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Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico

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ABSTRACT. Fifteen species of Lepidoptera occurred in large numbers in spring and early summer after the passage of Hurricane Hugo over the north-east of Puerto Rico. *Spodoptera eridania* (Noctuidae) was the most common of the larvae and fed on 56 plant species belonging to 31 families. All the Lepidoptera fed on early successional vegetation. Some of the plants represent new host plants for these species. The outbreaks appeared to be based on the flush of new foliage that developed in the Luquillo Mountains after the passage of the hurricane. The end of the *S. eridania* outbreak was concurrent with the consumption of its preferred host plants and to an apparent increment in parasitism by ichneumonids (Hymenoptera). Parasitism by tachinids (Diptera) may have contributed to the reduction in abundance of other Lepidoptera species that were temporarily very abundant. Natural enemies of *S. eridania* were recorded for the first time in Puerto Rico.

KEY WORDS: Diptera, disturbance, Hymenoptera, insects, Lepidoptera, parasites, Puerto Rico.

INTRODUCTION

A map showing the accumulated paths of tropical cyclones in the Caribbean would cover most of the Caribbean basin including both land and sea. On average, 10 cyclones (six hurricanes and four storms) occur each year in the Caribbean (National Weather Service 1988). Fassig (1929) estimated that 50 cyclones have passed over Puerto Rico in 450 years.

Tropical cyclones can have drastic effects on insect abundance. Osborn (1935) found a severe reduction in the abundance of homopterans in 1929, one year after the passage of Hurricane San Felipe throughout Puerto Rico. Hurricane San Ciprían (26–27 September 1932) destroyed most of the cottony cushion scale, *Icerya purchasi* Maskell (Wolcott 1941). In contrast the soft green scale, *Coccus viridis* Green, increased in abundance and became highly destructive in coffee areas denuded of shade by Hurricane San Felipe in 1928 (Smith 1942, Wolcott 1932, 1933). Scale abundance depends on humidity, and numbers are strongly reduced by entomogenous fungi that thrive in wet conditions. Hurricane San Ciprían eliminated the pink bollworm, *Pectinophora gossypiella* Saunders (a pest of

cotton) from some areas on the north coast when it destroyed the fruiting portions of maga (*Thespesia grandiflora* Urban) trees; the fruits of *T. grandiflora* were the most important alternate food of pink bollworm on the north coast of Puerto Rico. These examples show that hurricanes can affect insects directly or affect their abundance by destroying their enemies or their food sources. In addition, hurricanes can be an important factor in the dispersal of some insect groups (Torres 1988).

Although there is some information on the effects of cyclones on agricultural pests, there are no studies on forest insects immediately following the passage of a hurricane. The passage of Hurricane Hugo (17–18 September 1989) over the north-east of Puerto Rico provided an opportunity to make observations on insect responses to the vegetation changes ensuing from this catastrophic event.

In this paper, I report lepidopteran outbreaks during the spring and summer after the passage of Hurricane Hugo. The outbreak by *Spodoptera eridania* Cramer (Noctuidae) was the most conspicuous and it is discussed in greater detail. Also, I conducted captive rearing of wild-caught *S. eridania* final instar larvae on their original host plant to determine if different host plants could sustain adequate larval growth to permit the development of adults. Information on bark beetles and dipteran peaks of abundance is also presented.

SITE DESCRIPTION AND METHODS

Hurricane Hugo passed over the north-east of Puerto Rico on 17–18 September 1989. Maximum wind speed was approximately 225 km h^{-1}. The winds blew for about 18 hours in the Luquillo Mountains causing extensive damage to north and east facing slopes. Defoliation was ubiquitous along these slopes. Pre- and post-hurricane measurements of over 300 tagged trees in the Bisley watersheds (located on the north-east side of the Luquillo Mountains) indicated that 35% of stems were snapped at the base, uprooted or crushed (Scatena 1990). In the Bisley area the average height of standing trees was reduced by 38%. On the hillslopes nearly 10% of the land-surface had exposed mineral soils from landslides and tree uprootings (Scatena 1990). After the hurricane, an intensive invasion of early successional plant species took place. The percentage of herbaceous vegetation and vines increased remarkably. These changes were most prominent at the lower elevations of the forest, where the effect of the hurricane was most severe.

