Dump 4½, and 6—Red Tank Lake.

species known to have potential for controlling waterhyacinth, the mottled waterhyacinth weevil (*Neochetina eichhorniae* Warner) and the waterhyacinth mite (*Orthogalumna terebrantis* Wallwork), were already present in the Panama Canal. One fungal pathogen known to adversely impact waterhyacinth, the zonal leaf spot fungus [*Acremonium zonatum* (Saw.) Gams.], was also present. However, the impacts of these species on the plant populations were not known, nor was it known whether other species were present that were exerting significant impacts. Prior to considering the release of additional insects and plant pathogens for control of waterhyacinth in the Panama Canal, it was necessary to determine the full complement of species already present, and to define spatial and temporal variations in their impacts on the plant populations. Data obtained from this study would be used to develop strategies for increasing the level of waterhyacinth control through the use of biocontrol agents.

¹C. Von Chong. 1980. Personal communication.

²W. P. Murdoch, Jr. 1980. Personal communication.

METHODS

Six sites (Figure 1) were selected for study, four located on the Rio Chagres, one in a cove of Gatun Lake into which dredged material had been deposited, and one in Red Tank Lake near the Miraflores Locks. Each site contained a stable population of plants and was subjected to minimal water flow. At the beginning of the study, none of the sites had been recently treated with herbicides. However, all study sites except site 4 were periodically treated with 2,4-D during the study. By January 1980, most of the waterhyacinths in sites 5 and 6 had been destroyed.

Twenty-four randomly selected plants were collected from each site in January and April 1978, May and October 1979, and January 1980. The rainy season extends from May through November; thus, two sampling dates occurred during the rainy season and three occurred during the dry season. Collected plants were placed in plastic bags in groups of six, and the bags were stored in an air-conditioned building until processed.

The number of daughter plants (plants with little or no root development that were still attached to the parent plant on erect stolons) and the number of leaves with an expanded pseudolamina were recorded.

Each plant was examined for the presence of arthropods and their associated damage. The number of *N. eichhorniae* adults and pupae on each plant was recorded. The degree of feeding by *N. eichhorniae* adults on each pseudolamina of each parent plant was estimated using the following rating scale:

Category	Number of Feeding Scars/Pseudolamina
0	0
1	1-50
2	51-100
3	101-200
4	>200

Feeding activity of *Cornops aquaticum* Bruner, a grasshopper that fed on waterhyacinth by excising sections of the pseudolamina or by rasping the epidermis, was quantified using the following rating scale:

Category	% of Pseudolamina Damaged
0	0
1	<50
2	≥50

O. terebrantis, a galumnid mite, characteristically produced tunnels in the intervascular areas of the pseudolamina. The extent of *O. terebrantis* tunnelling was estimated for each pseudolamina of each parent plant by use of the following rate scale:

Category	% of Pseudolamina Tunnelled
0	0
1	<50
2	≥50

Oviposition chambers of a small fly, *Thyripticus* sp. (Diptera: Dolichopodidae), on each petiole of each parent plant were counted and recorded.

Each plant was also examined for symptoms of plant pathogens. Because *A. zonatum* had been commonly observed during the cursory inspection, the following index was used to describe its level of activity on each pseudolamina of each parent plant:

Category	% of Pseudolamina Infected
0	0
1	<50
2	≥50

Symptoms produced by other microorganisms were described and recorded. Two 16-mm² sections of pseudolamina exhibiting each symptom were excised and processed to identify the associated microorganism. To identify bacteria, one of the excised sections was macerated in a Petri dish containing 1 ml of sterile saline solution (0.85%). A loop of the resulting supernatant was streaked onto a plate of Difco nutrient agar and incubated for 2 days at room temperature. Microtubes of the API-20 Enterobacteriaceae System (API20E) were inoculated with the resulting isolates and incubated at 30 C for 2 days. Results of the biochemical tests were recorded and used for identification of bacterial species (3). To identify fungi, the other excised section of pseudolamina was surface-sterilized with a 0.5% NaClO solution for 2 min. and rinsed twice in containers of sterile, deionized water. The section was then placed on a potato dextrose agar (PDA) plate and incubated at room temperature for 7 to 10 days. Morphology of resulting colonies, hyphae, and fruiting structures on the PDA plates, and spore characteristics on slide cultures were used to identify fungi (1, 2).

