

Variation in Waterhyacinth/Weevil Interactions Resulting from Temporal Differences in Weed Control Efforts

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ABSTRACT

Waterhyacinth (*Eichhornia crassipes*) populations, weevil (*Neochetina eichhorniae*) populations and plant damage were compared at Canal-M, Palm Beach Co., FL, in summer 1983. Three sections of the canal were studied. History of waterhyacinth control differed between the upstream section and the two other sections. Upstream plants were harvested 16 mos. before this study and regrowth plants were large with little weevil damage. Downstream and middle sections were controlled with 2,4-D 34 mos. before this study. Regrowth plants were small, due to intense weevil damage, and were sinking. Weevils per shoot were greatest in the middle but absolute densities were comparable in upstream and middle. Standing crop and shoot size were inversely related to number of weevil larval galleries and proportion of the laminae eaten by adults. Long duration of weevil attack reduced plant size causing proportionately greater weevil effects. Adult weevils were smaller and sex ratios favored males where plants were heavily damaged. No differences in flight muscle development or female fecundity were found. By fall 1983 the middle and downstream sections were completely controlled by insects. By summer 1984 weevils had also killed most of the upstream plants. This suggests that biological control can be very effective but a minimum time period is required. Plant size and weevil intensity determine the length of this interval.

Key words: biological control, herbivory, insect-plant interactions, *Eichhornia crassipes*, *Neochetina eichhorniae*, aquatic weeds.

INTRODUCTION

Biological control is a proven, effective method for managing growth of floating aquatic vegetation. Successful programs have been implemented against alligatorweed (*Alternanthera philoxeroides* (Mart.) Griseb.; Coulson, 1977), *Salvinia molesta* D. S. Mitchell (Room *et al.*, 1981), and waterlettuce (*Pistia stratiotes* L.; Harley *et al.*, 1984). Recent successes with biological control of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) have now been reported worldwide (Center, 1982; DeLoach and Cordo, 1983; Cofrancesco, 1984; Goyer and Stark, 1984; Wright, 1979; Bashir *et al.*, 1984; Irving and Bashir, 1984). Results in Florida have been less spectacular than in other regions

possibly due to extensive and efficient chemical control programs (Haag, 1985). Intensive management has likely obscured the impact of biological control agents.

Elimination or reduction of waterhyacinth populations correspondingly reduces populations of host-specific herbivores such as the weevil *Neochetina eichhorniae* Warner. Although no data are available, herbivore populations seem depauperate in young waterhyacinth mats which form as regrowth after control operations. If true, this suggests that current management practices are not compatible with biological control. It also suggests that better methodology is needed to provide an integrated approach towards waterhyacinth control. We recently studied adjacent canal sections in which waterhyacinth differed in degree of herbivore damage and time since respective sections had last been cleared of plants by chemical or mechanical methods. This provided an opportunity to examine the effects of disturbance on the interactions between the weevils and their host plant. It also enabled us to acquire data on the time required for effective biological control and on the effect of dramatic reduction of plants on herbivore pressure.

We were interested in two aspects of the plant-herbivore interaction. First, we wished to compare the effects of the insects on the plants. Second, we wanted to compare aspects of the biology of the weevils on healthy, robust plants with plants in poor condition due to sustained attack. Two adjacent sections of the canal were studied to provide these comparisons. Waterhyacinth were large, robust, and healthy with little apparent weevil damage in the upstream section. Plants there had last been removed in March (16 mos. earlier) by mechanical means. Plants just downstream (middle section) were small, with spindly petioles and curled leaf blades. Weevil damage was heavy and many plants were clearly dying. Plants in this section were removed ca. 34 mos. earlier (fall 1980) by application of herbicide (2,4-D). A distant section much further downstream was similar to the middle section. This section was included to control for the effects of location within the canal since plants upstream may alter nutrient supplies to those downstream.

METHODS AND MATERIALS

Studies were conducted at Canal-M, in Palm Beach County. Two of the three sections studied were located just west of the Sunshine State Parkway overpass while the third was just east of Haverhill Rd. Distance between the upstream and middle sections was only ca. 100 m while distance between the middle and bottom sections was ca.

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1.8 km. The length of the upstream mat was ca. 1.2 km, the middle mat was ca. 1.4 km, and the downstream mat was ca. 0.4 km. The farthest point downstream was ca. 3.2 km upstream from Lake Mangonia. A log control structure just west of the downstream section and floating barricades both above and below the middle section prevented mixing of the three waterhyacinth populations.

Plants were sampled ten times at equal intervals along transects within each canal section. Data were analyzed to determine if sample location accounted for variability. Sample spacing was determined by the time interval required to travel each canal segment in an airboat with the engine at constant rpm (2200), dividing the total time by ten, then repeating the run while dropping markers at appropriate time intervals. The markers designated the ten sample locations. The sampling intervals were ca. 130 m in the upstream area, and 150 m in the middle area, but only ca. 40 m in the smaller downstream area. All samples were near the center of the canal to avoid shoreline effects.

Plant characteristics, insect damage, and insect populations

The modular unit in a waterhyacinth population is a shoot. A plant may consist of one or several shoots, depending upon the number of offsets. We considered individual shoots to be our sampling unit, provided they were capable of independent survival. Our criteria for including a shoot in a sample stipulated that each must possess one live leaf and be of sufficient maturity to possess visible root initials.

Sampling was first done on 12-13 July 1983. A square frame measuring 50 cm X 50 cm (0.25 m²) was thrown into the mat near each marker to delineate the sample. First, ten shoots were removed from each frame and adult weevils were picked off, counted, and placed into a plastic vial marked with the sample location. All other plants were withdrawn from the frame and placed in a plastic bag with the original ten. Each bag was labelled to indicate sample location.

