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Aquatic Plant Control Research Program

Influence of *Pistia stratiotes* Plant Quality on the Growth and Development of the Biological Control Agent *Spodoptera pectinicornis*

by G. S. Wheeler, T. D. Center, T. K. Van,
Agriculture Research and Education Service

Prepared for Headquarters, U.S. Army Corps of Engineers

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U.S. Department of Agriculture
Agriculture Research and Education Service
Aquatic Plant Management Laboratory
3205 College Avenue
Fort Lauderdale, FL 33314

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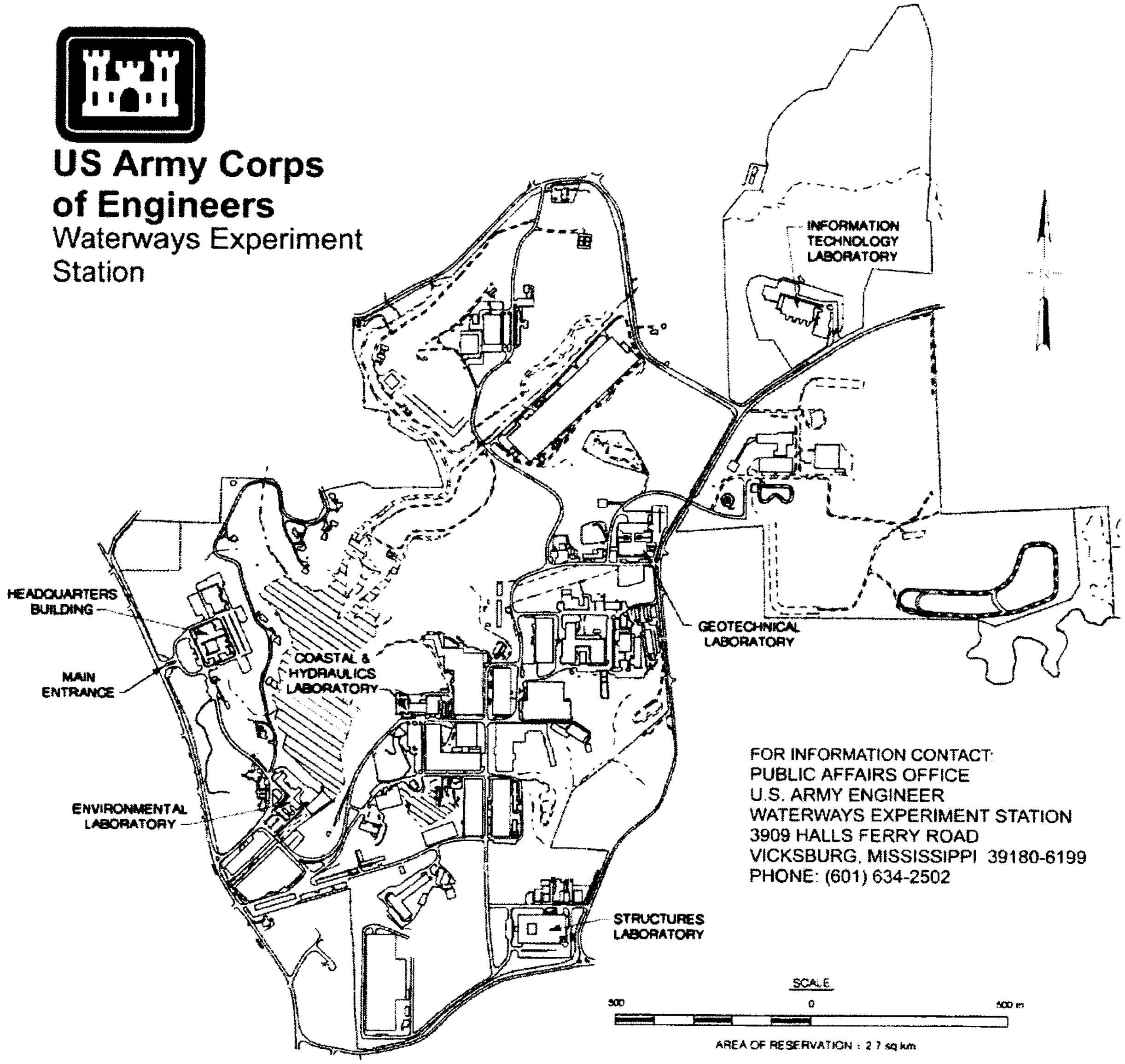

FOR INFORMATION CONTACT:
PUBLIC AFFAIRS OFFICE
U.S. ARMY ENGINEER
WATERWAYS EXPERIMENT STATION
3909 HALLS FERRY ROAD
VICKSBURG, MISSISSIPPI 39180-6199
PHONE: (601) 634-2502

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Contents

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32406. The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Center for Aquatic Plant Research and Technology (CAPRT), Dr. John W. Barko, Director. Mr. Robert C. Gunkel, Jr., was Assistant Director for the CAPRT. Program Monitors during this study were Mr. Timothy Toplisek and Ms. Cheryl Smith, HQUSACE.

This report was prepared by Drs. G. S. Wheeler, T. D. Center, and T. K. Van, United States Department of Agriculture - Agriculture Research Service (USDA-ARS), Aquatic Plant Control Research Center, Fort Lauderdale, Florida.

This investigation was performed under the supervision of Dr. Alfred F. Cofrancesco, Jr., Leader, Biomanagement Team, APCRP, EL; Dr. Edwin Theriot, Chief, Aquatic Ecology Branch, EL; Dr. Conrad Kirby, Chief, Ecological Research Division, EL; and Dr. John Harrison, Director, EL.

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1 Introduction

Biological control of the floating aquatic weed *Pistia stratiotes* have been conducted in Florida for a little over a decade. These activities have been successful in the release and establishment of a leaf-feeding weevil, *Neohydronomous affinis* from South America (Dray et al. 1990). Presently, the weevil is widely distributed throughout the state and in some locations has had a dramatic impact on *P. stratiotes* populations. However, the weed continues to be a problem, and therefore additional biological control agents are needed to augment the control exerted by the weevil. The noctuid *Spodoptera pectinicornis* is a very effective control agent of *P. stratiotes* in Thailand. Following extensive host testing in quarantine, this species has been cleared for release in the United States (Habeck and Thompson 1994). Despite releases in numerous sites, this species may be only sporadically established, and its general status in the remaining sites is unknown.

Knowledge of the factors that limit the performance of *S. pectinicornis* may improve success in establishing this species by providing the information needed to select the most conclusive release site(s) for rapid population growth. One of the most important factors that limits the growth and development of herbivorous insects is the nutritional quality of plants, especially percent nitrogen and leaf tissue toughness. This species oviposits on plants that contain the highest nitrogen levels, generally considered an adaptive response as the survival, growth, and development of herbivorous insects is dramatically improved on plants containing relatively high concentrations of nitrogen (Slansky and Feeny 1977, Mattson 1980). Tissue toughness also significantly affects herbivorous insects (Wheeler and Center 1996, 1997), especially relatively small species that feed and develop inside plant tissues (Hagen and Chabot 1986, Kimmerer and Potter 1987). Together these two factors are among the most important biotic determinants of establishment of insects on plants (Coley 1983, Wheeler and Center 1996, 1997).