Qualitative observations were made on the abundance of insects in the Luquillo Mountains during the year following the passage of Hurricane Hugo. The Luquillo Mountains are located in the north-east corner of Puerto Rico and contain four subtropical life zones: wet forest, rain forest, lower montane wet forest, and lower montane rain forest (sensu Holdridge 1967). Most peaks in abundance of Lepidoptera occurred during April, May, and June of 1990 (in spring and early summer, seven months after the passage of the hurricane) in all the life zones. During these months all forest areas close to asphalt roads, the

Bisley, Palo Hueco, and El Verde trails, were visited, and information on lepidopteran abundance, host plants, predators and parasites was recorded. The approximate level of defoliation of host plants species by *S. eridania* was classified in three categories: intense, moderate, and low. Intense defoliation described the situation when over 75% of a plant was defoliated and more than 80% of the plants observed were defoliated; moderate when 40–75% of the plant was defoliated and 10–40% of the observed plants were attacked; low when defoliation was below 40% and on less than 10% of the plants observed. Although most of the information presented is not strictly quantitative, the observations are based on the examination of large tracts of forest land, in many cases containing thousands of individuals of a given plant species.

Final instar larvae of *S. eridania* and other Lepidoptera species were placed in glass jars and fed leaves of the same host plant upon which they were feeding in the field. Final instar larvae were selected to estimate the level of parasitism at that stage. The first group of *S. eridania* larvae was collected on 29 April and 4 May and the second on 4 June. Vermiculite or sand was used as substrates for species that pupate in soil. Larvae were kept at ambient temperatures. The fate of each larva was recorded as follows: larva died before pupation, pupa died, adult eclosed, or parasite eclosed.

RESULTS

Spodoptera eridania (Noctuidae)

An outbreak of *S. eridania* had occurred by mid April 1990. The moth population structure was not single-stage (asynchronous – sensu Godfray & Chan 1990). The larvae were recorded feeding on 56 plant species belonging to 31 families (Table 1). The following species appeared to be favoured and suffered the heaviest defoliation: *Phytolacca rivinoides*, *Impatiens wallerana*, *Ipomoea tiliacea*, *Cestrum macrophyllum*, *Conyza bonariensis*, *Mentha piperita*, *Bacopa stricta*, and *Solanum americanum* (authorities for plant species are in Table 1). The first four plant species were very abundant, while densities of the last four species were low. *Phytolacca rivinoides* was defoliated in all the areas visited. Only a few plants of *P. rivinoides* were not attacked. *Impatiens wallerana* bordered the Luquillo Mountain roads for many kilometres; approximately 85% of the plants were completely defoliated (Figure 1). On many attacked plants, it was common to find over 30 medium size and large larvae during the peak of the outbreak. Many *I. wallerana* and *P. rivinoides* died after larval attack. Though *I. tiliacea* vines were heavily attacked, the level of defoliation on many vines did not exceed 60%. For that reason this species is included under moderate defoliation (Table 1).

In some areas of the forest, *Cayaponia americana*, *Mikania cordifolia*, *Clibadium erosum*, and *Lepianthes umbellatum* (Figure 1) suffered heavy defoliation, but the attack was not uniform on these species. The same occurred with some saplings of *Cecropia peltata* and *Solanum torvum*.

Some host plants were attacked with greater intensity when they were located

Table 1. Host plants of *Spodoptera eridania* in the Luquillo mountains.