Insect and plant samples were transported to our laboratory in Ft. Lauderdale. Weevil species (*N. eichhorniae* or *N. bruchi* Hustache) were identified and counts recorded for each species. (Less than 1% of the weevils were *N. bruchi* so species was not an important variable). Sex of each individual was determined but only after specimens from each section were pooled into a common sample. Hence, sex ratio was determined for each section but not each sample location. Twenty each of male and female *N. eichhorniae* from each canal section were randomly picked from the pooled samples (only 18 females were obtained from the downstream section), quick-frozen at -40°C, then freeze-dried in a lyophilizer. Each individual was weighed on a balance accurate to 10⁻⁴ mg. Average weights for both males and females were compared among canal sections.

Plant samples were cleaned and dead tissue was removed. Three shoots were randomly selected and root length, leaf measurements, and counts of live leaves determined. Leaf measurements were from the third nodal position leaves (usually the youngest mature leaf) and included total leaf length, lamina length, lamina width, and petiole length. Total number of shoots per sample was

counted. The sample was dried at 70°C to constant weight then weighed to the nearest gram.

Weevil damage to the three shoots subsampled from each plant sample was assessed. The leaf with the greatest number of feeding scars was selected from each shoot, its stem node position noted, the number of feeding scars on the adaxial lamina surface counted, and the proportional lamina area damaged estimated. Number of feeding scars and percentage lamina coverage was also determined on third position leaves. Number of weevil larval galleries within each shoot was also counted. Weevil density (no./m²) was determined as weevils/shoot x shoots/m²; weevil mass (mg/m²) as weevils/m² x mg/weevil (adjusted for sex ratio); weevil intensity (mg/kg) as weevil mass/m² x plant mass/m².

Size and age structure of the plant population vary in a manner dependent upon the degree and mode of vegetative growth. Sampling often biases data towards the larger shoots. Hence, best estimates were obtained by removing a group of shoots and sampling several from the group. Since we were not interested in variation within samples but rather variation within and among canal sections, data were averaged prior to analysis to provide one estimate per variable per sample. Initial analyses performed with a regression procedure (PROC GLM; SAS, 1983) used a model statement which included the class variable "section" and the nested variable "location within section." The purpose of the latter term was to analyze for linear upstream vs. downstream effects within each section. The nested effect was not significant for any variable. We concluded that upstream or downstream position of the sample had no bearing on the data. Hence, the nested term was deleted and data re-analyzed as one-way analyses of variance (PROC ANOVA; SAS, 1983) testing for effects of canal section upon the plant characteristics, insect damage, and insect populations.

Weevil size, flight muscle development, fecundity and sex ratio

Because of differences in sex ratios in the three areas we suspected differences in weevil flight activity and fecundity. Ten female weevils from each section were rehydrated by soaking them in 10% tri-sodium phosphate solution overnight. These were then dissected to determine if they were fecund and if indirect flight muscles were fully developed. We found fully developed eggs in 10% of downstream weevils, 40% of weevils in the middle section, and 70% of upstream weevils. Dehydration of the specimens precluded analysis of wing muscle development. Nonetheless, the preliminary information prompted initiation of another sampling scheme to examine these factors in more detail.

On 4 and 5 August 1983 we again marked sampling locations in the canal as previously described. We withdrew plants from the mat at each sampling location from any point within reach and hand-picked adult weevils from them. Collecting continued until we acquired at least 60 weevils at each location. This number assured acquisition of twenty females. Weevils were immediately placed in 70% isopropyl alcohol with each sample preserved separately. At the laboratory ten females from each sample

were dissected to ascertain fecundity and wing muscle development and ten males for wing muscle development only. An additional ten males and ten females from each sample were weighed. Because these were stored in alcohol, they were first air-dried overnight, then sorted to species and sex, then freeze-dried and weighed as before. This differed from the earlier sample in that the weevils were killed immediately rather than held alive for several hours without food before we weighed them. The effect of the alcohol storage on the dried weights was unknown.

Only 22 (1.1%) from the total of 1958 weevils collected were *N. bruchi*. Hence, data were only collected from the *N. eichhorniae* specimens with regard to weight, wing muscle development, fecundity, and sex ratio.

RESULTS

Plant characteristics, insect damage, and insect populations

Weevil population data are shown in Figure 1. Means were quite different among canal sections but differences were not statistically significant ($p = .05$) due to high variability within sections. Number of weevils per shoot was over twice as great in the middle section as opposed to downstream and the upstream section was slightly greater than downstream. In terms of weevil density (number/m²) upstream and middle sections were nearly identical. Hence, populations were about the same size in both areas but weevils were dispersed over more shoots upstream. Weevil mass (mg/m²) was slightly greater upstream than in the middle, but very low downstream. The most revealing index was weevil intensity. The value for the upstream area was slightly greater than the downstream area. Weevil intensity in the middle section was nearly three times greater than downstream and over twice the upstream value.

Figure 2 shows degree of larval and adult weevil injury to the plants. Although data varied, significant differences ($p = .05$) occurred. Upstream and downstream sections were similar whereas greater injury occurred in the middle section. Number of larval galleries per shoot was not significantly different upstream and downstream (0.70 vs. 1.20) but was nearly twice as great in the middle (2.27). The same pattern held for percentage of lamina area eaten on third position leaves, on leaves with maximum feeding, and for number of feeding scars on third position leaves. Number of feeding scars on leaves with maximum feeding was highest in the middle section, intermediate upstream, and lowest downstream. All differences were significant (258, 198, and 129 scars per lamina, respectively). Maximum feeding on young leaves indicates recent maximum weevil activity while on old leaves it indicates a past peak in feeding activity. Although maximum feeding occurred on somewhat younger leaves in the middle section, the average nodal position of leaves with maximum feeding was not significantly different among sections.