The importance of these two factors in the biological control of weeds is becoming widely recognized following the work conducted on other aquatic weeds like hydrilla (Wheeler and Center 1996, 1997) and salvinia (Taylor 1984, 1988). As with hydrillia, *P. stratiotes* plant quality may range widely at different sites in both the levels of nitrogen and leaf toughness. Possibly some plant populations are better suited than others for herbivore establishment and population increases of these biological agents. Similarly, depending upon plant quality, some plant populations will be more impacted than others. One of the primary factors determining outbreak populations in insect pests and beneficial species is the level of foliar nitrogen available to herbivorous insects (Myers 1987, White 1993). Furthermore, these plant qualities may be manipulated to stimulate desirable outbreaks in laboratory mass rearing or in field nurseries of these beneficial insects. The goal of this study was to determine the range of nitrogen levels and leaf toughness at various sites in Florida and to determine their impact on the survival, growth, and development of the *P. stratiotes* biological control agent *S. pectinicornis*. Additionally, these results were compared with those generated from tank studies where larvae are fed leaves from *P. stratiotes* plants grown at known fertilizer levels.

2 Methods and Materials

Plant Collections

Pistia stratiotes plants were collected from eight sites in south Florida from November 1995 through January 1996. The sites included Tory Island, Palm Beach Co. (TI); Corkscrew Swamp Sanctuary, Collier Co. (CS); Pioneer Park, Palm Beach Co. (PP); Loxahatchee Everglades Nutrient Removal (ENR) site 1, Palm Beach Co. (E1); Loxahatchee ENR site 2, Palm Beach Co. (E2); and Christmas Park, Orange Co. (CM). The sites were typically located in small lakes or impoundments which were infested with *P. stratiotes*. Plants were returned to the laboratory where the first four leaves were removed and stored in plastic shoe boxes at 4 ºC until ready for feeding tests (about 2 days).

Two additional treatments were included to determine the effect of fertilizer alone on insect performance. These treatments consisted of *P. stratiotes* plants (4-5 leaves per plant) cultured in 64-ℓ pots (0.16 m^2 surface area) inside a 3- by 2-m cage at a relatively high fertilizer (5 ppm nitrogen with Peter's 15-5-15 and 2 ppm Fe, changed weekly) and low fertilizer rate (0.25 ppm nitrogen with Peter's 15-5-15 and 0.1 ppm Fe, changed weekly). Three plants and four plants were grown in each pot for the high and low fertilizer treatments, respectively, and each treatment was replicated four times. The plants were grown for four months until they completely covered the water surface of the pots in which they were grown. Leaves were cut from plants as needed and refrigerated as described above.

Plant Quality

The percent nitrogen, phosphorus, and potassium were determined on a dry weight basis. Leaf digests were conducted by a Kjeldahl method (Hach et al. 1987). Nitrogen content was determined by the ammonia-selective electrode method, phosphorus by the ascorbic acid method, and potassium by atomic absorption chromatography (Greenberg, Clesceri, and Eaton 1992). Standard reference material (tomato leaves; National Institute of Standards and Technology (NIST)) were analyzed as controls, and values were adjusted for percent recovery. Leaves were tested for toughness using a modified gram gauge (Wheeler and Center 1996, 1997) which estimated the pressure required to puncture leaf tissues. Leaf toughness was measured on leaves 1-4 (counting from the inner-most leaf outward) and each leaf was sampled at four leaf locations: tip, apical quarter, halfway point where the leaf begins to enlarge, and leaf base. Replicates consisted of 20 leaves of each position. Leaf percent dry weight (dw) was determined gravimetrically for leaves by weighing each when fresh and after drying (60 ºC for 48 hr).

Larval Survival, Growth, and Development

Neonates were transferred to individual leaves (leaf positions 1-4) and reared to pupation. The larvae were reared in plastic petri dishes lined with moistened filter paper and sealed with Parafilm. All rearing was conducted at 28 ºC 50-percent relative humidity (RH) and under a 14:10 hr photoperiod. Data were collected on larval survival, consumption, growth, and development. The final dw (dried at 60 ºC for 48 hr) of each pupa (±0.1 mg) and the time (days) required to reach pupation were recorded. Leaf consumption was estimated gravimetrically according to the following method. Each leaf was cut length-wise and each half was weighed fresh. One half served as the control leaf and was dried (60 ºC for 48 hr) directly to estimate the initial percent dw of the entire leaf. The other half was fed to a larva until approximately 60 percent of the leaf area had been consumed. The uneaten portion of this leaf half was then dried and weighed. With the estimate of initial dw and the final dw of the leaf material not consumed, dw consumption could be estimated by subtracting the final dw from the initial dw. Both growth and consumption rates were estimated on an average dw basis to derive the relative growth rates (RGR) and relative consumption rates (RCR), respectively (Gordon 1968). Insect frass was collected and dried to estimate the nutritional indices for digestion (approximate digestibility, AD) and efficiency of conversion of digested food (ECD) (Slansky and Scriber 1985). Finally, the nitrogen consumption, nitrogen assimilation (mg nitrogen consumed minus mg nitrogen excreted), and nitrogen utilization efficiency (NUE, mg nitrogen assimilated/ mg nitrogen consumed) were calculated as described by Slansky and Feeny (1977).

Data Analysis

All analyses were conducted with SAS/PC unless otherwise noted (SAS Institute, Inc. 1988). The results of leaf toughness were analyzed on each leaf (1-4) and at different locations on the leaves (e.g., tip, quarter, half, base). Means were compared with the Ryan's Q test (probability $P = 0.05$). The significance of plant quality factors on larval performance was determined by stepwise multiple regressions of percent nitrogen, percent phosphorus, percent potassium, leaf toughness, and percent dry weight of the leaves as the independent variables. Nitrogen consumption, assimilation, and efficiency of utilization were analyzed by linear regression.

3 Results

Plant Quality

Leaf nitrogen and phosphorus concentrations differed significantly among site and fertilizer treatments (Table 1). The E1, E2, and CM sites had higher nitrogen concentrations compared with the remaining sites. Phosphorous concentrations were significantly higher in the E1, CM, E2, and TI sites. Percent dry weight of the *P. stratiotes* leaves was highest in the CM and E2 sites and lowest in the E1 and CS sites. Potassium concentrations did not differ among the different sites. All nutrient concentrations were significantly higher in the high fertilizer treatment compared with the low fertilizer treatment. Percent dry weight was higher in the low fertilizer treatment than the high treatment.