Family	Species	Defoliation
Acanthaceae	*Odontonema strictum* (Nees) Kuntze	low
	Sanchezia speciosa Leonard	low
	Teliostachya alopecuroidea (Vahl) Nees	moderate
Araceae	*Xanthosoma* spp.	low
Araliaceae	*Didymopanax morototoni* (Aubl.) Decne & Pl.	low
Balsaminaceae	*Impatiens wallerana* Hook. f.	intense
Commelinaceae	*Commelina diffusa* Burm. f.	moderate
	Tripogandra serrulata (Vahl) Handles	moderate
Compositae	*Clibadium erosum* (Sw.) DC.	moderate
	Conyza bonariensis (L.) Cron.	intense
	Conyza canadensis (L.) Cron.	low
	Eclipta alba (L.) Hassk.	moderate
	Elephantopus spicatus Jussieu ex Aublet	low
	Erechtites valerianaefolia (Wolf) DC.	low
	Mikania cordifolia (L.f.) Willd.	moderate
	Neurolaena lobata (L.) Cass.	low
Convolvulaceae	*Ipomoea tiliacea* (Willd.) Choisy	moderate
Cucurbitaceae	*Cayaponia americana* Lam.	moderate
	Cayaponia racemosa Mill.	low
Dioscoreaceae	*Dioscorea polygonoides* Humb. Bunpl. ex. willd.	low
	Rajania cordata L.	low
Euphorbiaceae	*Phyllanthus urinaria* L.	low
	Sapium jamaicense Sw.	low
Gramineae	*Ichnanthus pallens* (Sw.) Munroe	low
	Stenotaphrum secundatum (Walt.) Kuntze	low
Labiatae	*Mentha piperita* L.	intense
Lauraceae	*Ocotea* sp. (saplings)	low
Lobeliaceae	*Lobelia portoricensis* (Vatke) Urban	moderate
Malvaceae	*Hibiscus rosa-sinensis* L.	moderate
	Pavonia fruticosa (Mill.) Fawc. & Rendle	low
	Sida rhombifolia L.	low
Melastomataceae	*Heterotrichum cymosum* (Wendl.) Urban	low
Mimosaceae	*Leucaena leucocephala* Lam.	moderate
	Mimosa pudica L.	low
Moraceae	*Cecropia peltata* L.	low
Ochnaceae	*Sauvagesia erecta* L.	moderate
Onagraceae	*Ludwigia* sp.	low
Papilionaceae	*Centrosema pubescens* Benth.?	moderate
	Desmodium adscendens (Sw.) DC.	moderate
Passifloraceae	*Passiflora edulis* Sims.	low
	Passiflora sexflora Juss.	low
Phytolaccaceae	*Phytolacca rivinoides* Kunth & Bouché	intense
Piperaceae	*Lepianthes umbellatum* (L.) Rafinesque	moderate
Plantaginaceae	*Plantago major* L.	low
Rosaceae	*Rubus rosifolius* Smith	low
Rubiaceae	*Hamelia patens* Jacq.	moderate
	Gonzalagunia spictata (Lam.) Maza	low
	Hemidiodia ocimifolia (Willd.) K. Schum	moderate
	Psychotria berteriana DC.	low
Scrophulariaceae	*Bacopa stricta* (Schrad.) Robins	intense
Solanaceae	*Cestrum macrophyllum* Vent	intense
	Solanum americanum Schulz	intense
	Solanum rugosum Dunal	low
	Solanum torvum Sw.	low
Verbenaceae	*Citharexylum fruticosum* L.	low
Zingiberaceae	*Alpinia purpurata* Vieill ex k. Schum	low

close to specimens of *P. rivinoides*, *I. wallerana* or *C. macrophyllum*, suggesting that the latter plants served as attractants to *S. eridania*. Sometimes the larvae moved from one plant to another when the food was exhausted, but *S. eridania* eggs were also found deposited on less acceptable host plants such as *Rubus rosifolius*.

In areas of the forest such as El Verde, which suffered light to moderate destruction by the hurricane, plants experienced only a mild attack by *S. eridania*. Parts of the forest from which *I. wallerana*, *C. macrophyllum* or *P. rivinoides* were absent (e.g. Jimenez road) did not suffer conspicuous defoliation by the caterpillars.

Most of the highly acceptable host plants were consumed by the end of May. *Cestrum macrophyllum* is common on the peaks of the mountains and was the last of the highly acceptable host plants to be defoliated. The attack on *C. macrophyllum* was very intense during June in the highlands.

The larvae of *S. eridania* were preyed on by *Podisus sagitta* F. (Hemiptera: Pentatomidae) and by the pearly-eyed thrasher, *Margarops fuscatus*, Vieillot (Aves: Mimidae). A tachinid fly, *Winthemia* sp. (Diptera: Tachinidae) and two ichneumonid wasps, *Enicospilus luquillo* Gauld, and *Ophion flavidus* Brullé (Hymenoptera: Ichneumonidae) parasitised the larvae. However, wasps were the main enemy of the moth, and only two tachinids emerged from captive-reared larvae. The overall level of parasitism in wild-caught captive-reared larvae was 19% (N = 109: Table 2); those collected on 29 April–4 May suffered 18% (N = 61), and those on 4 June 27% (N = 48). Although the differences were not significant ($X^2 = 0.80$, $P > 0.05$), the parasitic wasps were ubiquitous attacking *S. eridania* larvae in the forest during June.