Differences in plant characteristics among canal sections were distinct from either weevil population or damage data. Plants were about the same in the middle and downstream sections but consistently and significantly greater upstream in terms of shoot density, standing crop, and stature (Figure 3). This was also true of lamina length,

lamina width (see Table 1), leaf length and leaves per shoot. Root length followed a different pattern, with length upstream significantly greater than in the middle section. Downstream root lengths were intermediate and not significantly different from either of the other sections. Root length to shoot length ratio increased downstream (0.44, 0.56, 0.68) but differences were not significant. Nonetheless, this constant change in a downstream direction indicated possible nutrient differences. Hence, we checked for correlation between these ratios and sample location within sections, since sections were generally longer than distances between them. Sample location accounted for very little of the variation in root to shoot ratio (1.1%, 24.5%, and 0.2%, upstream to downstream) and the low correlation coefficients were negative (-0.11, -0.50, -0.05, respectively) rather than positive as would have been anticipated if nutrient differences were great.

As we examined the three sections, our impression was that plants in the middle section were heavily damaged by weevils and were in poor condition, plants upstream were not heavily damaged and were in good condition, and plants downstream were intermediate in both regards. Data analysis showed this impression to be true for plant condition, although the downstream section was more similar to the middle section than we anticipated, and the two were not statistically different.

In terms of weevil damage, however, our impression was wrong. Adult damage upstream was equal to or greater than downstream. Only larval damage conformed to expectations and even this was not significantly different. The same pattern was true of weevil population numbers with smaller average numbers in the downstream section but no significant differences.

Examination of the data revealed other unexpected patterns. Within sections, weevil damage did not correspond with weevil population numbers. Nor did plant condition within sections correspond with weevil damage. Correlation analyses were therefore done both by section and over all sections. Both means and coefficients of variation (CV) were used to determine if damage correlated with plant condition or variability of plant condition. In the upstream area leaf length CV was directly correlated with number of larval galleries per shoot ($r = .704$, $p = .023$, 8 df). Thus, shoot size was more homogeneous when larval damage was low.

In the middle section the CVs of plant characteristics were often correlated with insect population or damage. For example, variability in shoot size (leaf length) was inversely correlated with weevil population in terms of mass or density ($r = -.620$, $p = .056$, 8 df) and intensity ($r = -.638$, $p = .047$, 8 df) but less so in terms of weevils per shoot ($r = -.554$, $p = .096$, 8 df). The number of feeding spots on leaves with maximum feeding was inversely correlated with root length CV ($r = -.634$, $p = .049$, 8 df), with root to shoot ratio CV ($r = -.627$, $p = .052$, 8 df), with lamina length to width ratio CV ($r = -.681$, $p = .030$, 8 df) as well as with means of lamina ratios ($r = -.650$, $p = .042$, 8 df) which were also inversely correlated with proportion of lamina area eaten on third position leaves CV ($r = -.667$, $p = .035$, 8 df). Therefore, high weevil intensities in this section were associated with smaller shoots. Heavy feeding damage by

