INTRODUCED PURPLE LOOSESTRIFE AS HOST OF NATIVE SATURNIIDAE (LEPIDOPTERA)

James G. Barbour[1] and Erik Kiviat[2]

ABSTRACT

Purple loosestrife (*Lythrum salicaria*, Lythraceae) arrived in North America nearly 200 years ago. In 1969 we first found larvae of the native Cecropia (*Hyalophora cecropia*) and Polyphemus (*Antheraea polyphemus*) moths (Lepidoptera: Saturniidae) on loosestrife in the Hudson River Valley, New York, and we have since found Io (*Automeris io*) on this plant. A census of 4th and 5th instar saturniids in four 0.25 ha plots in purple loosestrife—gray dogwood (*Cornus racemosa*) wet meadows near Saugerties in 1984 indicated that Polyphemus and Cecropia larvae occurred much more frequently on loosestrife than on dogwood, a native host. The switch from native woody hosts to an introduced herb may have been facilitated by the dense shrub-like habit, high productivity, and high tannin content of loosestrife.

The ecological relationships between native species and introduced species are of theoretical and practical interest (Mooney and Drake 1986). Complex interactions of insects with native and introduced hosts may affect population and range dynamics of biota, pollination, herbivore impacts on plant community composition, decomposition and nutrient cycling, agriculture, and the potential for biological control of weeds.

Purple loosestrife, *Lythrum salicaria* L. (Lythraceae), was introduced from Europe to the northeastern United States in the early 1800s (Thompson et al. 1987). Loosestrife is a broad-leaved, cespitose, perennial herb 1–3 m tall with a woody root system and herbaceous aerial stems that die but persist erect through winter. In older plants the root crown may become an elevated pedestal greater than 30 cm in diameter and 30 cm high that supports 25–50+ stout stems. Loosestrife leaves are sessile, 3–12 cm long and 1–2 cm wide. Loosestrife is abundant in ditches, shores, wet meadows, nontidal marshes, low-salinity tidal marshes, and disturbed upland soils in many regions of the northern United States and southern Canada. Many animals eat loosestrife leaves, but rarely are more than a few plants defoliated at a site (Hight 1990; Barbour and Kiviat, personal observations).

Many Saturniidae (silk moths) are known for the large size and bold color patterns of the adults and larvae. *Antheraea polyphemus* (Cram.) (Polyphemus), *Hyalophora cecropia* (L.) (Cecropia), and *Automeris io* (F.) (Io), have broad host and habitat niches, and large geographic ranges, in eastern

---

[1]5 Fish Creek Road, Saugerties, NY 12477.

[2]Corresponding author; Hudsonia Ltd., Bard College Field Station, Annandale, NY 12504-0217.

North America (Tuskes et al. 1996). Here we report purple loosestrife as a larval host for these native Saturniidae (Lepidoptera) in New York.

MATERIALS AND METHODS

Our general study area in northeastern Ulster and western Dutchess counties has elevations of 0–150 m adjoining the Hudson River midway between New York City and Albany, New York. Annual precipitation is ca. 1000 mm. Woody vegetation, mostly post-agricultural, covers about half the landscape, and wetlands cover perhaps 5–10%.

Barbour conducted censuses 18–21 August 1984 in shrubby wet fields 1.5 and 4 km north of Saugerties (Ulster County), elevation 45 m, where he had found the highest local densities of saturniid larvae the previous two years. These sites are 1.6–2.0 km from the tidal Hudson River on deep, nearly level, somewhat poorly drained to poorly drained soils on glaciolacustrine silty clay and glacial outwash (Tornes 1979). At each of the two sites, two 50 × 50 m (0.25 ha) plots, at least 50 m from forest edges, were selected as representative. Each plot bordered a drainage ditch or mowed right-of-way, and was divided into 25 subplots (10 × 10 m). Barbour searched each subplot once, recording 4th and 5th instar saturniids, and visually estimating the cover of purple loosestrife and gray dogwood (*Cornus racemosa* Lam.). We believe the census was complete for 5th instar and nearly complete for 4th instar saturniids. There were no trees in the plots, and few other plants except aster (*Aster*) and goldenrod (*Solidago*). The plots rarely flood and did not flood in 1983–84.