Mean numbers of *N. eichhorniae* adults and pupae and oviposition sites of *Thyripticus* sp. per plant were calculated for each site for each sampling date by dividing the total counts for each by the total number (24) of plants examined from each site. Mean index values of feeding by *C. aquaticum* and adult *N. eichhorniae*, the extent of *O. terebrantis* tunnelling, and the degree of infection by *A. zonatum* per pseudolamina were computed by dividing the sum of the respective rating categories for each species by the number of pseudolaminae examined for each site on each date. A two-way analysis of variance was used to determine if means for the above parameters varied significantly within sites among sampling dates, and Duncan's multiple range test was used to identify means that were significantly different at the 0.05 probability level (8). Spatial variation in overall activity of these species on waterhyacinth was determined by summing mean index values for the four species for each site averaged across sampling dates. Temporal variation in the overall activity of these species on waterhyacinth was determined by summing mean index values for the four species for each date averaged across study sites. To examine interspecific relationships between the four major species on waterhyacinth, Spearman's method (7) for determining rank correlation coefficients

between species was applied to all rating data for each sampling date and study site.

RESULTS AND DISCUSSION

Waterhyacinth growth. Mean numbers of daughter plants and leaves with unfurled pseudolamina per plant are presented in Table 1. Temporal variation in the number of daughter plants was negligible, with significantly different means occurring with time only at sites 4 and 5. However, spatial variation was more pronounced. Greater numbers of daughter plants occurred at site 6 than at other sites, presumably due to the predominance of small, bulbous petioled plants (Stage I morphotype³) resulting from the more frequent application of herbicides at this site. The waterhyacinth populations on other sites were composed of a mixture of all three morphotypes, but were predominantly Stage III. Uniformly high temperatures and levels of solar insolation characteristic of tropical regions provided optimum growth conditions for waterhyacinth, and uniform mats of Stage III plants would normally be expected to occur. However, the combination of localized herbicide spraying and limited nutrient availability in backwater sites due to low rates of water exchange and competition for available nutrients by other species, such as hydrilla [*Hydrilla verticillata* (L.f.) Royle], resulted in mixed stands of all three morphotypes.

Variation in mean number of leaves per plant (Table 1) was only slight with respect to both time and location. Spatial variation was greatest between plants at site 6 (\bar{X} = 6.5 leaves/plant) and site 3 (\bar{X} = 10.5 leaves/plant) in January, 1978. The larger, predominantly Stage III plants at site 3 generally had greater numbers of leaves than the smaller Stage I plants that were present at site 6. Because Stage III plants have greater leaf surface area than Stage I plants, and Stage I plants channel a greater percentage of net photosynthate into daughter plant production than

³Stage II plants have both leaves with bulbous petioles at the base and erect leaves toward the apex that have slender petioles, while Stage III plants have only the erect, slender petiole type.

Stage III plants, the production of new leaves in Stage III plants in the Panama Canal occurs twice as rapidly as in Stage I plants. Thus, we would expect to find that Stage III plants have twice as many leaves as Stage I plants. This does not occur because of the greater frequency of arthropod and pathogen damage on leaves of Stage III plants, which results in more rapid senescence. Although temporal variation in mean numbers of leaves per plant was minimal, the mean number of leaves per plant was greater late in the dry season (April 1978) than early in the dry season (January 1978 and 1980). This suggested an increased rate of growth of waterhyacinth during the dry season.

In addition to competition from submersed species such as hydrilla, other floating aquatic species such as water-lettuce (*Pistia stratiotes* L.) and salvinia (*Salvinia* spp.) were found to compete with waterhyacinth for available space and nutrients. In some areas, anchored waterhyacinth [*Eichhornia azurea* (Sw.) Kunth.] outcompeted floating waterhyacinth for space, and often occurred in monotypic stands. This was particularly true in areas of greater water flow.

Arthropod activity. Adult *N. eichhorniae* were found at all sites on all sampling dates, except at site 6 in April 1978 and January 1980 (Table 2). Temporal variation in the mean number of adults per plant was not pronounced, but significantly greater numbers occurred during the dry season than during the rainy season in sites 1-3. However, overall spatial variation was more pronounced, ranging from an average of 1.5 adults/plant at site 1 to 0.1 adults/plant at site 6. This was probably due to the concentration of plants containing adult and larval *N. eichhorniae* near site 1 by river flow. Site 1 was located very near the permanent boom across the Rio Chagres, and plants floating downstream were concentrated in this area. This provided a constant source of insects to supplement the existing population at site 1. In fact, there was a definite gradient in mean numbers of adult *N. eichhorniae* per plant within Rio Chagres sites, with progressively decreasing mean numbers of individuals in sites upstream from site 1.

N. eichhorniae pupae (Table 2) were infrequently en-

TABLE 1. MEAN NUMBERS¹ OF DAUGHTER PLANTS AND LEAVES OF WATERHYACINTH.