Table 1
Mean ± SE Composition of Leaves of *Pistia* Plants That Were Either Field-Collected or Locally Grown and Fertilized[1]

Site/Tmt	% N	SE	% PO_4	SE	% K	SE	% dw	SE
Field Plants								
E1	2.9	0.1 a	0.45	0.03 a	5.1	0.2 ns	6.7	0.1 cd
CM	2.8	0.1 a	0.44	0.04 ab	5.1	0.1	8.9	0.3 a
E2	2.5	0.2 a	0.54	0.03 ab	3.9	0.3	8.6	0.2 a
PP	1.6	0.1 b	0.32	0.03 bc	5.2	0.4	7.9	0.2 bc
CS	1.5	0.1 b	0.26	0.02 c	4.8	0.5	6.3	0.1 d
TI	1.5	0.2 b	0.45	0.04 ab	4.6	0.4	7.3	0.2 b
Fertilized Plants								
High	2.6	0.1 a	0.70	0.01 a	5.4	0.2 a	4.9	0.2 a
Low	1.8	0.1 b	0.35	0.02 b	3.8	0.1 b	6.0	0.1 b

[1] Means within a column and plant group followed by the same letter are not significantly different ($P < 0.05$).

Leaf toughness differed significantly among the sites sampled, the positions on the leaf, and leaf positions on the plant. Leaf toughness was generally greatest in the leaf position half-way from the leaf tip (the leaf position where the leaf begins to enlarge; Figure 1a). The toughest leaves were collected at the CM site, where values ranged from 310 to 405 g/mm^2. The high fertilized plants had leaves significantly softer than those of the low treatment at all leaf positions (Figure 1b). Leaf toughness also differed according to leaf position on the plant, where, in general, the toughest leaves were located in the number four position and the softest leaves were located in positions two to three from the plant center (Figure 2). Leaf toughness was not determined for plants from the PP site.

Larval Survival, Growth, and Development

The number of molts required to pupate and the instar in which larval mortality occurred differed among the larvae fed field-collected and fertilized plants (Figures 3 and 4). Larval mortality occurred most frequently in the first instar, especially in larvae fed leaves from the CM, CS, E2, and the low fertilized plants. Larvae fed the field-collected plants pupated after either 6 or 7 instars (Figure 3), whereas those fed the high fertilized plants pupated after occasionally 5, but typically 6-7 instars (Figure 4). All or nearly all of the larvae fed leaves from the CM, CS, PP, and low fertilized plants pupated after 7 instars.

The results of the stepwise multiple regression analysis indicated that leaf toughness contributed significantly only to percent larval survival and relative growth rate (Figure 5). Neither percent phosphorus, percent potassium, nor dry weight significantly contributed to the variance of the performance parameters tested; therefore, these independent variables were dropped from the analysis. Tip leaf toughness was used instead of the toughness estimates from other leaf positions (e.g., quarter, half, or base) as it best predicted larval survival and RGR. Percent survival ranged from 72.5 to 13.3 percent and was greatest when the larvae were fed the softest leaves and decreased with the tougher leaves. Similarly, RGR values decreased by 50 percent when larvae were fed the tougher leaves.

Leaf nitrogen content contributed significantly to the larval development time, consumption, efficiency of conversion of digested food (ECD), relative consumption rate (RCR) and relative growth rate (Figure 6). Larvae fed the higher nitrogen leaves completed development in nearly half the time as larvae fed the low nitrogen plants. The development time ranged from 14.3 days on the high treatment to 26.6 days on the TI leaves. Consumption decreased by nearly 75 percent on the high nitrogen plants, ranging from 128.4 mg on the high treatment leaves compared with 516.0 mg on the TI leaves. The ECD values increased on the higher nitrogen plants, exceeding 20 percent on the high treatment leaves compared with 4.1 percent on the CS leaves. The RGR values decreased on the higher nitrogen leaves by more than 60 percent, ranging from 4.4 milligrams of weight gain divided by milligrams average weight multiplied by the number of days (mg/mg*d) on the CS leaves to 1.6 mg/mg*d on the high treatment leaves. The RGR values increased twofold on the higher nitrogen leaves, ranging from 0.09 on the PP and CM leaves to 0.18 on the high treatment leaves.

Despite the low nitrogen levels found in the leaves of several sites and the low treatment, the amount of nitrogen consumed and assimilated was stabilized by the larvae. Neither nitrogen consumption nor the nitrogen assimilation differed significantly when analyzed as a function of percent nitrogen of the leaves (Figure 7). However, the nitrogen utilization efficiency (NUE) increased significantly with increased nitrogen consumption rate, ranging from 65.6 percent when fed leaves from the low treatment to 84.7 percent when fed leaves from the CM site (Figure 8).

4 Discussion

A wide range in leaf toughness and percent nitrogen occurred in the *P. stratiotes* plants collected from various sites and produced from the fertilizer treatments. The *S. pectinicornis* larvae that fed on the tougher leaves had decreased survival and relative growth rates. The reduced numbers of larvae that survived these tougher leaves had reduced RGRs. Low nitrogen levels also significantly affected several performance parameters including increased development time and consumption and decreased ECDs and RGRs. The larvae responded to the low nitrogen levels in the leaves by exhibiting compensatory feeding resulting in more than doubled dry weight intake of food. This apparently compensatory response resulted in a stabilization in the amount of nitrogen consumed and assimilated by the larvae. This more than fourfold increase in consumption undoubtedly contributed to the increased survival and performance of the larvae fed the low nitrogen leaves. Despite this response to the low nitrogen leaves, the larvae required more than twice the number of days to complete development compared with those fed the high nitrogen leaves. This extended larval period increased their exposure to the many natural enemies (Damman 1987, Stamp and Bowers 1990) that are known to attack other lepidopterous herbivores feeding on *P. stratiotes* (Knopf and Habeck 1976).

A possible cost of this increased consumption was the increased processing of the ingested food. Greater toughness of plant tissue may be related to high concentrations of tissue lignin and fiber (Buendgen et al. 1990, Choong et al. 1992), constituents that decrease the digestibility of the ingested food (Martin 1988, Wheeler and Slansky 1991). Increased concentrations of these indigestible materials would result in decreased conversion efficiencies, e.g., ECD and NUE (Wheeler and Slansky 1991). As low nitrogen leaves are typically negatively correlated with leaf toughness (Wheeler and Center 1997), reduced conversion efficiencies are predicted on the low nitrogen, tougher leaves. The results of this study support this prediction as decreased ECD and NUE in the larvae fed the low nitrogen leaves were found.

The selection of areas or conditions in which the softer leaves are produced may have great importance in the establishment of this species in North America. The initial release site (September 1995) was located at Christmas Park where, as it turned out, the study found the toughest leaves and the lowest percent survival of larvae. Although the nitrogen content of these leaves was among the highest found, the surviving larvae fed these leaves had increased development times and RGR values.