We computed Spearman's rank correlations (*rho*), Kruskal-Wallis one-way analysis of variance by ranks, Wilcoxon matched-pairs tests (T), and two-tailed Fisher exact tests with Statistica version 5.1 (StatSoft, Tulsa, OK).

RESULTS

In 1969 Barbour found 2 Cecropia and 1 Polyphemus (all 4th instar) on purple loosestrife near Kingston, New York. In 1976, Kiviat found a copulating pair, eggs, and larvae (instars 1–3) on purple loosestrife in the towns of Clinton and Wappinger, Dutchess County. In 1979 Barbour found several Cecropia cocoons in loosestrife in a highway intersection "island" where there were no potential woody hosts. In September 1980 he found 45 5th instar Cecropia feeding on purple loosestrife in a highway intersection island at Kingston, and 63 on loosestrife near Stone Ridge (Ulster County). In the early 1980s he found more Polyphemus larvae on loosestrife in Ulster County. In 1991, Barbour found 3 Cecropia larvae on loosestrife at West Point Military Academy (Orange County, New York), and in 1992 he found Cecropia and Polyphemus larvae on loosestrife in the Bethlehem train yards (Albany County, New York). We have seen 1st instars of both moths feeding on loosestrife. Since 1984 there has been no obvious change in saturniid use of loosestrife in the Hudson Valley. In the 1980s, Robert Dirig (Cornell University, pers. communication 1997) found a Cecropia cocoon on loosestrife in Ithaca (Tompkins County, central New York), suggesting use of this plant for food elsewhere in the state.

On the 4 census plots combined (total = 1 ha) there was a total of 79 4th and 5th instar saturniids, comprising 50 Polyphemus, 27 Cecropia, and 2 Io. All larvae were on loosestrife except 4 Polyphemus on gray dogwood. Polyphemus was significantly more abundant than Cecropia (Wilcoxon

Table 1. Probabilities of Spearman rank correlations (*rho*) for saturniid larvae and vegetation cover for n = 100 subplots (each 10 × 10 m) at four sites; * indicates a negative correlation. The number of plots (50 × 50 m, n = 25) with *rho* significant ($\rho < 0.05$) follows the probability.

	Polyphemus		Cecropia		Total saturniids		Loosestrife	
Cecropia	0.00011	2						
Loosestrife cover	0.03	2	0.26	0	0.06	2		
Dogwood cover	* 0.038	1	* 0.024	2	* 0.0045	1	* 0.0017	4
Ls. + dw. cover	0.56		* 0.69		* 0.87			

T = 117, $\rho = 0.01$). ANOVAs indicated that numbers of total saturniids and Polyphemus differed significantly among the 4 plots ($\rho = 0.0039, 0.012$, respectively), but Cecropia did not differ ($\rho > 0.05$). Loosestrife cover and dogwood cover were negatively correlated (Table 1). Loosestrife cover was 0–1.00 (mean 0.317, median 0.25) and dogwood cover 0–0.70 (mean 0.128, median 0.10). Loosestrife cover was significantly greater than dogwood cover (Wilcoxon T = 783.5, $\rho = 0.00001$).

Polyphemus was correlated with Cecropia and with loosestrife cover, and Polyphemus and Cecropia were each negatively correlated with dogwood cover (Table 1). Total saturniids were negatively correlated with dogwood cover but were not correlated with loosestrife cover (Table 1, Fig. 1). Saturniids separately or combined, however, were not correlated with total "brushy" cover (i.e. dogwood + loosestrife).