Site		Jan 1978	Apr 1978	May 1979	Oct 1979	Jan 1980	Means for Site
1	P ²	0.4a	0.7a	0.6a	0.3a	0.7a	0.5
	L ³	8.1b	9.8a	10.0a	8.2b	7.7b	8.8
2	P	0.8a	0.3a	0.5a	0.9a	1.0a	0.7
	L	9.2ab	9.5a	8.1b	8.3ab	8.9ab	8.8
3	P	0.8a	0.7a	0.6a	1.0a	1.1a	0.8
	L	10.5a	9.5a	9.1a	8.5a	9.8a	9.5
4	P	0.5ab	0.4ab	1.2a	0.1b	1.0ab	0.6
	L	9.1a	10.2a	8.5a	10.0a	9.0a	9.4
5	P	1.1a	0.3b	1.2a	0.4ab	0.6ab	0.7
	L	6.5b	8.9a	8.9a	8.6a	8.3a	8.2
6	P	0.1a	1.0a	1.8a	1.9a	2.3a	1.4
	L	7.4b	10.4a	7.8b	9.1ab	8.5b	8.6
Mean for sampling date	P	0.6	0.6	1.0	0.8	1.1	0.8
	L	8.5	9.7	8.7	8.8	8.7	8.9

¹Analyses performed only within rows. Means followed by the same letter in each row are not significantly different at the $p > 0.05$ level.

²P = mean number of daughter plants per plant.

³L = mean number of leaves per plant.

TABLE. 2 MEAN NUMBERS¹ OF *N. eichhorniae* ADULTS AND PUPAE PER PLANT.

Site		Jan 1978	Apr 1978	May 1979	Oct 1979	Jan 1980	Means for Site
1	A ²	1.3b	3.4a	1.1b	0.6b	1.1b	1.5
	P ³	0.3a	0.0a	0.2a	0.2a	0.0a	0.1
2	A	1.0a	0.3a	0.2a	0.7a	0.5a	0.5
	P	0.0b	0.0b	0.2a	0.0b	0.0b	0.0
3	A	1.5a	0.2b	0.4b	0.2b	1.6a	0.8
	P	0.1a	0.0a	0.1a	0.0a	0.0a	0.0
4	A	0.6a	0.2ab	0.0b	0.7a	0.2ab	0.3
	P	0.0a	0.0a	0.1a	0.0a	0.0a	0.0
5	A	0.2a	0.3a	0.8a	0.2a	0.1a	0.3
	P	0.0b	0.0b	0.2a	0.0b	0.1ab	0.1
6	A	0.1a	0.0a	0.2a	0.3a	0.0a	0.1
	P	0.0a	0.0a	0.2a	0.0a	0.0a	0.0
Mean for sampling date	A	0.8	0.7	0.5	0.5	0.6	0.6
	P	0.0	0.0	0.2	0.0	0.0	0.0

¹Analyses performed only within rows. Means followed by the same letter in each row are not significantly different at the $p > 0.05$ level.

²A = mean number of *N. eichhorniae* adults per plant.

³P = mean number of *N. eichhorniae* pupae per plant.

countered in plant samples, and means varied significantly with time only at sites 2 and 5. The greatest abundance of pupae were found in May 1979. Since the life cycle of (*N. eichhorniae* requires 120 days (4), it appears that reproduction occurs at a greater rate during the dry season, and that the adult population increases early in the rainy season.

Mean index values for adult *N. eichhorniae* feeding scars per pseudolamina (Figure 2) ranged from a high of 2.5 (moderate feeding⁴) at site 1 in April 1978 to 0.6 (slight feeding) at site 2 and site 4 in May 1979. As expected, these data were closely related to mean numbers of adults (Table 2). Rankings of sites averaged across time were identical with respect to mean numbers of adults and index of feeding scars. Although temporal variation in mean index of feeding scars could be partially explained by seasonality, an intensified herbicide spray program beginning in early 1979 also contributed to the observed variation by destroying

waterhyacinths containing larval and pupal stages of the insects, thereby reducing the population of *N. eichhorniae*.

Mean index values of *C. aquaticum* feeding damage per pseudolamina ranged from a maximum of 1.2 (moderate feeding⁵) at site 3 in January 1978 to a minimum of 0.1 (slight feeding) at site 4 in April 1978 (Figure 3). Although not as pronounced as the gradient described for *N. eichhorniae*, there was a decrease in the mean level of *C. aquaticum* feeding damage in Rio Chagres sites from site 1 to site 4. This was probably due to concentration of individuals near site 1 by river flow and the predominance of Stage III plants in the site 1 area as compared to the predominance of Stage I plants in site 4. Whether the greater feeding activity by *C. aquaticum* on Stage III plants was related to a true preference for the larger plants or was due primarily to increased protection afforded the insects by Stage III plants is not known. Evaluation of temporal variation in

⁴Maximum possible mean index value was 4.0.