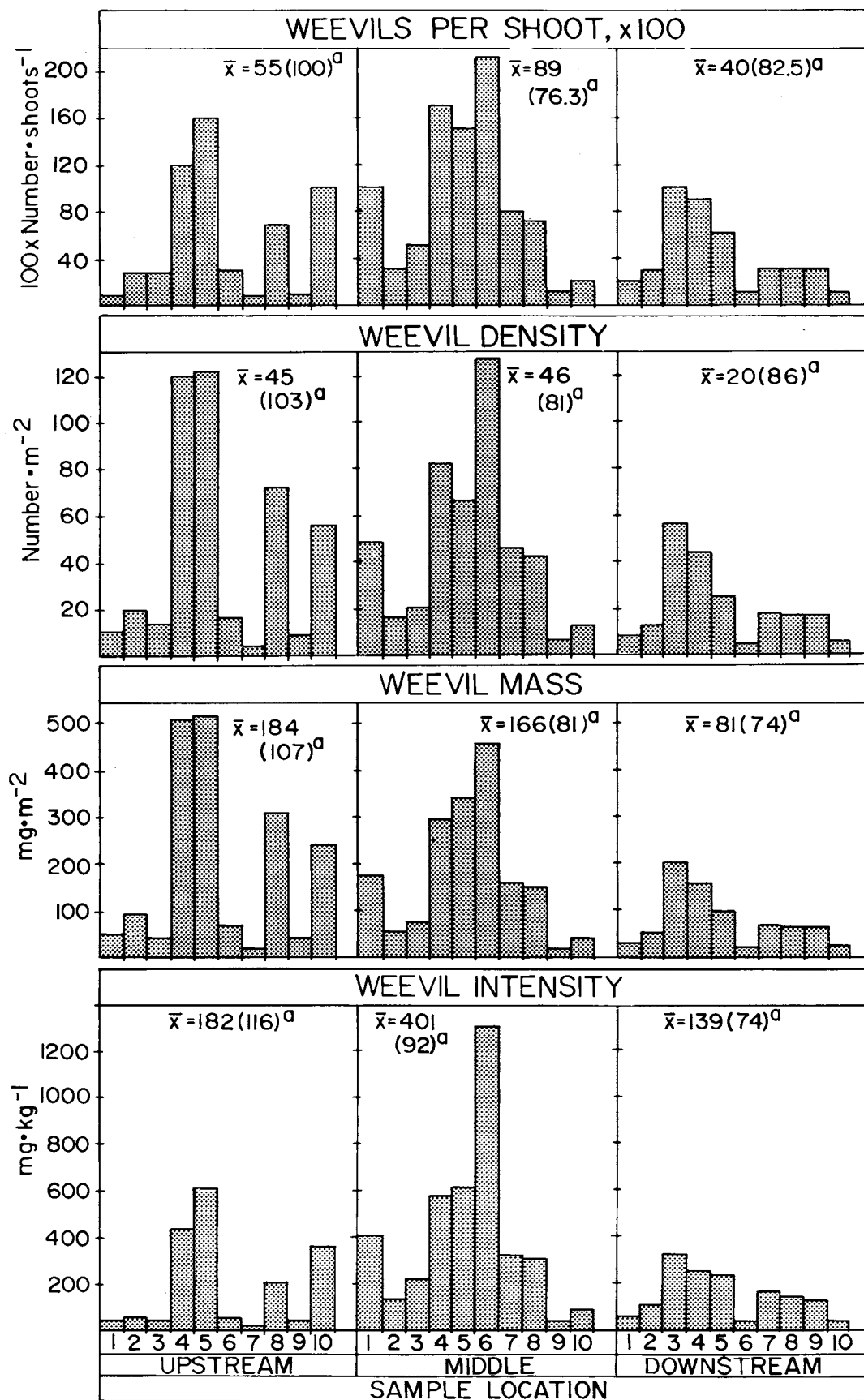


Figure 1. Data for estimates of weevil populations in the three sections of Canal-M. Sample locations are numbered from the upstream end to the downstream end of each section. Data for weevils per shoot represent adults and have been multiplied by 100 to avoid fractional numbers. Weevil density represents adults per square meter. Weevil mass represents dry weight of adult weevils per square meter. Weevil intensity represents weevil mass per unit of plant mass. Numbers at the top of each graph represent means for each section with coefficients of variation in parentheses and are based upon sample means (n=10). Mean values superscripted with the same letters indicate no significant difference (p=.05) between sections based upon the Duncan-Waller K-ratio.

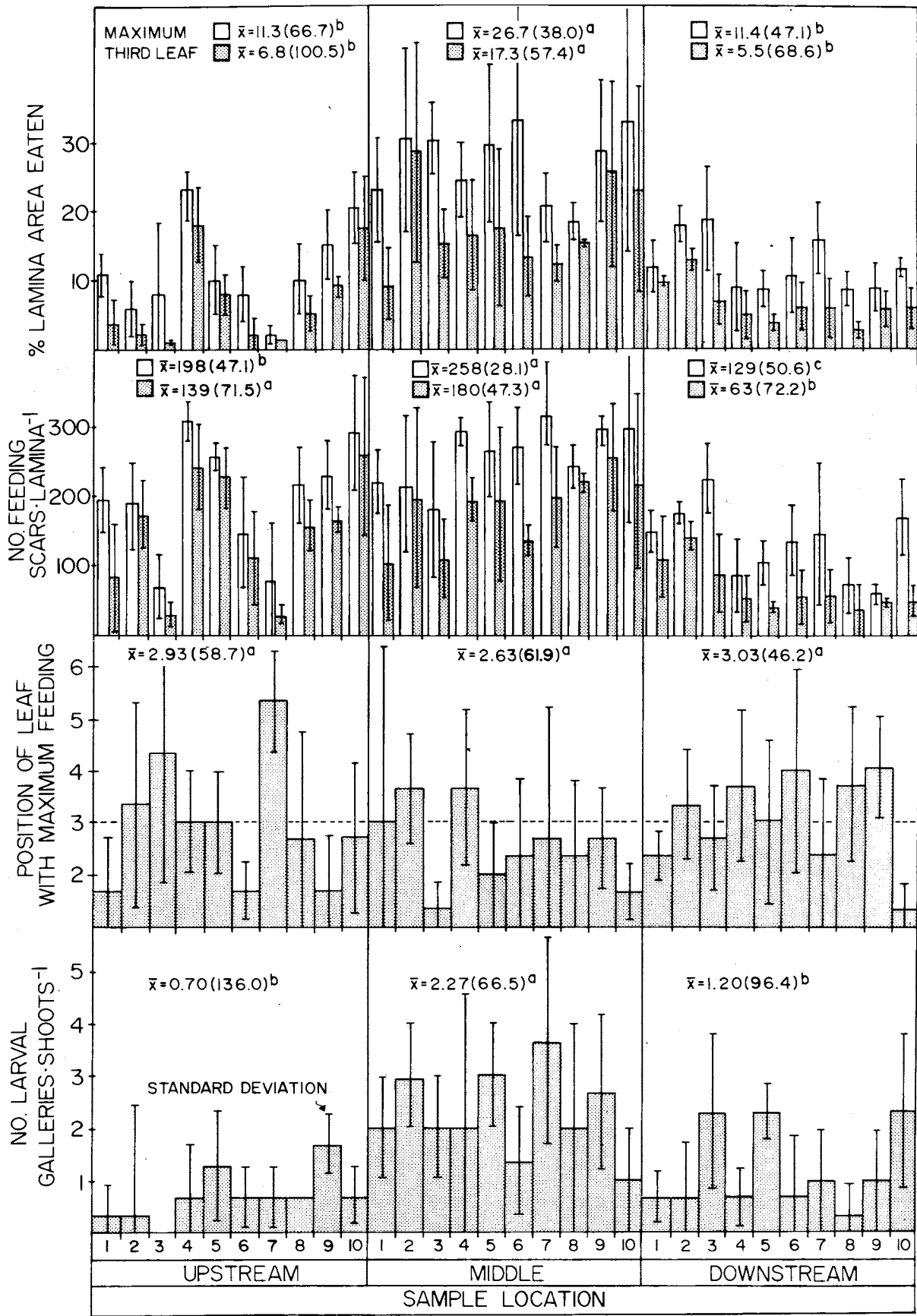


Figure 2. Data showing the extent of weevil adult and larval damage to waterhyacinth shoots in the three sections of Canal-M. Percentage of lamina area eaten and number of feeding scars per lamina are derived from leaves with maximum feeding (open bars) and third position leaves (shaded bars). The stem node position of the leaf with the greatest amount of feeding on each shoot is depicted in the third set of bar graphs. Vertical lines on each data bar represent standard deviations within samples (n=10).