The August censuses were in the early part of the 5th instar period for Polyphemus, and between the two peaks for late instar Cecropia (adult Cecropia exhibit bimodal emergence and oviposition [Waldbauer and Sternburg 1973]). On 5 September 1984, Barbour re-censused 1 plot. There were 3 Polyphemus, 9 Cecropia, and 3 Io (compared to 5 Polyphemus, 2 Cecropia, and 0 Io on 21 August). The numbers of Polyphemus and Cecropia were not significantly different between the two dates (Fisher $\rho = 0.074$). On 2 September 1984, Barbour censused 4th and 5th instar saturniids along 835 m of wet drainage ditches with loosestrife and other plants (habitat width 1–2.5 m, habitat area ca. 0.15 ha) in a hay field near one plot. There were 3 Polyphemus, 27 Cecropia, and 2 Io, all on loosestrife. Saturniid density was equivalent to 213 ha^{-1} (Polyphemus 20 ha^{-1}, and Cecropia 180 ha^{-1}).

DISCUSSION

Cecropia and Polyphemus are associated with savanna-like habitats (scattered trees and shrubs), forest ecotones such as riparian and lacustrine margins, open shrubby wetlands (Stratton-Porter 1910), old fields and burned forests (Waldbauer 1996:90, 257), and barrier beach shrublands (John Cryan, New York, NY, pers. communication 1988). Polyphemus also occurs in deciduous forests. Both moths readily colonize disturbed habitats and may abound in suburbs and cities (Scarbrough 1970, Waldbauer 1996), post-industrial shrublands, and railroad rights-of-way. We have found saturniids feeding on loosestrife in wet meadows, pond shores, ditches, and wetland fill. Kiviat has found Cecropia cocoons on loosestrife distant from woody plants in a freshwater-tidal marsh of the Hudson River. Loosestrife stands supporting

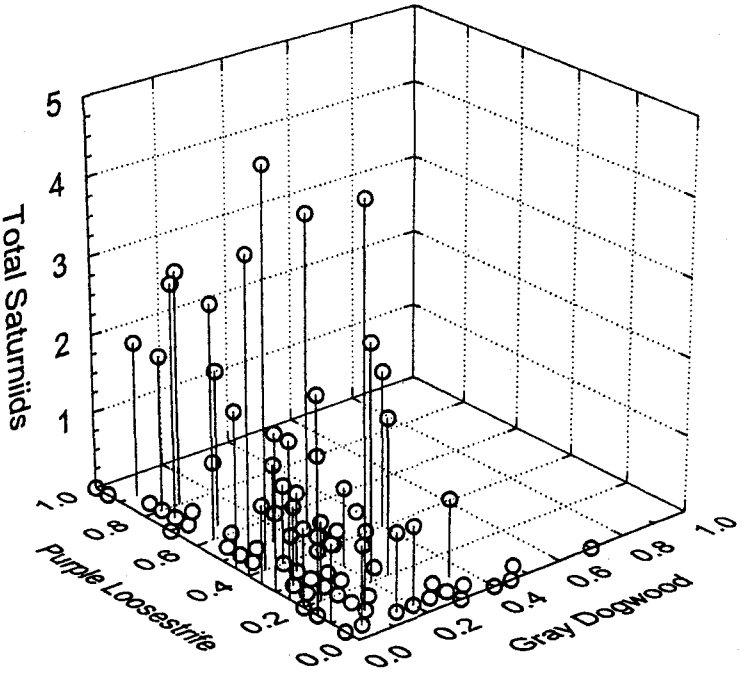

Figure 1. Occurrence of 4th and 5th instar saturniids (*Antheraea polyphemus*, *Hyalophora cecropia*, and *Automeris io* combined) in 10 × 10 m subplots (n = 100) in relation to cover of purple loosestrife and gray dogwood.

saturniid larvae comprise denser, larger plants more often than sparser, smaller plants. Figure 2 shows a Cecropia larva on loosestrife.