Therefore, in addition to less than 20 percent of the larvae surviving on these plants, the survivors had reduced performance that would seriously threaten their establishment and impact on the target weed. On the other hand, the larvae fed plants produced in the experimental tanks, fertilized with relatively high rates produced the softest leaves, and the larvae that ate these leaves had among the highest survival, lowest developmental periods and greatest ECD and RGR. Coincident with this was a significant decrease in both the amount of food consumed and the rate of food consumption. Possibly, the larvae acquired sufficient nutrients to complete development despite the lower consumption rates because of the increased nutritional value of the food. The larvae fed the softer, more nutritious plants would be expected to have the greatest biotic potential as they require less time between generations, would have the least duration exposed to natural enemies, and, based upon their greater size, produce greater numbers of progeny (Wheeler, Van, and Center 1998).

Finally, a rapid field evaluation technique is being devised to predict plant quality. Field observations suggest that plant quality could be related to the intensity of the green color of the leaves. Therefore, the authors of this study are relating the leaf color using Munsell color charts to leaf toughness and nitrogen content. These results should be useful in the field for quickly predicting the suitability of *P. stratiotes* populations for *S. pectinicornis* growth and development.

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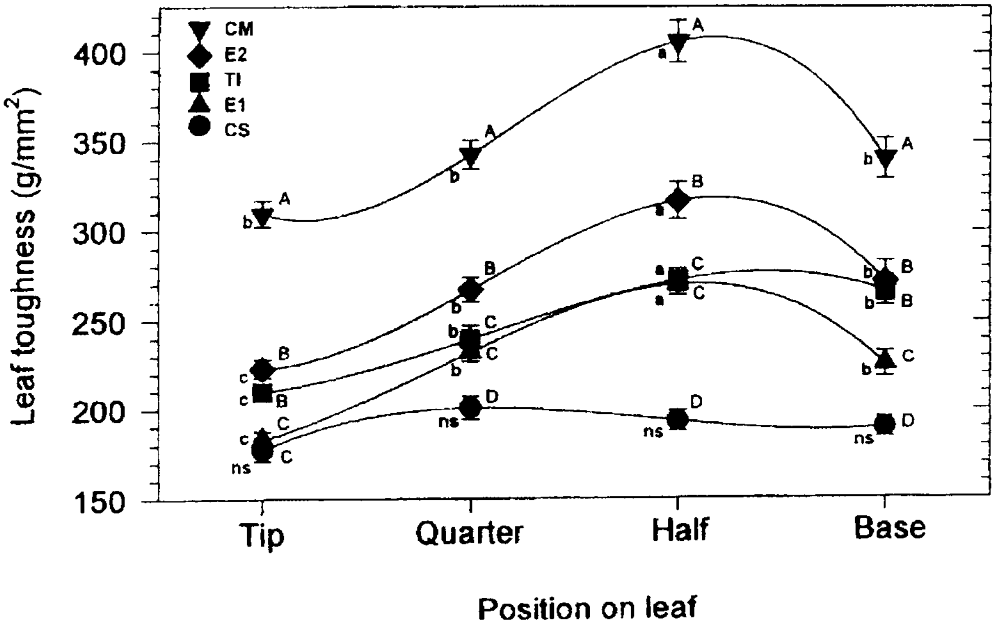
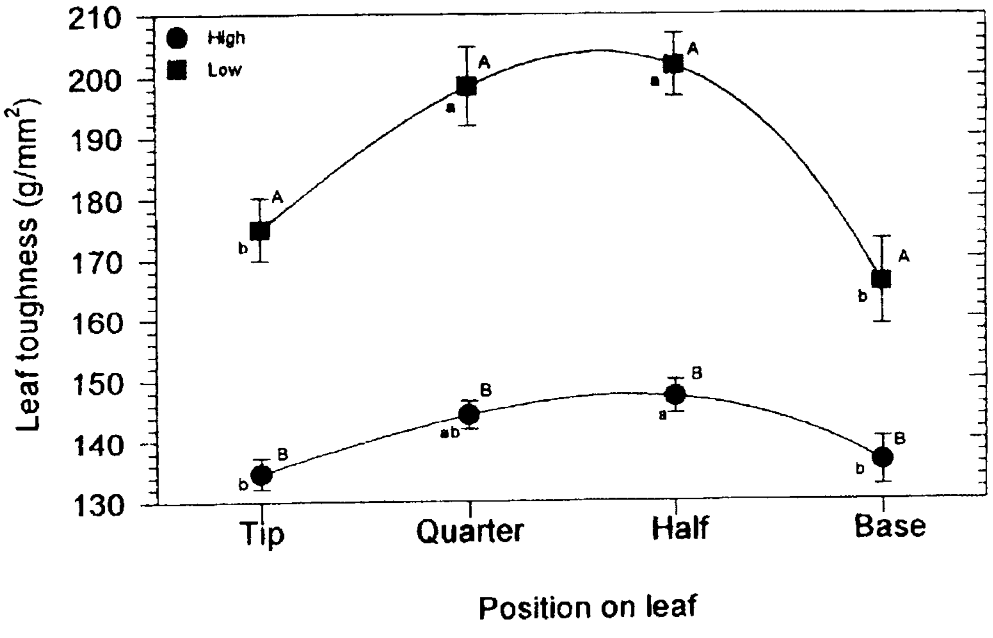
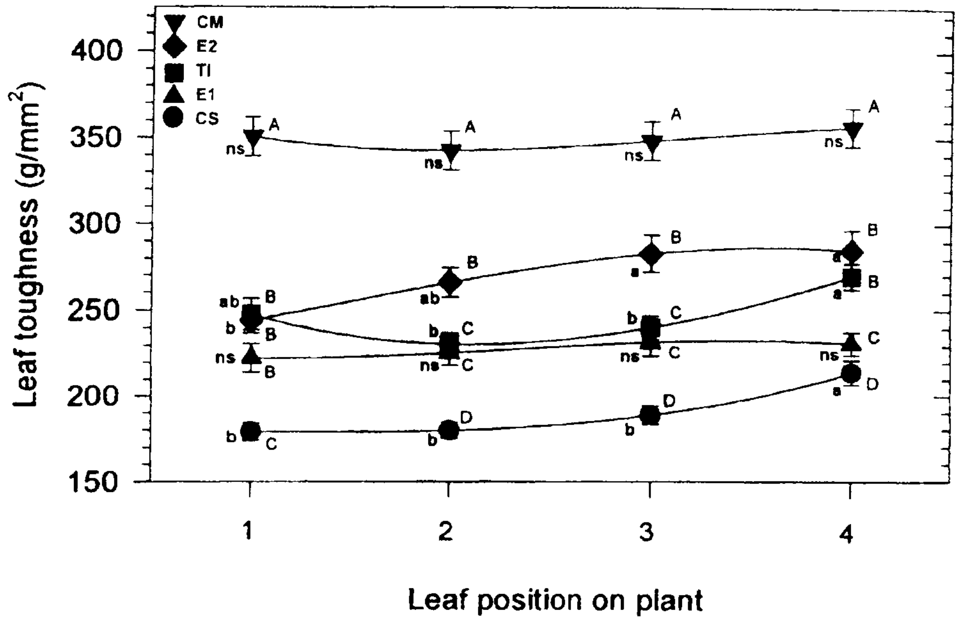