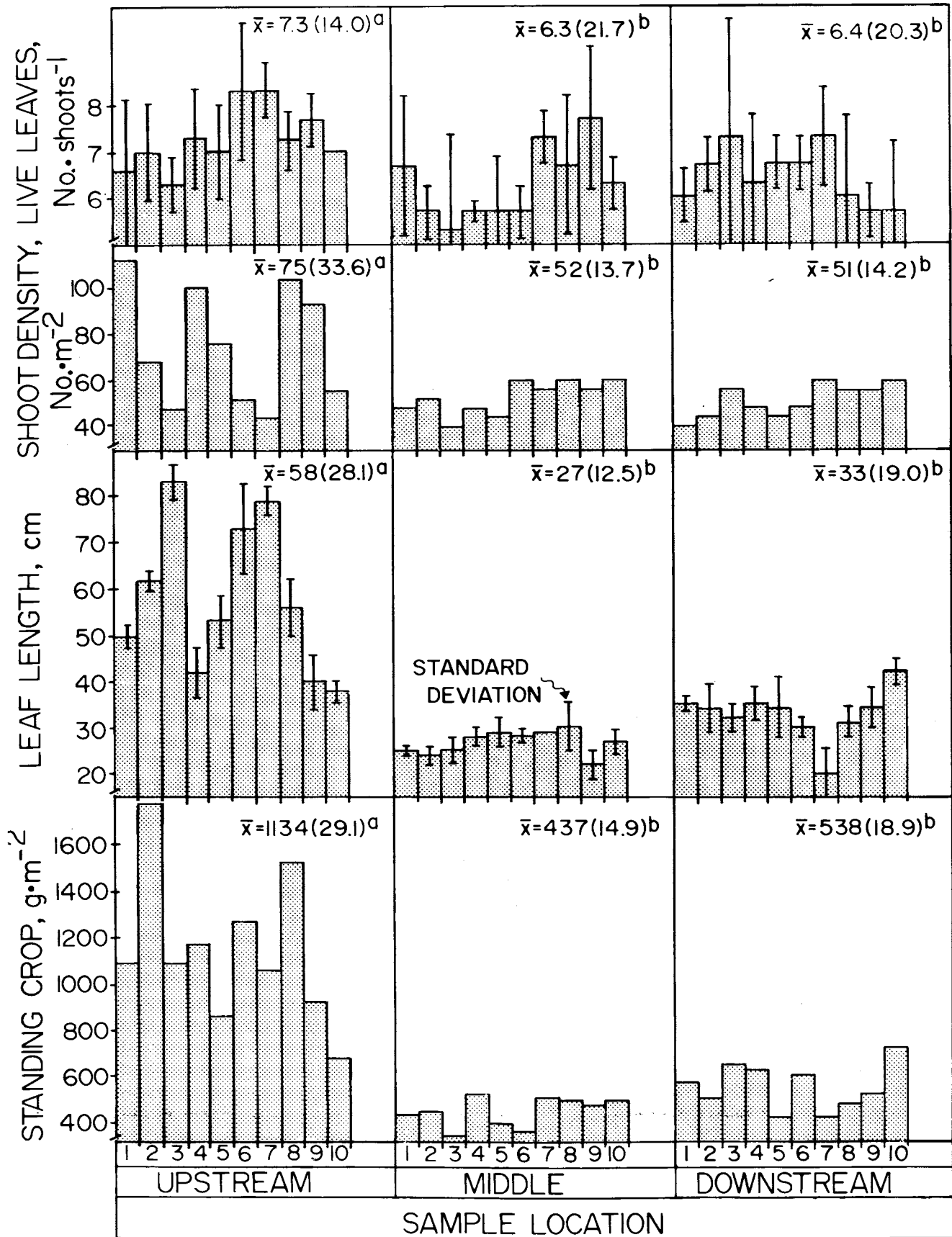


Figure 3. Data for plant characteristics within the three sections at Canal-M. Labels and numbers as in Figure 2.

TABLE 1. DATA FOR PLANT CHARACTERISTICS WITHIN THE THREE CANAL SECTIONS AT WEST PALM BEACH, CANAL-M. NUMBERS SUPERSCRIBED WITH THE SAME LETTER INDICATE LACK OF SIGNIFICANCE ($p = .05$) USING THE DUNCAN-WALLER K-RATIO. NUMBERS REPRESENT MEANS AND COEFFICIENTS OF VARIATION (IN PARENTHESES) UNLESS OTHERWISE INDICATED. ROOT:SHOOT DENOTES RATIO OF ROOT LENGTH TO TOTAL LEAF LENGTH (LAMINA + PETIOLE).

Variable	Upstream	Middle	Downstream	F (Pr>F)
Lamina Length (cm)	12.55 (18.99) ^a	7.15 (14.09) ^b	8.45 (12.51) ^b	30.50 (.0002)
Lamina Width (cm)	9.73 (24.79) ^a	5.37 (14.77) ^b	6.25 (11.47) ^b	22.96 (.0001)
Root Length (cm)	25.47 (46.98) ^a	14.80 (36.30) ^b	21.53 (53.33) ^{ab}	2.87 (.0740)
Lamina L:W	1.33 (5.53) ^a	1.34 (6.39) ^a	1.37 (8.48) ^a	0.37 (.6973)
Root:Shoot	0.44 (33.83) ^a	0.56 (36.34) ^a	0.68 (58.35) ^a	1.96 (.1604)

adult weevils was associated with greater homogeneity of shoot size, root length, root to shoot ratio, and lamina shape, as well as with a more rounded lamina shape (low length to width ratio).

Few correlations between plant characteristics and weevil population or damage were apparent downstream. Interestingly the proportion of the lamina area eaten on the leaves with maximum feeding was correlated with the number of live leaves per shoot ($r = +.66$, $p = .036$, 8 df).

When data from all sections were pooled and correlation analyses performed, relationships between plant characteristics and weevil populations or damage were more apparent. Waterhyacinth standing crop and shoot size were inversely correlated with number of larval galleries per shoot ($r = -.520$, $p = .003$, 28 df; and $r = -.535$, $p = .002$, 28 df) and with proportion of lamina area eaten on the leaf with maximum feeding ($r = -.530$, $p = .003$, 28 df; and $r = -.642$, $p = .001$, 28 df). Variability in number of feeding spots on third position leaves was related to leaf shape variation as evidenced by the direct correlation of the lamina length to width ratio CV with feeding spot counts on third position leaves CV ($r = +.509$, $p = .004$, 28 df). Hence, a more uniform dispersion of feeding spots leads to more homogeneity of leaf shape, or vice versa.