Purple loosestrife is probably as abundant in the Hudson Valley as anywhere in North America. Other regions with extensive loosestrife include central and western New York, the St. Lawrence River corridor in Quebec, the Lake Erie shore of Ohio, areas of Michigan and Wisconsin, and northeastern Massachusetts (Thompson et al. 1987). Cecropia larvae were found on purple loosestrife in Orange County, New York in 1986–87 (Hight 1990). A population of the *Hemileuca maia* (Drury) complex in Wisconsin (Tuskes et al. 1996:121) and *Saturnia pavonia* (Linnaeus) in Europe (Stone 1991) are the only other saturniids reported to feed on loosestrife to our knowledge.

Loosestrife thrives in disturbed, moist or wet soils, and often forms thickets adjoining or intermingled with native hosts of Polyphemus and Cecropia such as shrubby dogwoods (*Cornus* spp.) and willows (*Salix* spp.). On our study plots, Polyphemus and Cecropia occurred in areas with low dogwood cover and moderate to high loosestrife cover (Fig. 1). Larvae occurred almost exclusively on loosestrife, in close proximity to dogwood. Our qualitative observations also indicate that Polyphemus and Cecropia are at least as common on loosestrife as on their native woody hosts.

Figure 2. *Hyalophora cecropia* larva on purple loosestrife, Ulster County, New York. Photo by Anita F. Barbour.

Polyphemus and Cecropia share many woody hosts, especially shrubby dogwoods, willows, maples (*Acer* spp.), and cherries (*Prunus* spp.) (Tuskes et al. 1996; Barbour, personal observations). Besides purple loosestrife, only 3 herbs have been reported as Cecropia hosts: *Decodon verticillatus* (L.) Ell. (Lythraceae), a native species similar to and in the same family as purple loosestrife, native hops (*Humulus lupulus* L., Moraceae), and introduced garden peony (*Paeonia officinalis* L., Ranunculaceae) (Eliot and Soule 1902, Stone 1991, Waldbauer 1996:89). The *Decodon* record was based on cocoons over water (Eliot and Soule 1902:251), suggesting oviposition on this plant. Only 1 herb has been reported as a Polyphemus host, wild-indigo (*Baptisia tinctoria* [L.] Vent., Fabaceae) (Stone 1991).

The host niche breadth of Saturniidae is indicated by lists of larval food plants in Stone (1991) which we analyzed for nominate subspecies of moths only. These lists are a useful index although Stone (1991) presumably in-

cluded laboratory as well as wild host records, and some wild host records are probably based on cocoon locations (e.g. mature Cecropia larvae may move up to 10 m from host plant to a spinning site on another species [Waldbauer and Sternburg 1967a]). Larval food plants listed by Stone (1991) for Polyphemus, Cecropia, and Io comprise 40, 49, and 56 genera, respectively (arbitrarily combining *Pyrus, Malus,* and *Sorbus*). For 9 native species of Saturniidae now found in the Hudson Valley but that we have not found on purple loosestrife, Stone (1991) listed 4–31 (median = 6) genera of larval food plants. For Polyphemus, Cecropia, and Io, 1, 2, and ca. 9 genera of herbs are among the food plants listed, whereas only 0–1 (median = 0) herb genera were listed for the other 9 saturniids. (For two additional saturniids, the introduced ailanthus silk moth [*Samia cynthia* Drury] and the historically present imperial moth [*Eacles imperialis* Drury], Stone (1991) listed 41 and 42 genera of food plants, respectively.) These figures suggest that, of the saturniids in long contact with loosestrife in the Hudson Valley, the species with the broadest host niches and the most herbaceous food plants are the moths that have accepted loosestrife as host. It is also significant that the saturniid species using loosestrife pupate aboveground, as the soil is often wet under loosestrife.