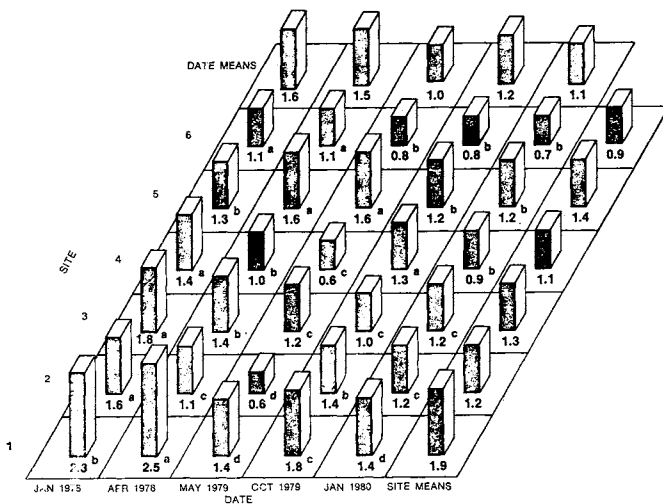


Figure 2. Mean index values of adult *N. eichhorniae* feeding scars per pseudolamina for sites during the study. Analyses performed only within sites. Mean values designated by the same letter within sites are not significantly different at the $p > 0.05$ level.

⁵Maximum possible mean index value was 3.0.

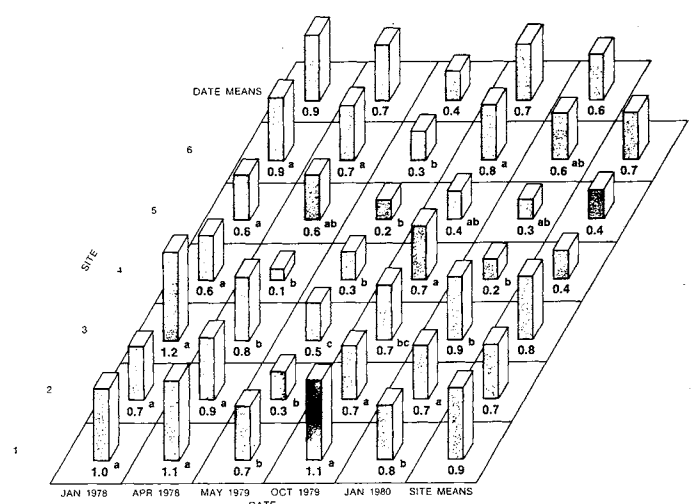


Figure 3. Mean index values of *C. aquaticum* feeding damage per pseudolamina for sites during the study. Analyses performed only within sites. Mean values designated by the same letter within sites are not significantly different at the $p > 0.05$ level.

the level of *C. aquaticum* feeding damage per pseudolamina within sites revealed that significantly greater levels of feeding occurred during the dry season than during the rainy season. Overall temporal variation ranged from 0.9 in January 1978 to 0.4 in May 1979. The lower values in May 1979 may have been related to the increased use of herbicides for waterhyacinth control, which resulted in an increased abundance of Stage I plants on the study sites.

Tunnelling activity by *O. terebrantis* varied considerably with respect to both time and location (Figure 4). Mean index values for tunnelling by *O. terebrantis* averaged across time varied from 0.8⁶ at site 2 to 0.0 at sites 4 and 6. The low values obtained for these relatively isolated sites suggested that *O. terebrantis* had very limited mobility. However, the mite was found at both sites in May 1979, and failure of the mite to develop to significant population levels on either site by January 1980 indicated that some environmental factor must have limited activity of *O. terebrantis*. Temporal variation in *O. terebrantis* tunnelling activity was also pronounced. Mean index values were significantly higher in October 1979 and January 1980 on all sites except sites 4 and 6 than in January 1978, and progressively greater levels of tunnelling occurred on three of the sites with time. Overall temporal variation ranged from

0.0 in January 1978 to 0.7 in October 1979 and January 1980. In fact, *O. terebrantis* was the only species that increased in level of activity on waterhyacinth during the study. However, the factor or factors responsible for this increased level of *O. terebrantis* activity were not evident.