Generally, variability of insect counts decreased as mean values increased. This was evidenced by inverse correlations between number of adult weevils per shoot CV and mean number of weevils per shoot, weevil mass per square meter, and weevil intensity ($r = -.521$, $p = .003$, 28 df; $r = -.510$, $p = .004$, 28 df; and $r = -.516$, $p = .004$, 28 df, respectively) and between means and CVs of number of larval galleries per shoot ($r = -.735$, $p = .0001$, 28 df). Hence, we might conclude that weevil populations are more evenly distributed when they are larger and patchy when populations are low.

Correlations also existed between adult weevil numbers and extent of adult feeding. The proportion of the lamina area eaten on the leaf with maximum feeding was positively correlated with weevil intensity ($r = +.491$, $p = .006$, 28df). The number of feeding spots on leaves with maximum feeding was correlated with number of weevils per shoot ($r = +.497$, $p = .005$, 28 df), weevil mass per square meter ($r = +.541$, $p = .002$, 28 df), weevil density per square meter ($r = +.535$, $p = .002$, 28 df), and weevil intensity ($r = +.476$, $p = .008$, 28 df). Significant correlations were apparent among all four estimates of weevil populations and among all measures of weevil damage (except for larval galleries with number of feeding spots on third position leaves).

Weevil size, flight muscle development, fecundity and sex ratio

Female weevils averaged 4.64, 4.34, and 3.96 mg from upstream to downstream sections respectively. Differences were significant ($p = .05$) between upstream and downstream sections but not between middle and either end. Males averaged 3.64, 3.25, and 3.28 mg respectively, no differences significant ($p = .05$). The male to female sex ratio differed among sections. In the middle, where plants were in poor condition, over twice as many males were present (2.12:1) as females. Upstream, where plants were in good condition the ratio favored females (0.75:1) Downstream the ratio was more even. This resulted in nearly identical average weights per adult weevil in middle and downstream sections (3.6 mg) but greater values upstream (4.2 mg).

When insects were collected for the second time the sex ratios were found to be different. The male to female ratio was again 1.17 in the downstream area but was also 1.17 in the upstream area where it had favored females only 22 days earlier. The middle area remained skewed towards males (1.38) but not to the previous extent (2.12). The second set of samples was based upon more individuals (595, 732, and 610 vs. 52, 86, and 39 respectively for upstream, middle, and downstream sections) which perhaps provided better estimates. Overall the sex ratio did not change greatly (1.32 before vs 1.23 later) so it seemed that redistribution of individuals within the canal had occurred. The sex ratio was significantly different from 1:1 only in the middle section ($\chi^2(p) = 12.6(.18)$, $19.5(.02)$, $6.24(.72)$, 9 df, upstream to downstream).

As noted earlier, examination of ten females from each section revealed that 70%, 40%, and 10% (up to down) were gravid in the July sample. One hundred females from each section (ten per sample location) were examined from the August samples and most were gravid. The lowest proportion was in the middle section where 82% of females contained one or more fully developed eggs as compared to 88% upstream and 93% downstream. Adjusting for sex ratio, 41%, 35%, and 43% of the population were reproductive females in the upstream, middle, and downstream sections, respectively.

Wing muscle development was checked to determine if individual weevils might be moving among sections. Only 11 of the 600 examined (1.8%) had any degree of wing muscle development and eight of these were in the upstream section (4.0%). Four of the 11 had rudimentary wing muscles and only six from the upstream section

(3.0%) and one from the middle section (0.5%) had well-developed flight muscles. Only two of the 11 with flight muscles were females of 300 females examined (0.7%) and both were upstream. One of the females with flight muscles was gravid, the other was not.

Data for weevil dry weights are shown in Figure 4. Means, standard deviation and range for each sample location within each section on 4 August are compared with data gathered 13 July. Mean weights of each sex by section were compared between the two dates using Student's t-test for unpaired data and no significant differences were found (Males: $t=1.6, 0.2, -.8$; $\text{prob.}>t=0.11, 0.85, 0.42$. Females: $t=0.3, -0.1, -1.1$; $\text{prob.}>t=0.78, 0.92, 0.26$; upstream, middle, downstream, respectively).

Comparisons of weights among sections within each sampling date revealed interesting differences (see Figure 4). For example no differences in weight of males were apparent among sections in July ($F=2.61, p=0.08$), but in August males in the downstream section were heavier than those in the middle, but nearly the same as those upstream ($F=2.90, p=0.06$). Those upstream were not significantly different than those in the middle. Because of the small differences in F-values and the low proportion of variation accounted for (8.4% in July, 1.9% in August), actual weights of adult males probably did not change between dates and did not differ among canal sections. Apparent changes probably resulted from the increase in error degrees of freedom (57 vs. 297).