a. Field samples



b. Grown and fertilized locally samples

Figure 1. Mean (± SEM) toughness of *P. stratiotes* leaves as a function of different positions on the leaf. Plants were field-collected (a) or grown and fertilized locally (b). Notice the different y-axis scales. Means within the same graph with different uppercase letters differ significantly among sites (a) or fertilizer treatments (b). Means within the same graph with the different lowercase letters differ significantly among leaf positions



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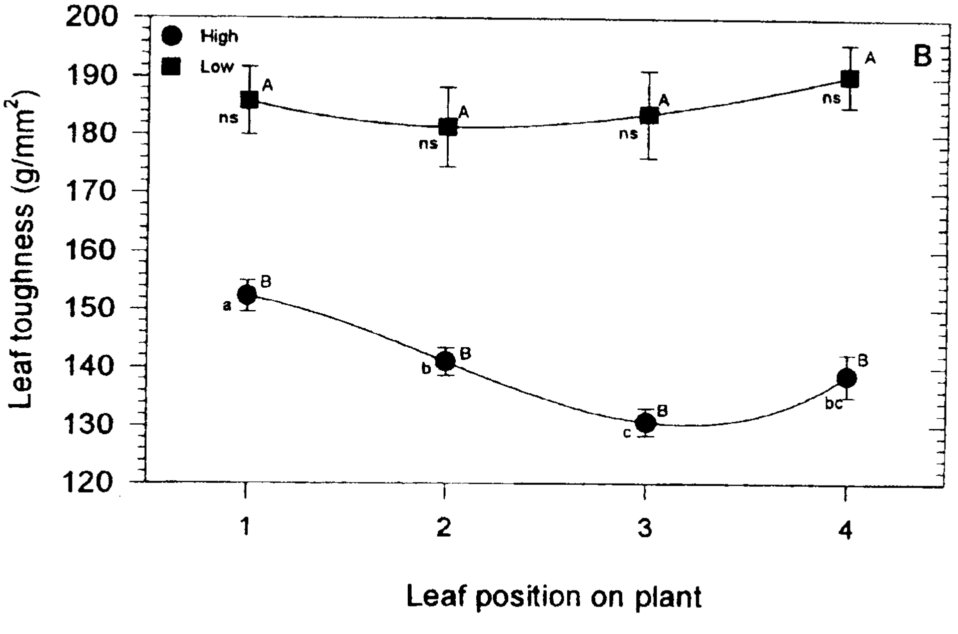

b. Grown and fertilized locally samples

Figure 2. Mean (± SEM) toughness of *P. stratiotes* leaves as a function of different positions on the plant. Plants were field-collected (a) or grown and fertilized locally (b). Notice the different y-axis scales. The number 1 position leaves are the inner-most, youngest leaves. Means within the same graph with different uppercase letters differ significantly among sites (a) or fertilizer treatments (b). Means within the same graph with the different lowercase letters differ significantly among leaf positions

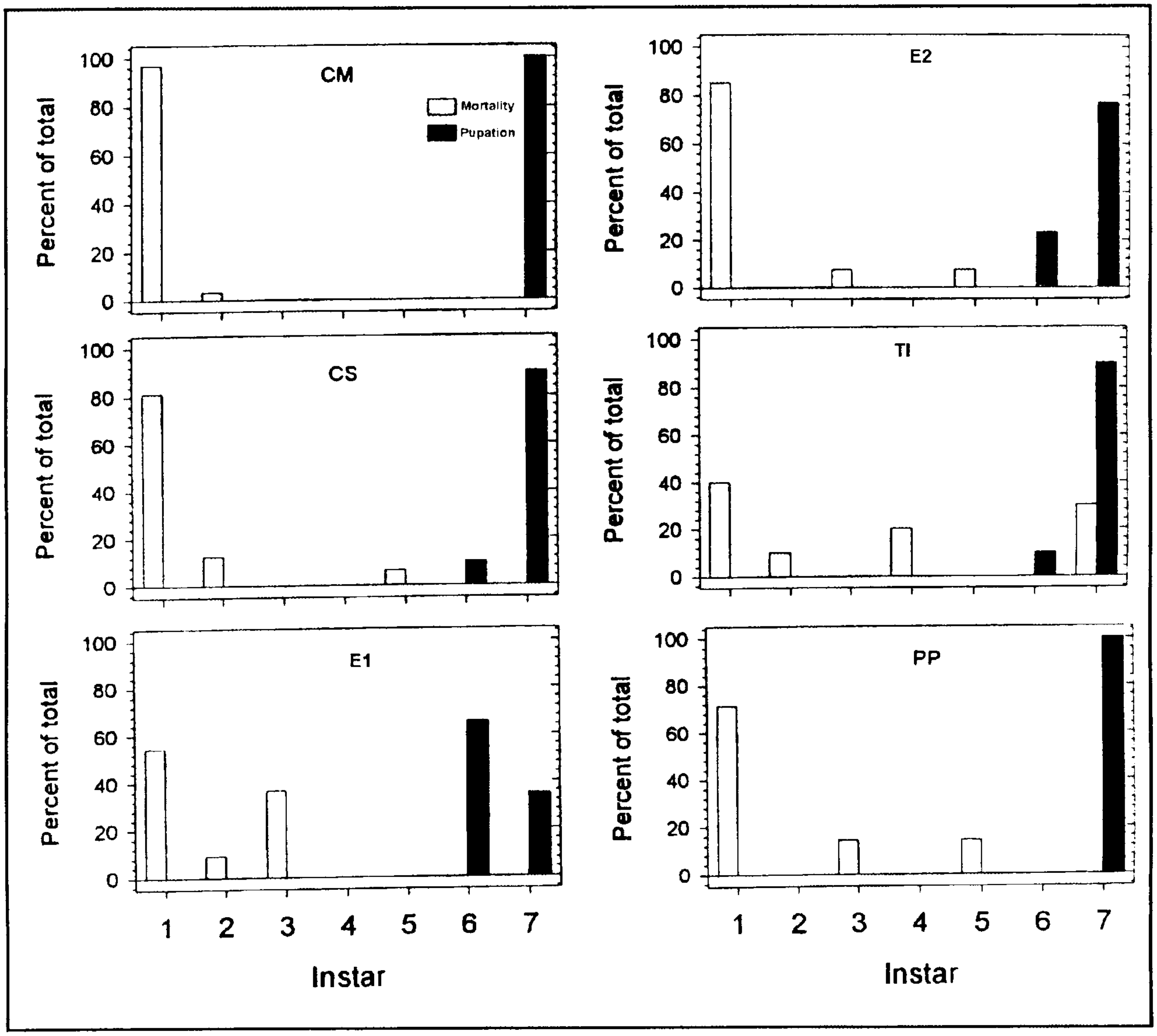

Figure 3. Larvae fed field-collected *P. stratiotes* plants. Percent of the total number *S. pectinicornis* larvae that died or pupated in different instars

