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THE GROWTH AND SURVIVAL OF EARLY INSTARS OF *BELLURA OBLIQUA* (LEPIDOPTERA: NOCTUIDAE) ON *TYPHA LATIFOLIA* AND *TYPHA ANGUSTIFOLIA*

J. M. Penko¹ and D. C. Pratt^{2,3}

ABSTRACT

Larvae of the noctuid moth *Bellura obliqua* are frequently encountered on *Typha latifolia*, but less commonly on *Typha angustifolia*. Experiments were conducted to compare the growth and survivorship of early *B. obliqua* instars on the two species of cattail. In short-term growth chamber experiments there were no significant differences in the survivorship, relative growth rate (RGR), relative consumption rate (RCR), or the efficiency of conversion of ingested food (ECI) between first-instar larvae reared on leaves of the two species. Third-instar larvae fed stems, however, had a greater RGR and higher ECI when reared on *T. latifolia*. Differences in growth are apparently not related to differences in hostplant nitrogen or acid-detergent fiber content. In a long term greenhouse experiment, using transplanted cattails, larvae reared on *T. latifolia* grew somewhat larger and had a significantly higher survival rate than those reared on *T. angustifolia*. Host plant structure is postulated to influence larval survivorship. *Typha* is under consideration for use as a bio-energy crop and planting *T. angustifolia* may help to reduce infestations in cultivated stands.

Larvae of the noctuid moth *Bellura obliqua* Walker feed primarily on cattails (*Typha* spp.). In Minnesota, egg masses and larvae are encountered more frequently on *T. latifolia* than on *T. angustifolia* (Penko 1985). Elsewhere, *B. obliqua* has been reported to utilize *T. latifolia* or *Typha*, but not specifically *T. angustifolia* (e.g., Claassen 1921, Kellicott 1883).

The apparent ovipositional preference for *T. latifolia* suggests that this species may be a more suitable host plant for *B. obliqua* larvae. To test this hypothesis, studies were conducted to compare the growth and survivorship of early *B. obliqua* instars on leaves and stems of *T. angustifolia* and *T. latifolia*. The results may be of some agronomic significance because *Typha*, a highly productive aquatic macrophyte, is under consideration as a possible bio-energy crop (Pratt et al. 1984). Small cultivated stands of *T. latifolia* and *T. glauca* can be heavily infested by *B. obliqua* (Andrews et al. 1981, Pratt et al. 1982).

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MATERIALS AND METHODS

Typha spp. are perennial aquatic macrophytes with tall (ca. 1.5–3 m) vegetative shoots composed entirely of erect, linear leaves. In mature stands new aerial shoots are produced each spring, for the most part, from rhizomes (underground stems) produced during the previous growing season (see Linde et al. 1976). Leaves are produced sequentially from a centrally located meristematic region situated at the base of a shoot (Kaul 1974, Yeo 1964). For several decimeters above the shoot base, leaves of a mature shoot are in close contact and form a well defined stalk or "stem."

Both *T. latifolia* and *T. angustifolia* are widely distributed in the eastern United States (Smith 1967) and are found in habitats ranging from roadside ditches to extensive marshes. In Minnesota, *T. glauca* (or *T. × glauca*), a hybrid between *T. angustifolia* and *T. latifolia* (Smith 1967), is also common. Vegetative shoots of *T. latifolia* have broader and more numerous leaves, and a greater basal diameter than those of *T. angustifolia*.

The life history of *Bellura obliqua* has been studied in the northern United States by Claassen (1921) and Penko (1985). Eggs are deposited in masses on cattail leaves in June and July. First-instar larvae are leaf miners. Second-instar larvae feed on leaf sheaths or stems. Later instars are typically solitary stem borers which kill the central leaves of infested plants. Mature larvae overwinter in cattail stalks or upland locations and pupate in the spring.

Leaves, stems, and young shoots used in these experiments were collected from a natural stand at the Carlos Avery Wildlife Management Area (Anoka County, Minnesota). Leaves and stems were transported on ice and stored at 4°C until use (always within 12 h of collection).

Egg masses used in these experiments were collected from roadside populations of *T. latifolia* near Aitkin and Zim, Minnesota on 14 and 26 June 1982. Third-instar larvae used in experiments 2 and 3 were reared in *Typha glauca* leaves and stems collected from stands near the St. Paul campus of the University of Minnesota.

Experimental Design and Methodology

Experiment Number 1. This experiment was designed to compare the growth of first-instar larvae on upper leaves of *T. angustifolia* vs. those of *T. latifolia*. The relative growth rate (RGR), relative consumption rate (RCR), and the efficiency of conversion of ingested food (ECI) were determined on a dry weight basis using standard gravimetric techniques (Scribner & Slansky 1981, Waldbauer 1968). Mean larval biomass was calculated as the average of initial and final weights (Waldbauer 1962).