The outbreak declined by 20 May in the lowlands, but persisted in the highland forest until the end of June. Foerster & Dionisio (1989) found that generation time of *S. eridania* feeding on bracatinga (*Mimosa scabrella*, Bentham) was 33 days at 30°C. Generation time varies with host plant (Mattana & Foerster 1988). Based on the above information the outbreak of *S. eridania* lasted for about three generations.

When attacked by parasites or touched, larvae of *S. eridania* immediately let go of the host plant and fall to the ground. This defence mechanism is important because the dark coloured larvae of *S. eridania* are easily seen in the well illuminated disturbed habitats. This behaviour is similarly found in hemileucine saturniid caterpillars in Costa Rica (Janzen 1984). Polyphagous species are more likely to relocate to at least an edible host than if they were monophagous, and therefore can use this escape behaviour.

Most of the plant species provided in the laboratory as food to final instar larvae were appropriate for larval growth (Table 2). The only exception appeared to be the vine *Mikania cordifolia*, but the sample size was too small to support a definitive conclusion. On *Mikania*, the larvae ate only a very small amount of the leaves offered.

Other Lepidoptera

Table 3 summarizes the other Lepidoptera species observed in large numbers and lists their host plants. Most of their food plants were early successional

a)

b)

Figure 1. Defoliation by *Spodoptera eridania* on: (a) *Clibadium erosum*, (b) *Impatiens wallerana*, (c) *Lepianthes umbellatum*, and (d) *Lobelia portoricensis*.

species. The population structure of these lepidopteran species did not consist of a single-stage. They were asynchronous (sensu Godfray & Chan 1990). Authorities for other Lepidoptera are in Table 3.

Cosmosoma myrodora (Arctiidae). Larvae intensively defoliated *Mikania cordifolia*

c)

d)

Figure 1. *Continued*

throughout the whole forest; on some vines, where only *C. myrodora* were present, 99% of leaves were eaten. Also, *Condica cupentia* (Noctuidae) and *S. eridania* fed heavily on *M. cordifolia*. Larvae of *C. myrodora* pupated on other trees and vines not used as larval food in the forest.

Ecpantheria icasia (Arctiidae). During May this species was highly abundant in the forest, where it fed on several herbs and vines (Table 3). This species is

Table 2. Survival of wild-caught last instar larvae of *Spodoptera eridania* on different hosts.

Host plant	Sample size	Larval death*	Parasitised (%)	% Survival
Cestrum macrophyllum	15	8	5 (33)	13
Clibadium erosum	17	9	5 (29)	18
Commelina diffusa	2	0	1 (50)	50
Desmodium adscendens	5	1	4 (80)	0
Impatiens wallerana	14	3	0	79
Ipomoea tiliacea	4	0	0	100
Lobelia portoricensis	5	2	0	60
Mikania cordifolia	2	2	0	0
Phytolacca rivinoides	3	0	1 (33)	66
Rubus rosifolius	13	2	0	85
Solanum americanum	14	1	1 (7)	86
Tripogandra serrulata	15	6	4 (27)	33
TOTAL	109	34	21 (19)	50

*Some deaths could be releated to parasites that did not complete their life cycle.

Table 3. Lepidoptera species in outbreaks after Hurricane Hugo.