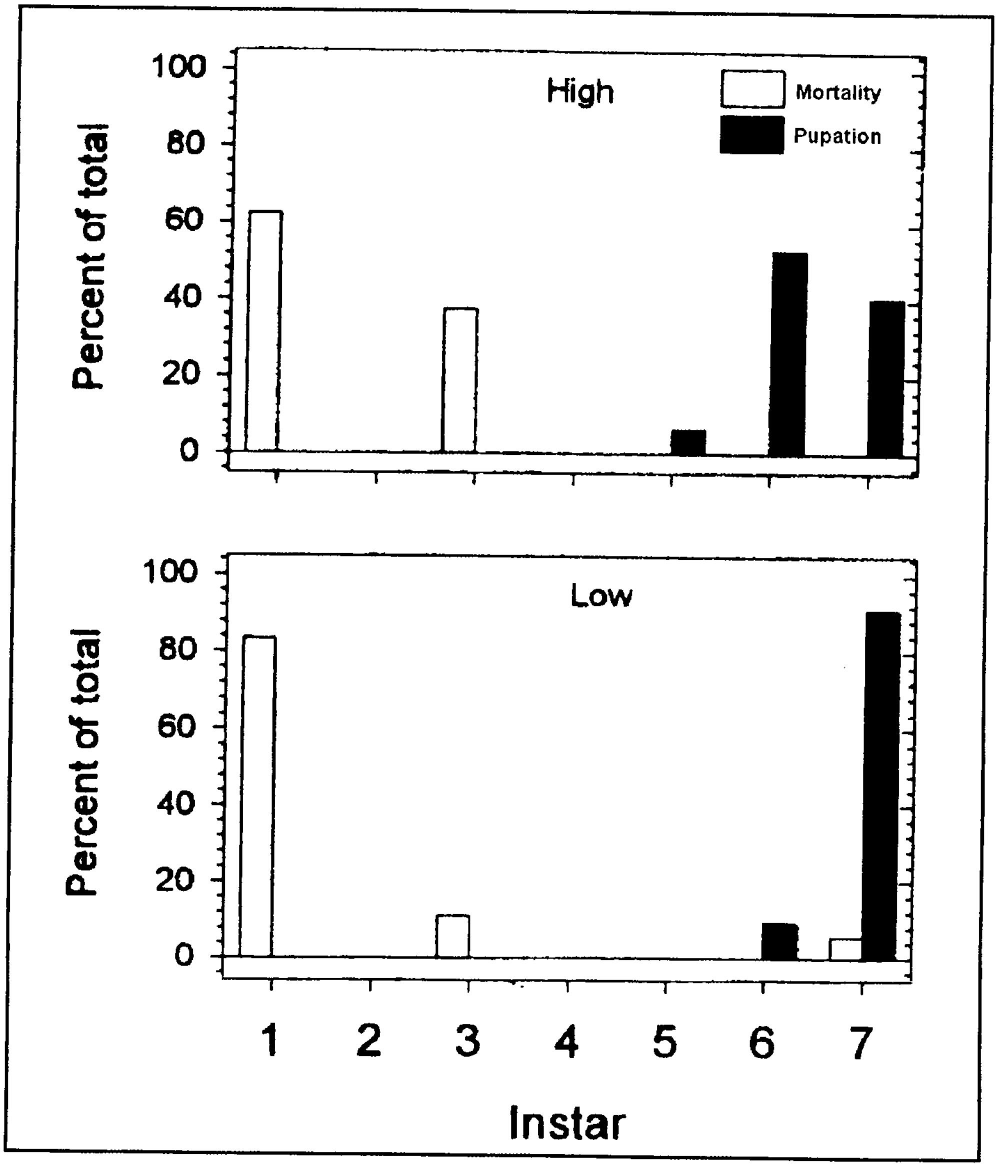

Figure 4. Larvae fed *P. stratiotes* plants grown and fertilized locally. Percent of the total number *S. pectinicornis* larvae that died or pupated in different instars