In the case of Cecropia, several factors may explain the successful switch to purple loosestrife: 1. Cecropia is a generalist that accepts many hosts; 2. Loosestrife is taller than most herbs and the same height as gray dogwood, and thus may intercept the flight path of ovipositing moths; 3. Loosestrife is very productive, and the dense, rapidly re-growing foliage of mature plants provides abundant food and concealment for large larvae (see Waldbauer 1996:90); 4. There is little competition for loosestrife leaves from other herbivores; 5. Loosestrife leaves appear to have a higher moisture content than leaves of common woody hosts e.g. *Cornus*, possibly increasing the availability of nutrients relative to woody plants (see Scriber 1975); 6. Cecropia cocoons among low dense shrub stems or basal tree shoots are more likely to escape bird predation (Waldbauer and Sternburg 1967b), and the stiff, crowded, winter-persistent loosestrife stems offer sturdy attachment and better concealment for the large cocoons than most trees and shrubs; 7. Saturniid larvae in general prefer tannin-rich leaves (Bernays and Janzen 1988), and although the leaves of most woody dicots contain tannins and herbaceous dicots do not (Bate-Smith and Metcalfe 1957, Swain 1979, Rhoades 1983), purple loosestrife leaves have high tannin levels (Vincent and Segonzac 1954, Gibbs 1974, Shishkin and Bobrov 1974). Except for factor 6, these factors may also apply to Polyphemus and Io.

We hypothesize that: 1. The switching of Polyphemus and Cecropia from native woody hosts to loosestrife was initially possible because of the wide host range of the moths, the abundance of dense mature loosestrife in association with traditional hosts in habitats that rarely flood, and the attraction of the moths to tannin-rich leaves; and 2. The switch was successful because abundant, moisture-rich foliage allows higher growth rates; also larvae feeding in dense loosestrife foliage and cocoons spun among crowded loosestrife stems are more likely to escape predators than larvae and cocoons on woody plants. Recent, large-scale switches from native to introduced leguminous herbs have been documented in the butterflies *Erynnis baptisiae* Forbes (Shapiro 1979) and *Glaucopsyche lygdamus* (Doubleday), ssp. *couperi* Grote (Dirig and Cryan 1992). (*Vicia cracca* L., the new host of *G. l. couperi*, may be native in New York, nonetheless this butterfly has two alien legume hosts in Canada [Robert Dirig, pers. communication 1997]).

Purple loosestrife is considered a pest in North America because it alters the marsh and wet meadow habitats of stenotopic species (Thompson et al.

1987), including plants, graminoid-feeding insects, graminoid-nesting marsh birds, and muskrat. European beetles have been released in the northern U.S. during the 1990s to control loosestrife (Malecki et al. 1993). Polyphemus, Cecropia, and Io moths are generalized herbivores that may switch from native woody hosts to purple loosestrife in regions other than the Hudson Valley as loosestrife becomes more abundant, and perhaps switch back to woody hosts where biological control causes loosestrife populations to decline. Other saturniids with broad food plant niches, such as ailanthus silk moth and imperial moth, might also switch to loosestrife. Monitoring these interactions would add to knowledge of loosestrife ecology in North America, and the ecology of invasions in general. The switching of native insects to an introduced host plant could indicate incipient "natural" control of purple loosestrife (perhaps akin to the control of Eurasian watermilfoil [*Myriophyllum spicatum* L.] by native insects, see Creed and Sheldon [1995]). We think it unlikely, however, that saturniid larvae can reach abundances sufficient to reduce Hudson Valley loosestrife populations.

ACKNOWLEDGMENTS

Anita F. Barbour participated in field work. John Bleiler and Stephen Hight provided literature citations. Robert Dirig and Gil Waldbauer commented on drafts. This is Bard College Field Station—Hudsonia Contribution 70.

LITERATURE CITED

Bate-Smith, E. C. and C. R. Metcalfe. 1957. Leuco-anthocyanins. 3. The nature and systematic distribution of tannins in dicotyledonous plants. Jour. of the Linn. Soc. of London; Botany 55:669–705.

Bernays, E. A. and D. H. Janzen. 1988. Saturniid and sphingid caterpillars: two ways to eat leaves. Ecology 69(4):1153–1160.

Creed, R. P., Jr. and S. P. Sheldon. 1995. Weevils and watermilfoil: did a North American herbivore cause the decline of an exotic plant? Ecol. Appl. 5(4):1113–1121.