Lepidoptera species	Hosts (Family)
Anartia jatrophae Munroe (Nymphalidae)	*Bacopa stricta* (Schr.) Robins (Scrophulariaceae)
Antillea pelops Drury (Nymphalidae)	*Justicia martinsoniana* Howard (Acanthaceae)
Condica cupentia Cramer (Noctuidae)	*Mikania cordifolia* (L. F.) Willd. (Compositae)
Cosmosoma myrodora Dyar (Arctiidae)	*Mikania cordifolia* (Compositae)
Dione vanillae Maynard (Heliconiidae)	*Passiflora sexflora* Juss. (Passifloraceae)
Ecpantheria icasia Cramer (Arctiidae)	*Cissus sicyoides* L. (Vitaceae)
	Elephantopus mollis Kunth (Compositae)
	Ipomoea tiliacea (Willd.) Choisy (Convolvulaceae)
	Ruellia coccinea (L.) Vahl (Acanthaceae)
	Solanum torvum Sw. (Solanaceae)
Gonodonta nitidimacula Guenée (Noctuidae)	*Piper* spp. (Piperaceae)
Heliconius charitonius L. (Heliconiidae)	*Passiflora sexflora* Juss. (Passifloraceae)
Historis odius Fabricius (Nymphalidae)	*Cecropia peltata* L. (Moraceae)
Hypanartia paullus Fabricius (Nymphalidae)	*Trema micrantha* (L.) Blume (Ulmaceae)
Perichares philetes Gmelin (Hesperiidae)	*Scleria pterota* Presl (Cyperaceae)
Perigonia lusca Fabricius (Sphingidae)	*Gonzalagunia spicata* (Lam.) Maza (Rubiaceae)
Syllepte silicales Guenée (Pyralidae)	*Didymopanax morototoni* (Aubl.) Dec & Pl. (Araliaceae)
Xylophanes tersa L. (Sphingidae)	*Psychotria berteriana* DC. (Rubiaceae)

quite polyphagous; Martorell (1976) listed 11 host plants, many of them agricultural crops. This is the first time the species is reported feeding on *Elephantopus mollis* and *Ruellia coccinea* in Puerto Rico. Of eight wild-caught larvae grown in glass jars, only two became adults; the others were parasitised by tachinid flies (*Calocarcelia* sp.).

Perichares philetes (Hesperiidae). By the end of May, larvae of this skipper were quite numerous on the grass *Scleria pterota*, which became abundant after the hurricane. Some plants were attacked by eight or more larvae and in some

instances defoliation of the plant reached 75%. Only three of eight wild-caught larvae grown in glass jars reached the adult stage; two died in the larval and one in the pupal stage (from unknown causes), and two died of parasitism by a tachinid fly. The insect is considered to be a minor pest of sugarcane which is its chief host plant (Martorell 1945, 1976); other host plants of *P. philetes* are Indian corn and bamboo (Riley 1975).

Condica cupentia (Noctuidae). This species fed heavily on *Mikania cordifolia.* On some vines, where only *C. cupentia* larvae were present, more than 95% of the leaves were consumed. This vine reached high levels of dominance in the forest after the hurricane; in the lowland parts of the forest, vines covered a high proportion of the ground and many standing trees. This is the first time this species is reported feeding on *Mikania* in Puerto Rico. The only other host reported for larvae in Puerto Rico is *Pluchea purpurascens* (Sw.) DC. (Compositae) (Martorell 1976). A tachinid (*Lespesia* sp.) parasitised the larvae of *C. cupentia.*

Gonodonta nitidimacula (Noctuidae). Larvae fed on members of the Piperaceae. During the spring after Hurricane Hugo, most pipers had at least one larva, but defoliation was minor due to the low density of larvae per sapling. Few plants had more than three larvae.

Antillea pelops (Nymphalidae). Adults were common in the forest by January 1990, but rare by March. Larvae were found feeding on *Justicia martinsoniana* at El Yunque Peak by the beginning of June. Defoliation on these small plants was about 50%.

Historis odius (Nymphalidae). According to Martorell (1976) this is a rare species in Puerto Rico, but after the hurricane (May 1990) the larvae were commonly observed feeding on the underside of leaves of *Cecropia peltata* saplings. *Cecropia peltata* is another plant species that specializes in colonizing disturbed sites in the Neotropics. Only one of ten wild-caught larvae grown in glass jars reached the adult stage; the other nine were parasitised by tachinid flies (*Calocarcelia* sp.). This species, along with *Ecpantheria icasia* (Arctiidae) above, suffered intensive parasitism by these flies. *Colobura dirce* (Nymphalidae) adults (another species which feeds on *Cecropia*) were common in the forest, but larvae were not seen.