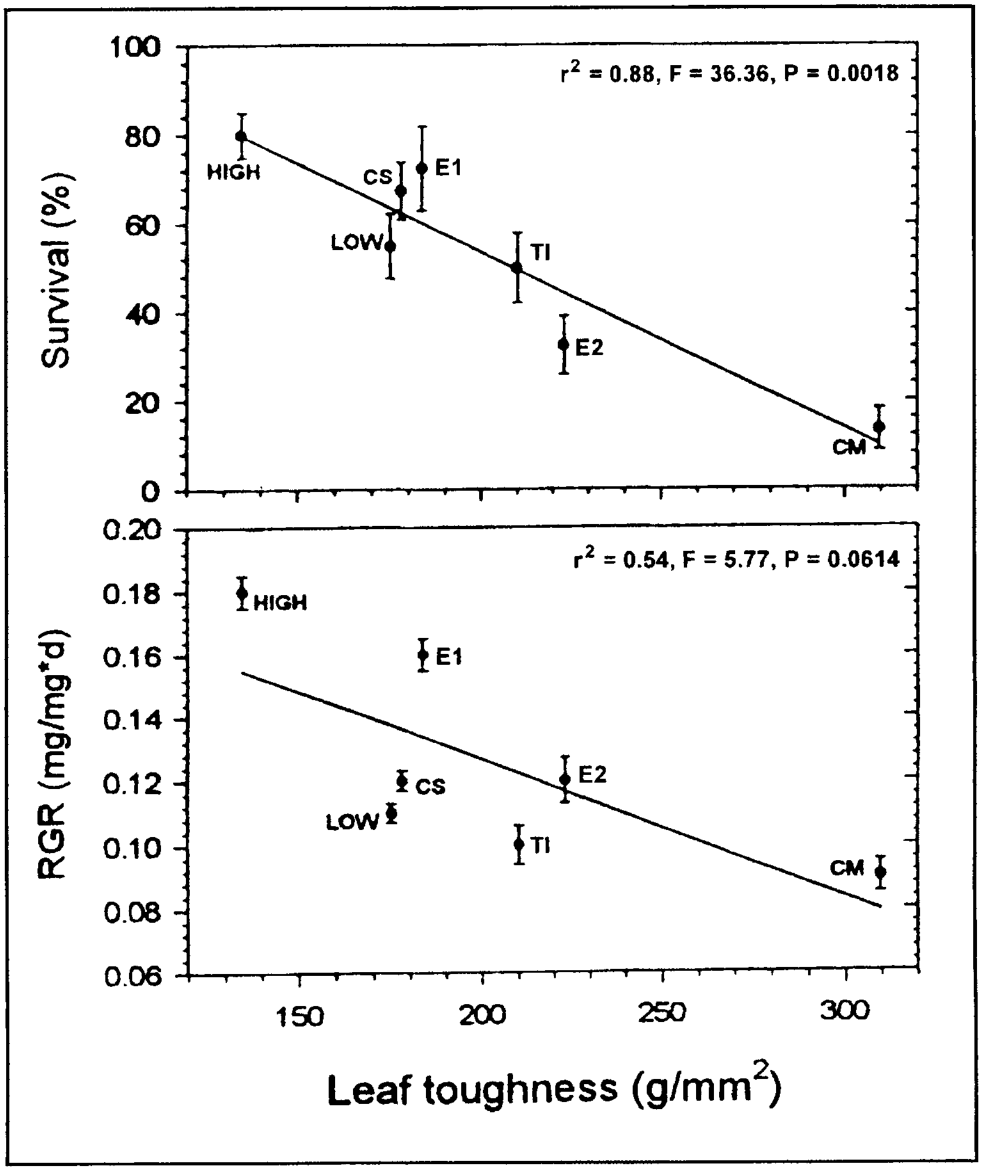

Figure 5. Mean (± SEM) *S. pectinicornis* percent survival and relative growth rate (RGR) of larvae fed *P. stratiotes* leaves collected from different sites having a range of leaf toughnesses. Regression r^2 values represent the partial r^2 from stepwise multiple regression analysis

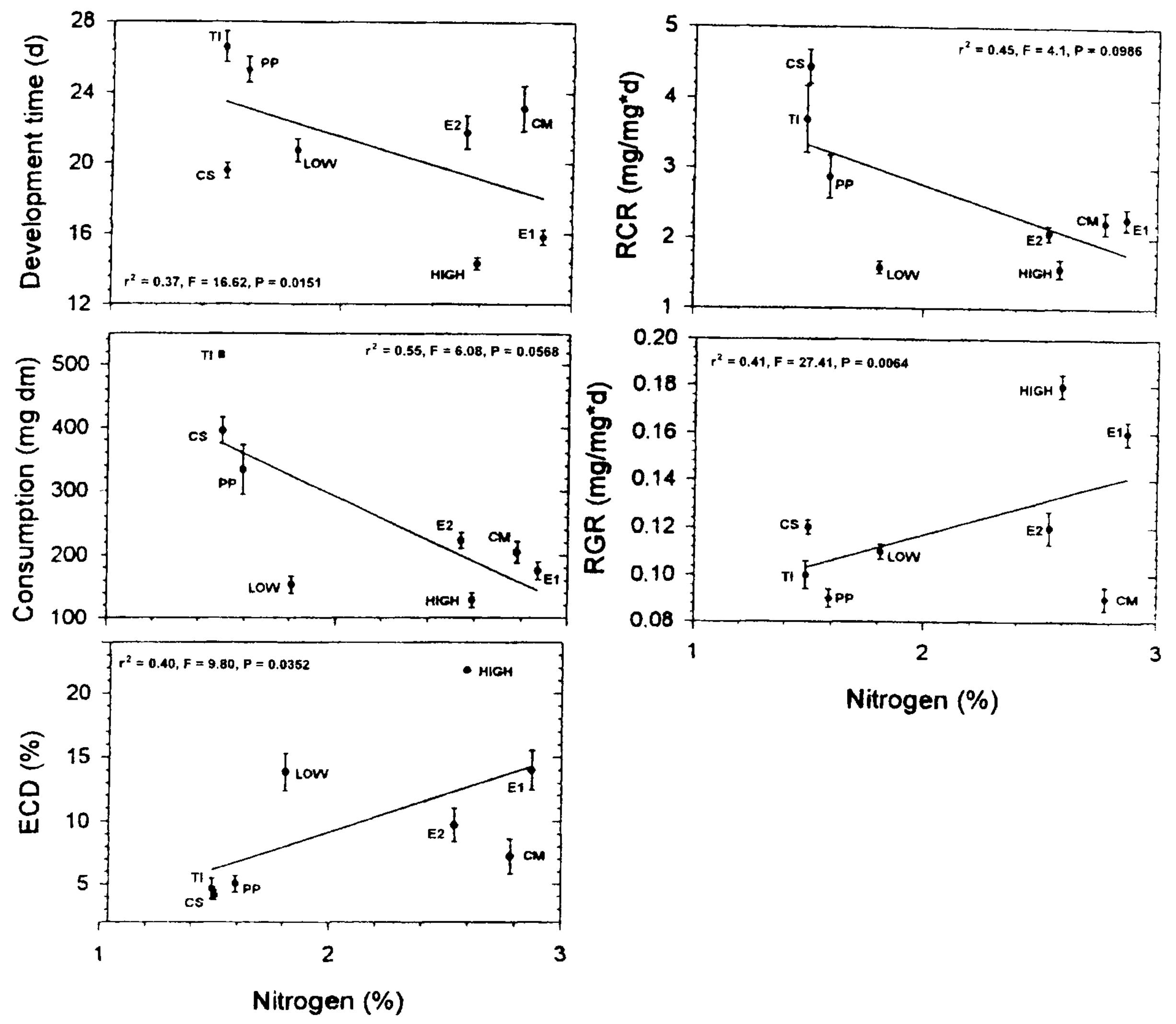

Figure 6. Mean (± SEM) *S. pectinicornis* larval performance parameters as a function of percent nitrogen when fed leaves from field-collected or fertilized *P. stratiotes* plants. The performance parameters included development time (d), consumption (mg dry mass (dm)), efficiency of conversion of digested food (ECD), relative consumption rate (RCR), and relative growth rate (RGR). Regression r^2 values represent the partial r^2 from stepwise multiple regression analysis