Mean numbers of *Thrypticus* sp. oviposition chambers per plant (Table 3) revealed that plants within the Rio Chagres were used more extensively than plants at other sites. Within the Rio Chagres, a gradient in mean number of oviposition chambers per plant was evident, progressively decreasing in upstream sites from site 1. Regardless of location of the plants, it was apparent that *Thrypticus* sp. used erect petioles of Stage III plants more extensively than those of Stage I plants. Thus, the predominance of Stage III plants at site 1 may have resulted in greater mean numbers of *Thrypticus* sp. oviposition chambers on these plants compared to the predominantly Stage I plants at site 4. Significantly fewer oviposition chambers occurred at sites 1 and 5 in January 1978 than for other sampling dates, but there were no evident trends in temporal variation of mean numbers of *Thrypticus* sp. oviposition chambers per plant. Although waterhyacinth petioles were heavily used as oviposition sites by *Thrypticus* sp. on some sites, the only potential effect of this species on waterhyacinth was that oviposition scars could serve as entry points into the plant for facultative pathogens or secondary invaders. The result would be an increase in the rate of senescence of individual waterhyacinth leaves.

Although *N. eichhorniae*, *C. aquaticum*, and *O. terebrantis* fed substantially on waterhyacinth in the Panama Canal during the study and produced locally heavy damage to the plants, these arthropod species appeared to exert a minimum controlling effect on the overall plant population. A major reason for the lack of a controlling effect was that none of the species utilized the newest leaves or meristematic zones of the plants as a significant food source. Although feeding scars produced by adult *N. eichhorniae* were occasionally found on pseudolaminae of the newest leaves, they seldom were present at levels required to significantly affect the photosynthetic capability of these leaves. *C. aquaticum* feeding was never observed on pseudolaminae of the two newest leaves, but significant feeding was often observed on leaves in the fourth through sixth positions. Whether the propensity for these species to feed predominantly on these leaves was due to the nutritional status of the leaves compared to younger or older leaves was not determined. *O. terebrantis* tunnelling was never observed on

⁶Maximum possible mean index value was 3.0.

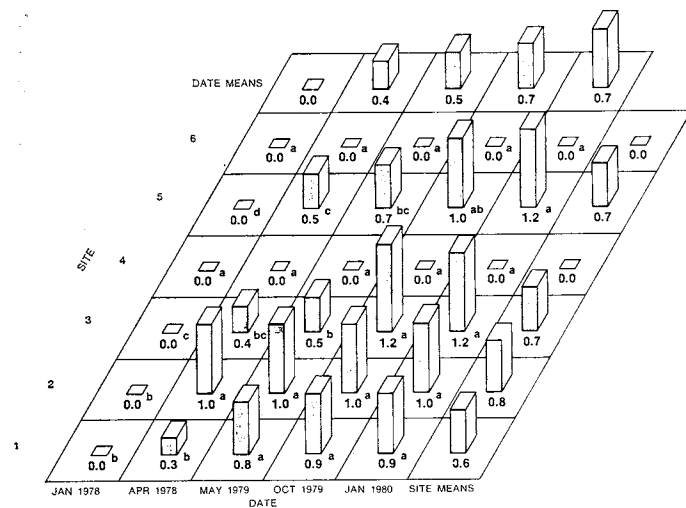


Figure 4. Mean index values of *O. terebrantis* tunnelling per pseudolamina for sites during the study. Analyses performed only within sites. Mean values designated by the same letter within sites are not significantly different at the $p > 0.05$ level.

TABLE 3. MEAN NUMBER¹ OF *Thrypticus* SP. OVIPOSITION CHAMBERS PER PLANT.

Site	Jan 1978	Apr 1978	May 1979	Oct 1979	Jan 1980	Means for Site
1	128.3d	303.0ab	239.1bc	369.6a	191.0cd	246.2
2	187.5a	256.8a	175.5a	194.1a	161.5a	195.1
3	217.1a	207.5a	218.6a	174.9a	297.5a	223.1
4	172.9a	173.8a	140.8a	205.5a	131.3a	164.9
5	65.2b	211.4ab	273.2a	161.3ab	151.5ab	172.5
6	90.1a	131.2a	83.0a	162.8a	127.6a	118.9
Mean for sampling date	143.5	214.0	188.4	211.4	176.7	186.8

¹Analyses performed only within rows. Means followed by the same letter in each row are not significantly different at the $p > 0.05$ level.

pseudolaminae of the three newest leaves; however, this was due to lag-time between egg-laying and eclosure of the eggs. By the time eggs had hatched, new leaves had been produced, thereby placing the newly produced juvenile mites on the pseudolamina of the leaf in the fourth or older position.