Leaf material was obtained from 10 to 26 cm below the tip of mature leaves. The central 8-cm section of this sample was weighed and placed in a 9.0-cm by 1.5-cm plastic petri dish lined with moistened filter paper. The remaining leaf material (two 4-cm sections) was weighed and dried at 60°C for two days (as was all material) to determine a dry/wet-weight ratio. The initial dry weight of the 8-cm section was calculated from this ratio and its initial wet weight. Leaves were sampled in this manner primarily to account for possible gradients in leaf moisture or leaf nitrogen content.

Six 4–10-h-old larvae were weighed and placed onto each 8-cm leaf section. Additional larvae were weighed, killed by freezing (as were all larvae), and dried so that an initial dry- to wet-weight ratio could be estimated. The mean initial dry weight (fresh weight × dry/wet weight ratio) of a larva was 0.12 mg. Larvae were allowed to feed for 24 h under controlled conditions (15: 9 h photoperiod; 25°C day, 19°C night; approximately 70% R.H.). Larvae were recovered from leaves, killed, and dried. Larval weight gain was calculated as the final minus the estimated initial weight. Leaves were carefully washed of frass, dried, and weighed. Consumption was calculated as the estimated initial leaf weight minus the final weight. The experiment was replicated 25 times and conducted over a three-day period in five blocks as larvae became available for use. To account for

any changes in leaf weight during the experiment not related to consumption by larvae, controls were run in which no larvae were placed on leaves.

Experiment Number 2. This experiment was conducted to compare RGR, RCR, and ECI of third-instar larvae on stems of *T. angustifolia* vs. those of *T. latifolia*. Stem material (without older dried leaves) was obtained from 12 to 24 cm above the shoot base. The central 6-cm section was weighed and placed in a 9-cm by 2.5-cm plastic petri dish lined with moistened filter paper. The remaining stem material (two 3-cm sections) were weighed and dried for determination of a dry- to wet-weight ratio. The initial dry weight of the 6-cm section was estimated using this ratio and its initial wet weight.

One third-instar larvae was weighed and placed onto each 6-cm stem section. Additional larvae were weighed, killed, and dried for determination of an initial dry- to wet-weight ratio. The estimated initial mean dry weight of a larva was 2.38 mg. Larvae were allowed to feed for 36 h under controlled conditions (see above). At the end of the experiment larvae were recovered from stems, killed, dried, and weighed. Stems were washed of frass, dried, and weighed. Larval weight gain and consumption were calculated as above. Controls (as above) were run concurrently. The experiment was replicated 32 times.

Experiment Number 3. This experiment was conducted to compare the long-term survival of larvae on live shoots of *T. latifolia* and *T. angustifolia*. Young shoots were collected in mid-May and planted in 19 1-l plastic pails. In early July, 30 shoots of each species were selected, and randomly arranged along a single greenhouse bench. *T. latifolia* shoots had a mean height of 133 cm (\pm SE 5) and a basal diameter (as measured by a micrometer) of 4.4 cm (\pm SE 0.2). *T. angustifolia* shoots had a mean height of 168 cm (\pm SE 6) and a diameter of 2.8 cm (\pm SE 0.1). One third instar larva was placed on the inner surface of an outer leaf of each plant. Larvae were allowed to feed for one month. At the end of the experiment, plants were inspected for insect damage and for larvae. Larvae were killed, dried, and weighed.

Upper Leaf and Stem Composition. Undamaged stem and upper leaf sections used in experiments 1 and 2 were analysed for nitrogen, phenolic, and water content. Tissues analysed for nitrogen and phenolics were ground in a Willey mill (1 mm mesh). Nitrogen content was determined for 10 stem and 10 upper-leaf samples using a micro Kjeldahl analysis. Phenolic content was determined for 10 stem samples and four composite samples of leaf sections using the folin-dennis determination (Swain & Hillis 1959). Phenolics were extracted with 50% methanol for 6 h at room temperature. The tissues were oven dried and had been stored at room temperature for approximately eight months prior to analysis, so it is necessary to view concentrations in relative, rather than absolute terms. Acid-detergent fiber content of stem ($n = 3$) tissue was also determined (Association of Official Analytical Chemists 1980).

Statistical Analysis. Data were analysed by ANOVA (Weisberg 1982) or by the non-parametric Mann-Whitney U test (normality approximation; Zar 1974).

RESULTS

Experiment Number 1. All larvae were recovered and were alive at the end of the experiment. There were no significant differences in the RGR, RCR, or ECI between larvae reared on leaves of *T. angustifolia* and *T. latifolia* (Table 1).