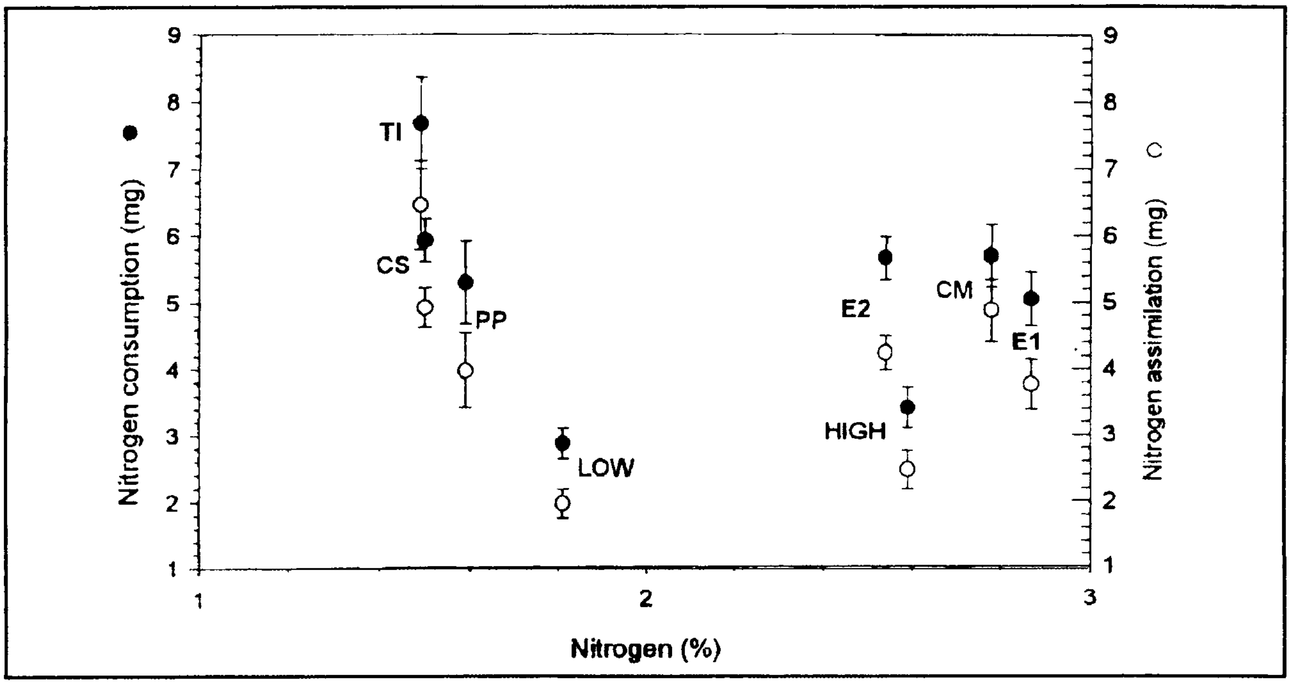

Figure 7. Linear regressions between larval nitrogen consumption, nitrogen assimilation, and leaf percent nitrogen when *S. pectinicornis* larvae were fed leaves from field-collected or fertilized *P. stratiotes* plants. The results of the regression analysis indicated that neither nitrogen consumption nor nitrogen assimilation changed significantly with the nitrogen content of the leaves

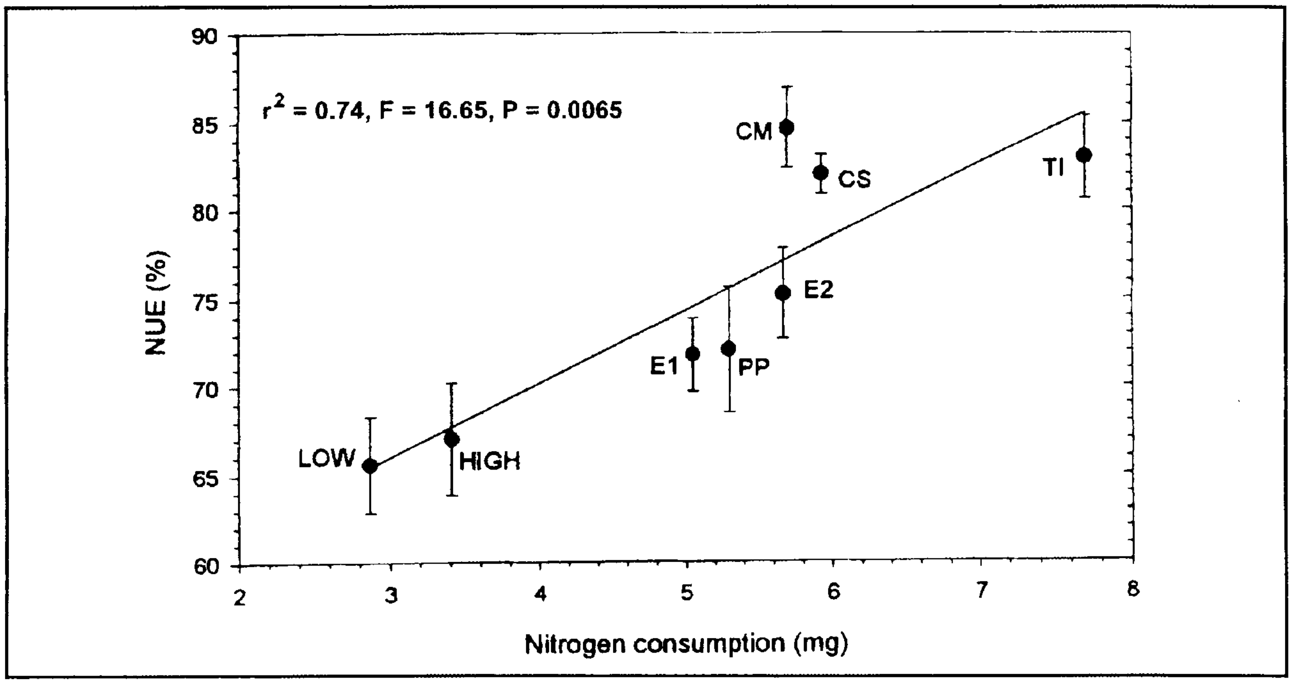

Figure 8. Linear regression results between nitrogen utilization efficiency (NUE) and nitrogen consumption when *S. pectinicornis* larvae were fed leaves from field-collected or fertilized *P. stratiotes* plants. The results indicated that the larvae with the greatest nitrogen consumption used the assimilated nitrogen most efficiently

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G. S. Wheeler, T. D. Center, T. K. Van

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Performance of the specialist herbivore *Spodoptera pectinicornis* (Hampson) (Lepidoptera: Noctuidae) was studied when fed the floating aquatic plant waterlettuce *Pistia stratiotes* L. (Araceae). Plants were either collected from six populations in south Florida or from plants grown with low or high fertilizer levels. Consumption of leaves with increasing toughness resulted in increased larval mortality to more than 80 percent; most mortality occurred during the first instar. Larvae fed low nitrogen leaves required up to twice the time and typically an extra instar to complete development. Larvae compensated for low nitrogen leaves by increasing fresh weight consumption threefold. Despite these dietary challenges, the biomass gained by the larvae was similar regardless of the quality of leaves consumed. These results are useful in understanding the adaptations and limitations of specialist herbivores to low nutrient foods. Additionally, they assisted in the selection of suitable release sites for this weed biological control agent. Finally, they improved mass rearing techniques for augmentative releases of this biological control species.

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