Pathogen activity. Mean index values of *A. zonatum* damage per pseudolamina for each site and sampling date (Figure 5) varied significantly. Mean values for sites 1-3 were higher than for other sites. Plants on these sites were predominantly larger, Stage III plants, and these plants had a higher percentage of mature or senescing leaves than plants from other sites. Smaller, more rapidly reproducing Stage I plants abundant in backwater sites may have actually repressed *A. zonatum* activity. Martyn (6) reported that small, actively growing waterhyacinths have higher levels of quinones, which result from degradation of polyphenols by polyphenoloxidase activity, than larger, more physiologically mature plants. This apparently has an inhibitory effect on *A. zonatum*. Thus, higher mean index values for *A. zonatum* in sites 1-3 than for other sites were attributed to the predominance of Stage III plants in sites 1-3. Overall temporal variation in *A. zonatum* damage ranged from 0.97 in April 1978 to 0.4 in May 1979. Mean values were higher during the dry season ($\bar{X} = 0.7$) than during the rainy season ($\bar{X} = 0.5$). Therefore, seasonal variation in environmental factors may partially explain the observed temporal variation. However, mean index values for 1979 and 1980 sampling dates were significantly lower than for 1978 sampling dates in four of the six sites regardless of season, which may be related to increased use of herbicides beginning early in 1979. Waterhyacinth regrowth following application of herbicides consisted primarily of small plants that would have had high levels of polyphenoloxidase activity. Therefore, development of *A. zonatum* on waterhyacinth regrowth was repressed in 1979 and 1980. Although *A. zonatum* was ubiquitous on waterhyacinth in the Panama

Canal, its impact was restricted to the older leaves of Stage III plants. *A. zonatum* lesions were never observed on pseudolaminae of the three newest leaves, nor was it observed on Stage I plants. The absence of *A. zonatum* lesions on the newer leaves of Stage III plants was due to the time required for infection and sufficient proliferation of hyphae to produce a perceptible lesion. Typically, isolated lesions first appeared near the apex of the fourth newest pseudolamina, lesions became larger and more numerous and coalesced on pseudolamina of leaves in the fifth and sixth positions, and infection became progressively more severe in older leaves. Therefore, the major effect of *A. zonatum* on waterhyacinth in the Panama Canal appeared to be hastening of leaf senescence, which decreased the total photosynthetic potential. However, the effect of this reduced photosynthetic capability was probably partially ameliorated by the increased rate of production of new growth in Stage III plants that was stimulated by inhibition of indoleacetic acid oxidase due to the presence of high levels of phenolic compounds in Stage III plants (6). The lack of *A. zonatum* symptoms on leaves of Stage I plants was probably due to the high levels of quinone, which inhibits fungal activity.

No other microorganisms occurred on waterhyacinth in the Panama Canal at sufficient levels to significantly affect the plant. A total of 16 genera of microorganisms were identified from plant samples, 10 of which were bacteria and 6 were fungi (Table 4). Although 7 genera were considered to be either secondary invaders or potential pathogens, none except *A. zonatum* were confirmed to be pathogens of waterhyacinth.

Combined activity. Temporal variation in combined activity of *N. eichhorniae*, *C. aquaticum*, *O. terebrantis*, and *A. zonatum* on waterhyacinth in the Panama Canal is presented in Figure 6. Greatest overall activity of these species occurred in April 1978, while the least activity occurred in May 1979. However, values for all species except *O. terebrantis* were highest in January 1978, and its absence on that date accounted for the lower level of combined activity in January 1978 than in April 1978. The level of activity of *O. terebrantis* progressively increased during the study, but there was a general decline in overall activity by the other species in 1979 and 1980.

Spatial variation in combined activity of the four major species impacting waterhyacinth in the Panama Canal (Figure 7) was more pronounced than temporal variation (Figure 6). Greatest combined activity occurred in site 1 while the least activity occurred in site 6. The level of combined activity was higher in sites 1-3 sites than in the isolated, backwater sites. Lower levels of combined activity at sites 4 and 6 were due primarily to the lack of a significant contribution by *O. terebrantis* activity on these sites. Although the greatest combined activity by these four species occurred in the sites 1-3, plants on these sites were larger than plants on other sites. Thus, it was evident that the combined activity of these species on waterhyacinth in the Panama Canal was insufficient to product a significant level of control.

Interspecific relationships. Correlation coefficients for all possible paired combinations of *N. eichhorniae*, *C. aquaticum*, *O. terebrantis*, and *A. zonatum* are presented in

[†]Maximum potential mean index value was 3.0.