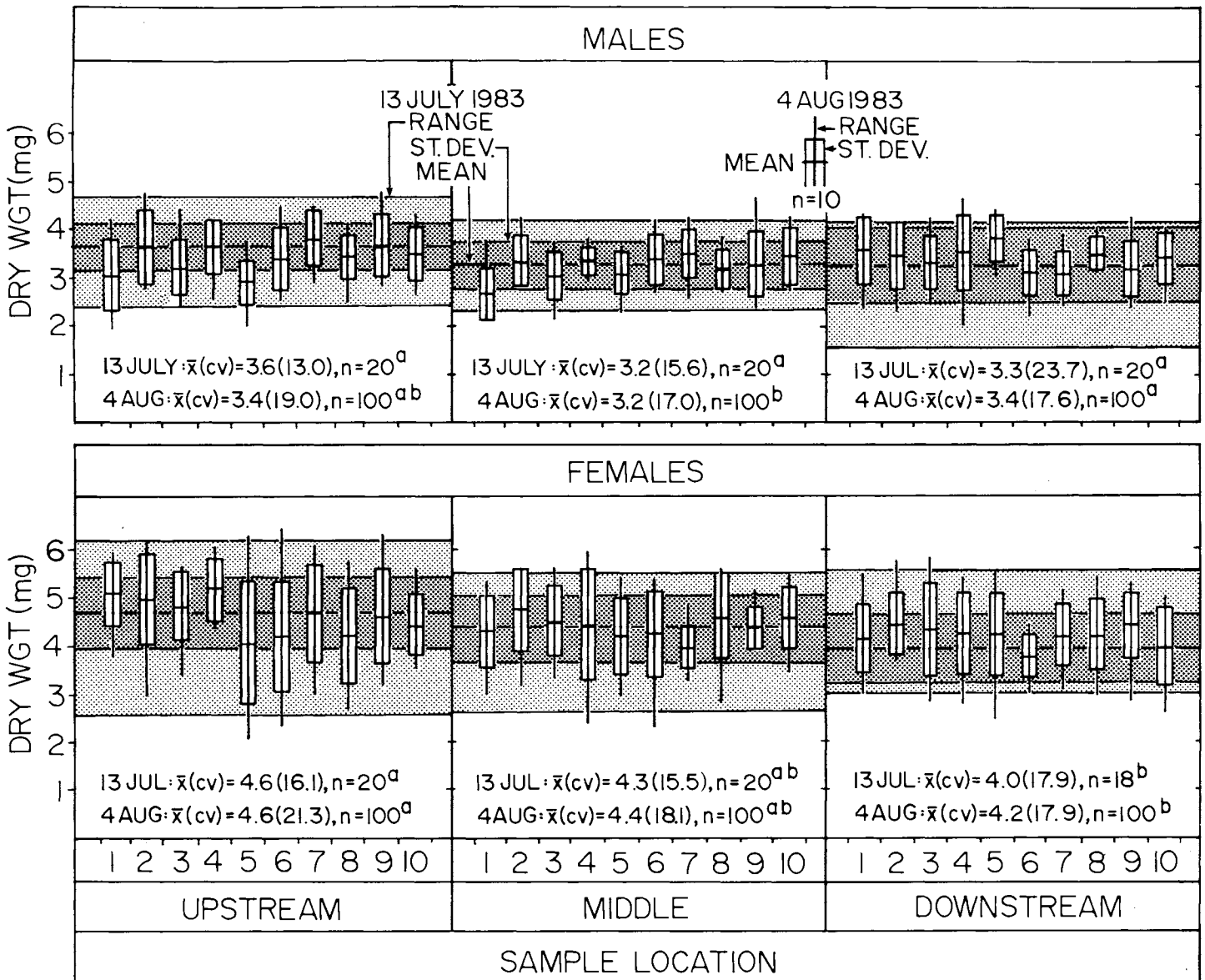


Figure 4. Data on average weights of male (top) and female (bottom) *N. eichhorniae* adults collected on 13 July (shaded bands) and 4 August 1983 (boxes) within each of the three canal sections at West Palm Beach. Data were only compiled by section on the earlier sampling date whereas later data were compiled for each sample location within each section. Differences between dates were not significant. Superscripts refer to tests of significance for differences among sections within dates using the Duncan-Waller K-ratio ($p=.05$), and means superscripted with the same letter are not significantly different. Comparisons between dates do not appear in the figure.

The pattern of distribution of females did not change. Weight decreased downstream, with upstream values significantly different from downstream values. Weights in the middle were not different from either end. Although analyses of variance showed significant F-values each time (July: $F=4.36$, $p < 0.02$; August: $F=5.69$, $p < 0.01$), coefficients of determination were small. Canal section only accounted for 14% and 4% of the variation in female weevil weight on the two successive dates. This indicates a low probability of identical mean weights among canal sections. It also indicates that the observed differences are not very meaningful.

DISCUSSION

This site has been very important to the development of several concepts relating to the integrated control of waterhyacinth. Both upstream and middle sections were originally cleared at the same time (September 1980) with herbicide treatment. Both areas had nearly filled in again by March 1982 when mechanical control was attempted in the upstream area. By summer 1983 the upstream area was covered with large waterhyacinth plants whereas those in the middle had dropped out. A brief chronology of these two sections is presented in Figure 5. Better long-term control was obtained without harvesting.

A reservoir of weevils was present in a marshy region in the upstream section which the canal crossed near sample locations 4 and 5. Weevils had spread from there into the canal and the plants in that region were showing adverse effects. Also weevils had spread upstream from the middle section and were affecting plants at the bottom end of the upstream section. It appeared that the upstream plant population had begun to decline but lagged about a year behind the middle section. By summer 1984 those plants were devastated by weevil attack and had dropped out. All three sections were then clear. This suggests that waterhyacinth control could be enhanced if refugia for weevils could be deliberately established.

We were able to determine beforehand that the plant population was declining in the middle section. The degree of damage to the plants was extensive. Adult feeding had destroyed over 35% of the lamina area in some cases. This caused desiccation of the leaves which then curled in response. Petioles became thin and spindly. Submerged, water-logged plant material pulled the shoot apices below the surface. Holes opened in the mat which were caused by the submergence of entire patches of plants. Areas of newest growth dropped out first which reflected the lesser ability of smaller plants to survive sustained attack. The canopy became very open such that the water was visible among the plants. Plant stature became much more uniform as did leaf size and shape. Perhaps these characteristics could be used in integrated control schemes to estimate degree of stress caused by biological control agents and to judge when and if a decline might be expected. If it is determined that the need for control is more immediate than could reasonably be expected from biological control then alternative control measures would be applied. Otherwise, the more expensive chemical or mechanical methods could be employed at higher priority target areas.

Harvesting simultaneously reduces the numbers of plants and weevils. When this is done at the peak of the growing season the plants come back rapidly but the weevils do not. Plants then attain large size before weevils begin to noticeably affect them. Conversely where plants are sprayed out near the end of the growing season, the timing enables insect and plant populations to recover simultaneously. The insects then prevent plants from becoming excessively large and are therefore effective more quickly. This suggests that chemical or mechanical control could be more effective if done in fall or early winter rather than spring. Also, a small amount of continual management is better than sporadic, large-scale attempts. Vigilance after harvesting and spot treatments with herbicide would avoid dramatic oscillations in plant abundance and be less disruptive to populations of biological control agents.