Experiment Number 2. Again, all larvae were recovered and were alive at the end of the experiment. Third instar larvae reared on stems of *T. latifolia* grew significantly larger than those reared on stems of *T. angustifolia* (Table 1). Differences in growth were probably related to differences in ECI between larvae reared on the two species ($P = 0.07$), because RCR was not significantly different.

Experiment Number 3. While there was no significant difference in the number of larvae that became established on the two species, a greater proportion of those established on *T. latifolia* were recovered at the end of the experiment (Table 2). Most missing larvae had probably migrated in search of new host plants. Some were collected on offshoots

Table 1. RGR, RCR, and ECI of *Bellura obliqua* larvae reared on leaves or stems of *T. angustifolia* and *T. latifolia*.

	Species		F or Z ^a	P
	<i>T. angustifolia</i>	<i>T. latifolia</i>		
RGR				
1st instar ^b	0.71 ± 0.04 ^c	0.74 ± 0.04	0.34	n.s.
3rd instar	0.30 ± 0.03	0.50 ± 0.03	23.04	<0.001
RCR				
1st instar	6.48 ± 0.44	6.41 ± 0.53	0.14 ^a	n.s.
3rd instar	6.38 ± 2.09	5.08 ± 1.54	0.21 ^a	n.s.
ECI				
1st instar ^d	12.35 ± 1.10	13.45 ± 1.29	0.45	n.s.
3rd instar	5.51 ± 1.17	8.73 ± 1.67	1.84 ^a	0.066

^aMann-Whitney U test.^bAnova performed on log₁₀ transformed data.^c± standard error.^dOne case deleted as outlier.Table 2. Long term growth and survival of *Bellura obliqua* larvae reared on *T. angustifolia* or *T. latifolia* shoots.

	Species		Significance
	<i>T. angustifolia</i>	<i>T. latifolia</i>	
Established Larvae	27	24	n.s. ($\chi^2 = 1.18$)
Surviving Larvae	13	18	$P = 0.05$ ($\chi^2 = 3.84$)
Mean Weight (mg) of Surviving Larvae	192.8 ± 16.5 ^a	249.9 ± 25.3	0.05 < P < 0.10 ($t = 1.73$)

^a± standard error.

produced by host plants. No dead larvae were found inside damaged stems. For damaged shoots of both *T. latifolia* and *T. angustifolia* the initial diameter of shoots in which larvae remained throughout the experiment was greater than for shoots without larvae at the end of the experiment (Table 3). Larvae remaining on *T. latifolia* at the end of the experiment were somewhat larger than those on *T. angustifolia*, but this difference was not quite significant (Table 2). Although not a statistically significant outlier, one larva found on *T. latifolia* was very small (34 mg) and appeared similar to stunted larvae occasionally noted in other experiments. If the data were reanalysed excluding this case, larvae growing on *T. latifolia* were significantly larger than those growing on *T. angustifolia* (262.6 ± 23.2 mg vs. 192.8 ± 16.5 mg, $df = 28$, $P < 0.05$).

Upper Leaf and Stem Composition. Upper leaves of both *T. angustifolia* and *T. latifolia* had significantly higher nitrogen levels than stems (Table 4; $P < 0.001$). Nitrogen content of the two species, however, was not significantly different for upper leaves or stems.

Phenolic content in upper leaves was significantly higher than that of stems (Table 4; $P < 0.001$). *T. angustifolia* stems had a significantly higher phenolic content than *T.*

Table 3. Influence of initial shoot diameter on larval survivorship.

Species	Initial diameter of plants (cm)		p ^b
	with larvae ^c	without larvae ^c	
<i>T. angustifolia</i>	3.1 ± 0.2 ^a (n = 13)	2.6 ± 0.2 (n = 14)	0.07
<i>T. latifolia</i>	4.8 ± 0.3 (n = 18)	3.7 ± 0.3 (n = 6)	0.06

^a± standard error.^bt test.^cAt the end of the experiment.Table 4. *Typha* nitrogen, phenolic, and water content.^a

Species	Upper Leaves	Stems
Kjeldahl nitrogen (%)		
<i>T. angustifolia</i>	2.87 ± 0.13	1.03 ± 0.13
<i>T. latifolia</i>	3.10 ± 0.22	0.98 ± 0.06
Phenolic content ^b		
<i>T. angustifolia</i>	1.80 ± 0.05	0.70 ± 0.03
<i>T. latifolia</i>	1.77 ± 0.08	0.45 ± 0.07
Water content (%)		
<i>T. angustifolia</i>	74.2 ± 0.4	87.6 ± 0.6
<i>T. latifolia</i>	72.8 ± 0.4	92.5 ± 0.3

^a± standard error.^bFolin-dennis determination (mg tannic acid equiv. per 100 mg dry tissue).

latifolia stems ($P < 0.001$). Phenolic content of upper leaves did not differ significantly between species.

Water content differed significantly between species, and between upper leaves and stems (Table 4; $P < 0.001$).