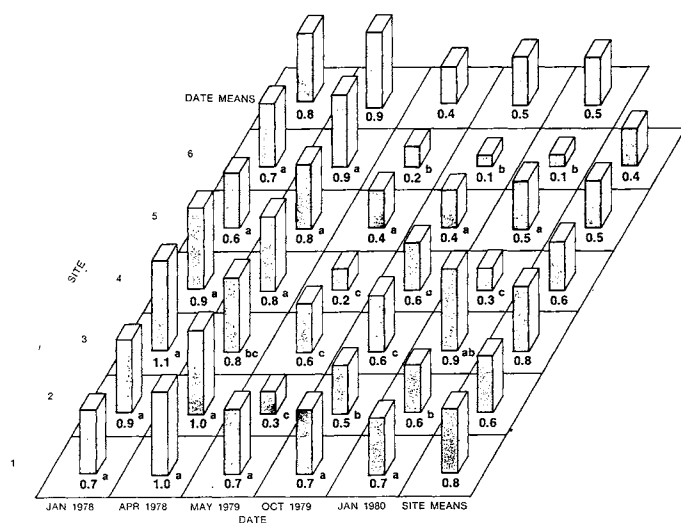


Figure 5. Mean index values of *A. zonatum* damage per pseudolamina for sites during the study. Analyses performed only within sites. Mean values designated by the same letter within sites are not significantly different at the $p > 0.05$ level.

TABLE 4. MICROORGANISMS IDENTIFIED FROM WATERHYACINTH IN THE PANAMA CANAL. NUMBERS UNDER EACH DATE REFER TO SITES IDENTIFIED IN FIGURE 1.

Taxon	Symptom	May 1979 ¹						October 1979 ¹						January 1980 ¹						Comments								
		1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6									
Bacteria																												
<i>Achromobacterium</i> sp.	Necrosis associated with insect damage																											Probable contaminant
<i>Aeromonas hydrophila</i>	Brown leaf spot																											Probable contaminant
<i>Alcaligenes</i> sp.	Chlorosis associated with <i>Neochetina</i> feeding scars																											Probable contaminant
<i>Corynebacterium</i> sp.	Brown leaf spot																											Possible pathogen
<i>Erwinia herbicola</i>	Leaf spot																											Probable secondary invader
<i>Enterobacter cloacae</i>	Wet leaf rot																											Probable contaminant
<i>Proteus inconstans</i>	Necrosis associated with insect damage																											Probable contaminant
<i>Pseudomonas</i> sp.	Necrosis associated with <i>Neochetina</i> feeding scars and <i>Acremonium</i> leaf spot																											Possible secondary invader
<i>Serratia liquefaciens</i>	Large leaf spot																											Probable contaminant
<i>Xanthomonas</i> sp.	Leaf spot associated with <i>Neochetina</i> feeding																											Possible pathogen
Fungi																												
<i>Acremonium zonatum</i>	Zonate leaf spot																											Pathogen
<i>Ascochyta</i> sp.	Necrosis associated with <i>Neochetina</i> feeding and <i>Acremonium</i> leaf spot																											Probable saprophyte
<i>Botrytis</i> sp.	Black leaf spot																											Possible pathogen
<i>Fusarium</i> sp.	Leaf necrosis																											Possible pathogen
<i>Paecilomyces</i> sp.	Necrosis associated with <i>Orthogalumna</i> damage																											Probable saprophyte
<i>Zythia</i> sp.	Leaf spot associated with <i>Neochetina</i> feeding																											Probable saprophyte

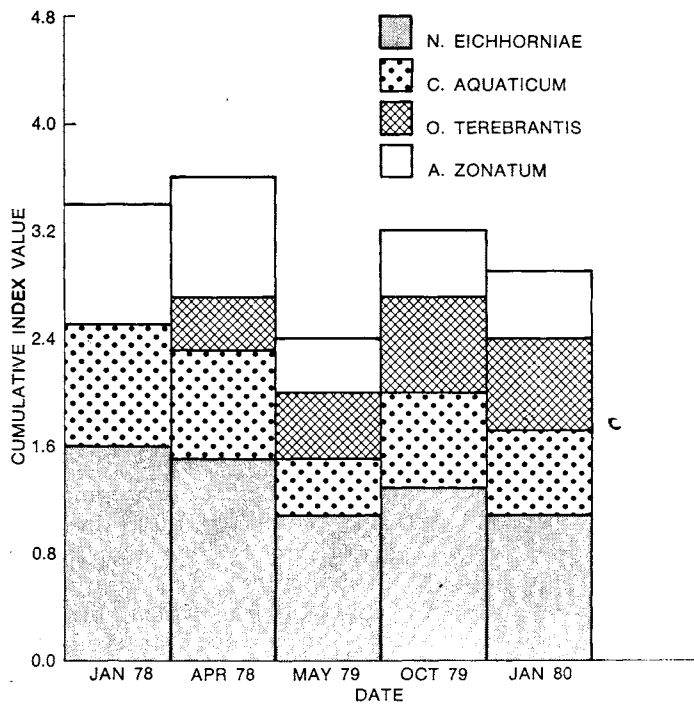


Figure 6. Temporal variation in combined activity of *N. eichhorniae*, *C. aquaticum*, *O. terebrantis*, and *A. zonatum* on waterhyacinth in the Panama Canal.