After control operations are implemented, the plant populations will undergo a recovery cycle as they recolonize, then increase in size. A later colonization by insects will reduce plant size, then decrease coverage. This cycle was nearly complete in the middle section of Canal-M and required a total of approximately 3 years. However, the decline phase only required approximately 18 months. The canal section which was nearly full in March 1982 was nearly empty by September 1983. Because of the barricades the reduction could not have been caused by the plants floating downstream.

It may be noted that the recovery to decline cycle was shorter in the upstream area, having taken place over a period of only 2 years. The major factor responsible for this was the shortened recovery phase. Recovery was more rapid for two reasons. First, harvesting was done at the onset of the peak growth period. Second, a fringe of plants along the banks remained after harvesting and this provided a large source of re-infestation. The decline phases were of similar duration in both sections.

Data from this site further show the potential for biological control in flowing water systems with relatively high nutrient loads. Although chemical analyses were not done, nutrient supplies were sufficient to support extremely rapid, luxuriant waterhyacinth growth. Further, the plants never showed chlorosis nor other signs of nutrient deficiencies and root to shoot proportions were normal. There was no evidence that distance from the source of nutrients affected the plants which would indicate sufficient supplies in all three sections. Hence, biocontrol was effective in a flowing system in which plants were not under obvious nutrient limitations. This is not easily observable because the plants usually drift away in flowing systems. On the other hand, perhaps retaining the plants within the barricaded area enhanced the biocontrol effects. Possibly mat fragmentation with small pieces drifting into open areas where a colonizing mode of growth may be sustained is an important adaptive characteristic enabling waterhyacinth to escape from or overcome the effects of herbivores.

Palatability and food quality of waterhyacinth tissue could deteriorate as a result of sustained herbivory. This could explain why waterhyacinth is rarely eradicated from sites. If so, growth rates of weevil larvae and size of adults



Figure 5. Photographs of the upstream (left) and the middle (right) sections of the Canal-M study area. These show the changes that took place within a period of ca. 18 months. The top pair of photographs shows the site in April 1982 about a month after the upstream area was harvested. Note the fringe of plants along the bank. By the following month this fringe had grown out and covered the entire canal section. The middle pair of photographs compares the two sections in July 1983, when data presented in this paper were taken. Note the extensive open water among the sinking plants in the middle area. The bottom photographs compares the two sections in Jan. 1984. The middle section was clear due to biological control. Insects were beginning to affect the upstream area and the impact was similar to that shown in the middle, right photo. Almost all plants in the upstream section were killed by weevils and had sunk by summer 1984.

would be expected to decrease. Adult weevils from the middle section would be expected to be smaller than from upstream if they remained on the same plants in which they developed. This hypothesis would be untestable if the weevils actively moved about but our data on flight muscle development do not indicate that they did. Weevils develop flight muscles rapidly and lose them equally rapidly (Buckingham, pers. comm.) so mixing among sections could have occurred. Since females eat far more leaf material than males (females eat ca. 10% of their body mass (dry) daily, males only 2% (unpublished data)), they would be expected to respond to poor quality food before males. If flight muscle development was a response to this, then females would be expected to disperse before males. This would nicely explain the paucity of females in the middle section and the over-abundance of females (at first) in the upstream section. Unfortunately, because of the low frequency of occurrence of wing muscles, our data are inconclusive on this. Nonetheless, weevils tended to be smaller in the middle and downstream sections and the possibility that this was due to deteriorating plant quality is intriguing.

Three biological control agents, i.e. *N. eichhorniae*, *N. bruchi*, and *Sameodes albiguttalis* (Warren) (Lepidoptera: Pyralidae) were active at this site (Center *et. al.* 1984). Effects of *S. albiguttalis* or *N. bruchi* were not apparent during this study. They were present earlier and probably slowed the build up of the plant population. If the site had not been studied over a relatively long period of time, one would assume that *N. eichhorniae* was the only biocontrol agent of importance. We are certain that biotic agents caused the plant decline but it is difficult to prove. Insect data were variable and differences among sections were not significant. Some of the differences in weevil damage were significant but others were not. Correlations were not as apparent as might have been assumed. The impact of the weevils at a given point in time is a function of the past history of the site (i.e. the phase of recovery or decline, time since last harvest or herbicide treatment, etc.) and plants size (equal weevil population has greater impact on smaller plants), as well as size, nature, and extent of the insect population. Relatively equal amounts of feeding resulted in more severe damage where the plants were small. Plants were small because chronic effects of insect damage over substantial periods of time made them that way. Conversely, plants upstream were large due to a temporary release from herbivore pressure, even though at the time of sampling weevil densities were comparable to the heavily damaged areas.

A common misconception about biological control is the time required for effective control. It is commonly assumed that as many as ten years are required. This applies to the time interval from the very first releases of insects to the onset of widespread control. Within individual sites the time frame is compressed and effective biocontrol can take place relatively rapidly and persist for long periods. For example, in Australia Wright (1979) showed collapse of a waterhyacinth population at Crescent Lagoon near Rockhampton beginning within two years after liberation of *N. eichhorniae* at that site. Goyer and Stark (1981, 1984) showed significant control by *N. eichhorniae* within 14

months at a site in Assumption Parrish, Louisiana. DeLoach and Cordo (1983) released *N. bruchi* at Dique Los Sauces in west-central Argentina in March 1974. They were able to show 67% control by Feb. 1978 and 90-95% control by Jan. 1980, 6 years after initial releases. Cofrancesco (1980) released *N. bruchi* in Texas at Wallisville reservoir in May 1980 and noticed a 90% reduction in the waterhyacinth infestation within 3 years. While acute conditions frequently exist where the need for immediate control supercedes all other considerations, it is more efficient and more effective over the long term to use integrated management approaches which minimize interference with biocontrol. Management techniques could certainly be developed or modified to minimize this interference but, unfortunately, very little research has been conducted along this line.

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