Dirig, R. and J. F. Cryan. 1992. The status of silvery blue subspecies (*Glaucopsyche lygdamus lygdamus* and *G. l. couperi*) in New York. Jour. of the Lepidopt. Soc. 45:272–290.

Eliot, I. M. and C. G. Soule. 1902. Caterpillars and their moths. Century Co., New York.

Gibbs, R. D. 1974. Chemotaxonomy of flowering plants. McGill-Queen's University Press, Montreal. 4 volumes.

Hight, S. D. 1990. Available feeding niches in populations of *Lythrum salicaria* L. (purple loosestrife) in the northeastern United States. Proceedings of the International Symposium on Biological Control of Weeds 7:269–278.

Malecki, R. A., B. Blossey, S. D. Hight, D. Schroeder, L. T. Kok, and J. R. Coulson. 1993. Biological control of purple loosestrife. BioScience 43(10):680–686.

Mooney, H. A. and J. A. Drake, eds. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Rhoades, D. F. 1983. Herbivore population dynamics and plant chemistry. pp. 155–222. *In*: R. F. Denno and M. S. McClure, eds. Variable Plants and Herbivores in Natural and Managed Systems. Academic Press, New York.

Scarbrough, A. G. 1970. The occurrence of *Hyalophora cecropia* (L.) as related to urbanization. Ph.D. Thesis, University of Illinois, Urbana-Champaign.

Scriber, J. M. 1975. Comparative nutritional ecology of herbivorous insects: general-

ized and specialized feeding strategies in the Papilionidae and Saturniidae (Lepidoptera). Ph.D. Thesis, Cornell University, Ithaca, New York.
Shapiro, A. M. 1979. *Erynnis baptisiae* (Hesperiidae) on crown vetch (Leguminosae). Jour. of the Lepidopt. Soc. 19:227–230.
Shishkin, B. K. and E. G. Bobrov, eds. 1974. Flora of the U.S.S.R. Volume 15. Malvales, Parietales, Myrtiflorae. Israel Program for Scientific Translations, Keter Publishing House, Jerusalem. (Originally published in Russian 1949, Akademiya Nauk SSSR, Moskva-Leningrad.)
Stone, S. E. 1991. Foodplants of world Saturniidae. Lepidopt. Soc. Mem. 4.
Stratton-Porter, G. 1910. Music of the wild, with reproductions of the performers, their instruments and festival halls. Jennings and Graham, Cincinnati, Ohio.
Swain, T. 1979. Tannins and lignins. pp. 657–682. *In:* G. A. Rosenthal and D. H. Janzen, eds. Herbivores; Their Interactions with Secondary Plant Metabolites. Academic Press, New York.
Thompson, D. Q., R. L. Stuckey, and E. B. Thompson. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Fish and Wildlife Service, Fish and Wildlife Research 2.
Tornes, L. A. 1979. Soil survey of Ulster County, New York. U.S. Department of Agriculture, Soil Conservation Service.
Tuskes, P. M., J. P. Tuttle, and M. M. Collins. 1996. The wild silk moths of North America. Cornell University Press, Ithaca.
Vincent, D. and G. Segonzac. 1954. Quelques donnees nouvelles sur la salicaire *Lythrum salicaria* L. et son action pharmacologique. Acta Phytotherapeutica 1(6):1–13.
Waldbauer, G. P. 1996. Insects through the seasons. Harvard University Press, Cambridge.
Waldbauer, G. P. and J. G. Sternburg. 1967a. Host plants and the locations of the baggy and compact cocoons of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Ann. Entomol. Soc. America 60(1):97–101.
Waldbauer, G. P. and J. G. Sternburg. 1967b. Differential predation on cocoons of *Hyalophora cecropia* (Lepidoptera: Saturniidae) spun on shrubs and trees. Ecology 48(2):312–315.
Waldbauer, G. P. and J. G. Sternburg. 1973. Polymorphic termination of diapause by Cecropia: genetic and geographical aspects. Biological Bull. 145:627–641.