Table 5. *N. eichhorniae* and *A. zonatum* were positively correlated ($p > 0.05$) on all six sites, and *N. eichhorniae* and *C. aquaticum* were positively correlated on all sites except at site 5. *C. aquaticum* and *A. zonatum* were positively correlated on sites 1-3, but not on sites 4-6. The predominance of Stage III plants in sites 1-3 and the constant

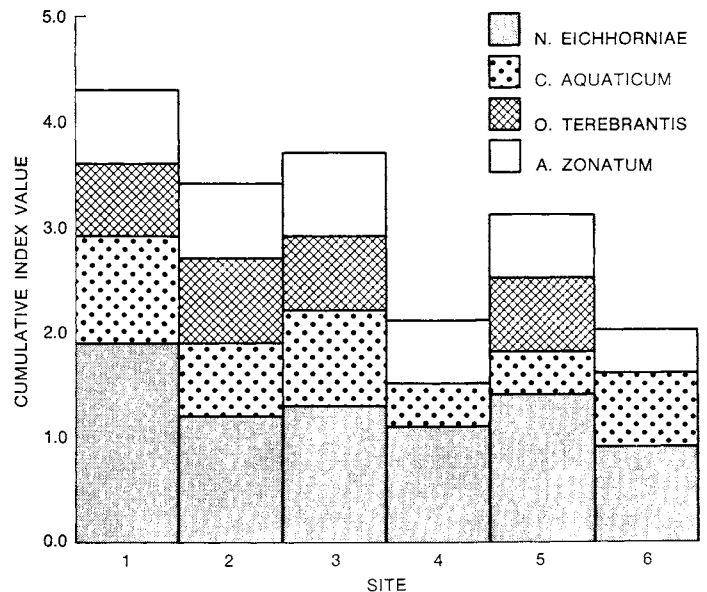


Figure 7. Spatial variation in combined activity of *N. eichhorniae*, *C. aquaticum*, *O. terebrantis*, and *A. zonatum* on waterhyacinth in the Panama Canal.

TABLE 5. CORRELATION COEFFICIENTS FOR SPECIES INTERACTIONS OF WATERHYACINTH IN THE PANAMA CANAL.

Species Combination	Manatee Lagoon	Las Cruces	Nevada	Stump Lake	Dump 4½	Red Tank Lake
<i>Neochetina</i> x <i>Cornops</i>	0.4260 ¹	0.3180	0.5350	0.3077	NS ²	0.2788
<i>Neochetina</i> x <i>Acremonium</i>	0.3848	0.3628	0.5461	0.5455	0.3615	0.6685
<i>Cornops</i> x <i>Acremonium</i>	0.4978	0.5187	0.5143	NS	NS	NS
<i>Neochetina</i> x <i>Orthogalumna</i>	-0.2635	NS	NS	NS	NS	NS
<i>Acremonium</i> x <i>Orthogalumna</i>	NS	NS	0.3009	NS	NS	NS
<i>Cornops</i> x <i>Orthogalumna</i>	-0.2119	NS	NS	NS	NS	NS

¹All numbers presented are significant at the 0.05 probability level.

²NS indicates values not significant at the 0.05 probability level.

concentration of plants in these areas by river flow were thought to be major factors influencing these positive correlations. *A. zonatum* and *O. terebrantis* were positively correlated, but only at site 2. Similar patterns in the timing of developmental sequences of these species on waterhyacinth probably accounted for this relationship, since neither species was ever found on pseudolaminae of the three newest leaves. There also appeared to be a relationship between the two species with respect to their entry into the plant. The first detectable *A. zonatum* lesion often occurred in the same area of the pseudolamina where *O. terebrantis* activity was first noted. Whether or not *O. terebrantis* served as a vector for *A. zonatum* was not determined; however, if *O. terebrantis* acted as a vector for *A. zonatum*, the relationship was not obligatory. *A. zonatum* was often present on pseudolaminae that had no *O. terebrantis* activity.

Two significant negative correlations were identified, both involving *O. terebrantis* at site 1. Negative correlations for *O. terebrantis* and *N. eichhorniae* and *O. terebrantis* and *C. aquaticum* were probably related to population shifts for these species during the study. *O. terebrantis* was absent from site 1 in January 1978 when the levels of activity of the other species were high. Its activity then increased during the study, while the activity of *N. eichhorniae* and *C. aquaticum* decreased.

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