Hypanartia paullus (Nymphalidae). The caterpillars fed on *Trema micranthum,* defoliating almost all the saplings observed in the forest. According to Wolcott (1948) the caterpillars are quite common, several often being present on a small single tree. *Trema micranthum* is a species typical of cutover second-growth forest at higher elevations, or in cuts along new roads in the mountains.

Perigonia lusca (Sphingidae). This sphingid defoliated most of the observed shrubs of *Gonzalagunia spicata* in the forest by May 1990. The attack was intense in both

the heavily hurricane-devastated part of the forest as well as in the less affected areas. *Spodoptera eridania* also fed on this shrub, but its effect was minor. In Puerto Rico, *P. lusca* caterpillars feed on other members of the Rubiaceae like *Coffea arabica* L. and *Rondoletia* sp. (Martorell 1976); in Costa Rica, it also feeds on Rubiaceae (Janzen 1984).

Xylophanes tersa (Sphingidae). This species was commonly found feeding on *Psychotria berteriana* saplings. Two other Rubiaceae, *Borreria verticillata* (L.) Meyer and *Diodia sarmentosa* Sw. are host plants in Puerto Rico (Wolcott 1948). *Xylophanes* also feeds on Rubiaceae in Costa Rica (Janzen 1984).

Syllepte silicalis (Pyralidae). This species is a leaf roller and caused more damage than did the other Lepidoptera species that fed on *Cecropia peltata* saplings. It was also feeding on saplings and damaged trees of *Didymopanax morototoni* by the end of May, and all inspected *D. morototoni* trees were attacked. Most leaves of *D. morototoni* suffered at least 50% surface loss. This was the only lepidopteran species that reached outbreak proportions on a damaged forest tree, this tree species being considered a successional species in tropical forests. The ichneumonid *Colpotrochia cerebrus* (Dewitz) parasitised *S. silicalis*.

Other observations

The following are the new host records for Lepidoptera in Puerto Rico: *Psuedoplusia* sp. (Noctuidae) larvae fed on *Lobelia portoricensis* (Vatke) Urban (Lobeliaceae); *Oxydia vesulia* Cramer (Geometridae) fed on avocado leaves (*Persea americana* Mill.), the woody vine *Securidaca virgata* Sw. (Polygalaceae), and the vine *Cissampelos pareira* L. (Menispermaceae).

In October (one month after the hurricane) there were conspicuous increases in the Diptera, especially fruit flies. This was probably a consequence of the increase of rotten fruits in the forest; although the possibility of vertical displacement of fruit flies cannot be ruled out. Peaks in abundance of bark beetles (Coleoptera: Scolytidae) and pin-hole borer (Coleoptera: Platypodidae) occurred during the months of November and December. This was related to the increase in dead or damaged timber.

DISCUSSION

Catastrophic disturbances like hurricanes are followed by large populations of young leaves, an effect that may accelerate herbivore action (Odum & Ruiz 1970). The new flush of successional vegetation resulting from Hurricane Hugo was probably the primary cause of the lepidopteran outbreaks described here. All the Lepidoptera fed on early successional plant species, and climax or mature species were not affected. Most of the Lepidoptera involved probably represent opportunistic species that survive in disturbed habitats such as agricultural land, and which moved or increased their abundance in response to the flush of

opportunistic plant species that followed the passage of the hurricane. The hypothesis that hurricanes can eliminate the natural enemies of an insect and cause temporal single-stage outbreaks (Godfray & Chan 1990) can be ruled out in this instance because outbreaks occurred seven months after the hurricane.

The response of herbivores to this new flush of vegetation was clearly observed in *Spodoptera eridania* larvae, which fed on opportunistic species that penetrated the forest when disturbances occurred. Pokeweed, *Phytolacca rivinoides*, was rare in the forest prior to the hurricane, but became very abundant afterwards. The increase in *P. rivinoides* and the presence of large populations of *I. wallerana* near the borders of forest roads seem to be two of the factors contributing to the outbreak. In Puerto Rico, pokeweed is found along road banks, trails, and disturbed areas (Edmisten 1970). Disturbance of soil appears to be the critical factor in the germination of pokeweed, with light being a secondary factor for the survival of the seedlings (Bell 1970). Also, high soil temperatures accelerate germination (Edmisten 1970). Disturbances of the soil due to landslides and tree uprootings, higher illumination, and elevated soil temperatures resulted from the passage of the hurricane. These conditions contributed to increases in the population of *P. rivinoides*, a light-demanding annual herb that colonizes disturbed areas like landslides but is not observed growing in treefall gaps (Guariguata 1989, Pérez 1986).