DISCUSSION

The results of experiment 2 suggest that the nutritional quality of *T. angustifolia* and *T. latifolia* stem tissue may differ. The higher growth rate of larvae reared on *T. latifolia* was probably related to differences in ECI, but not RCR. Differences in ECI were apparently not related to tissue nitrogen concentration. Differences in nitrogen "quality" (Mattson 1980), however, cannot be ruled out. Phenolics may play an anti-herbivore defensive role, but their importance in *Typha* requires further study. *Typha* spp. contain a variety of other secondary compounds (Chandler & Hooper 1979, McClure 1969, Smolenski et al. 1972, Su et al. 1973, Wall et al. 1959). Unidentified alkaloids have been detected in *T.*

angustifolia, but not *T. latifolia*. Also, young leaves of *T. angustifolia* appear to contain cyanogens, while those of *T. latifolia* do not (Gibbs 1974). Although significantly different, tissue water content in both species was high (i.e., above 60%), and thus was probably not a critical nutritional factor (cf. Scribner 1977). Differences in growth were also apparently not related to acid-detergent fiber content of stem tissue, which, in experiment 2, was approximately 40% for both species.

Larvae appeared more likely to remain on *T. latifolia* and on the larger diameter shoots of both species. If one assumes (I) that *Bellura* larvae which utilize larger shoots are required to switch host plants less frequently, and (II) that immigration in search of new host plants in the field would expose larvae to an increased risk of mortality due to predation, parasitism, or abiotic factors, selection would favor moths with an oviposition preference for *T. latifolia* relative to *T. angustifolia*. *T. latifolia* may also be a more suitable host morphologically because it tends to flower less frequently than *T. angustifolia* (Grace & Wetzel 1982, McNaughton 1966, Penko 1985). Flowering stems contain a tough central core, which is undoubtedly an inferior food resource for *B. obliqua* or other stem-boring insects.

The conclusions drawn from studies are tentative. A true measure of host plant suitability would consider the fecundity of moths reared on the two species. Also, the extent of intraspecies populational variation in *Typha* nutritional quality is unknown. Finally, although *T. latifolia* may be a more suitable host because of nutritional or possibly structural characteristics, the actual importance of these factors in the evolution of oviposition behavior remains uncertain since other ecological or abiotic factors may be ultimately responsible for the evolution of oviposition behavior in insects (Gilbert 1979, Holdren and Ehrlich 1982, Rausher 1981, Smiley 1978). Differences in larval growth and survivorship on the two species may simply indicate that *B. obliqua* is more finely adapted biochemically or morphologically to *T. latifolia* because *T. angustifolia* is less frequently utilized for entirely different reasons.

Because *T. angustifolia* is frequently noted to grow in deeper water than *T. latifolia* (e.g., Detmers 1912; see Grace & Wetzel 1981), water depth is one factor which could influence the relative suitability of the two species for *B. obliqua*. Although *B. obliqua* larvae may be competent swimmers (Fletcher 1903, Kellicott 1883), it is likely that mortality associated with dispersal, especially among early instars and overwintering larvae, may be higher in deep-water habitats where *T. angustifolia* predominates. If this is true, an oviposition preference for *T. latifolia* may have evolved because this species is more likely to grow in favorable shallow water habitats.

RGR and ECI of first-instar larvae reared on both species of *Typha* were higher than those of third-instar larvae. For other insects, RGR typically declines in latter instars and ECI may increase, decrease, or remain the same (Scribner & Slansky 1981). Changes in RGR and ECI are probably related both to differences in food quality between leaves and stems (nitrogen content was much lower in stems) and to ontogenetic changes in the digestive physiology of *B. obliqua* larvae. First-instar larvae may also have consumed less indigestible fiber than third-instar larvae because they were much smaller, and able to feed more selectively on leaf tissue. *Typha* stem tissue is quite low in nitrogen relative to mature leaves of other plants (see Mattson 1980, Scribner 1984). Low stem nitrogen content may explain the relatively low ECI and high RCR observed in this study.

B. obliqua can greatly reduce the productivity of *T. latifolia* shoots and may have reduced yields by up to 15% in some cultivated stands (Penko & Pratt, in press). Although cultivated *T. angustifolia* stands are not completely free of damage caused by *Bellura*, planting this species may offer an opportunity for partial biological control of *B. obliqua*. Other factors, however, must also be considered. *T. latifolia* may be more tolerant of stem borer damage than *T. angustifolia* so higher levels of infestation in *T. latifolia* may be acceptable. Also, information concerning the productivity, resource allocation patterns, nutrient and water requirements, ease of stand establishment, and harvestability, as well as susceptibility and tolerance to insect damage must all be evaluated when determining which *Typha* species is best suited for development as a bio-energy crop.

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