The first records of *S. eridania* in Puerto Rico are from 1880, as larvae feeding on *Amaranthus*, *Solanum torvum* and *Phytolacca*. Larvae also attack tomatoes, potatoes, peppers and tobacco, and are recorded from Swiss chard and mulberry (Wolcott 1948); most of these hosts belong to the Solanaceae. Though *Solanum torvum* seems to be an acceptable host in agricultural areas, it was not highly acceptable during the forest outbreak. This is the first time *S. eridania* has been reported attacking forest vegetation in Puerto Rico.

Spodoptera eridania was always observed feeding on saplings, herbs, grasses, sprouts from fallen trees etc., and never seen in crowns of mature trees. The absence of feeding on mature tree leaves could be related to their low digestibility compared with leaves of non-woody plants (Scriber & Feeny 1979, Soo & Fraenkel 1966a, 1966b). Larvae of *S. eridania* feeding on leaves of the tree bracatinga (*Mimosa scabrella* Bentham) required an extra (7th) instar to complete their larval stage (Mattana & Foerster 1988). The additional instar compensated for a slower initial performance on this diet. In the absence of a highly acceptable host, *S. eridania* can cause severe defoliation in reforested areas with bracatinga in southern Brazil (Foerster & Dionisio 1989). Manuwoto & Scriber (1986) found that tannins from many tree species suppressed the growth of first instar larvae of *S. eridania*. The absence of *S. eridania* larvae on crowns of mature trees might also be explained by the adult oviposition preferences for low growing vegetation, and the defence mechanism of the larvae (letting go of the plant) when attacked or disturbed by natural enemies.

Wild-caught larvae of *S. eridania* fed on their original host plants appeared to find adequate nutrition. Though feeding rates were not measured, some plant

species were consumed faster than others and the amount of food consumed varied with different plants. These factors can affect the development, survival and fecundity of larvae feeding on a particular plant (Barbosa & Wagner 1989). Also host plants vary in the amount of cover provided for the larvae, and thus there is variation in protection against natural enemies and the weather. Ichneumonid parasites appear to locate larvae more easily on plants with small leaves. It was observed that when temperatures rose in the forest, larvae sought protection from the sun by hiding parallel to the shaded side of remaining parts of the plants.

Larvae of *S. eridania* crossed forest roads in the Luquillo Mountains when their food was exhausted. USDA Forest Service personnel assigned to the Luquillo Mountains observed larvae feeding on tomatoes, potato skins, and lettuce inside trash cans. Larvae entered houses in the forest and even fed on dog food. In Florida (USA), outbreaks of *S. eridania* occurred in sunflower containing dense stands of pigweed (*Amaranthus*), a primary host plant of this species; after consuming the pigweed, the larvae moved *en masse* to the sunflower (Mitchell 1984). This behaviour could explain the increase in feeding on some less acceptable plants that were near *P. rivinoides*, *C. macrophyllum* or *I. wallerana*. Similarly, in stands that contain both highly acceptable and less acceptable host plants for the gypsy moth in the USA, the less acceptable are sometimes defoliated by older larvae after the earlier instars defoliated the more acceptable. In this way, the density of more acceptable species can account for differences in the degree of defoliation among stands (Barbosa & Wagner 1989).

Scriber (1986) found *S. eridania* feeding on *Phytolacca rigida* Small growing on recently disturbed sandy soils in Florida. In contrast to the present study, he found low levels of *S. eridania*, and these only on pokeweed, although dozens of other food plants existed in the immediate vicinity.

Impatiens wallerana, one of the heavily defoliated species, is an introduced garden plant in Puerto Rico and thrives well in disturbed wet locations such as road borders. Owing to its short stature (less than 1 m), *I. wallerana* did not suffer much damage during the hurricane and was able to increase as a result of the canopy opening. This is the first report of a lepidopteran feeding on *I. wallerana* in Puerto Rico.

Little is known about the natural food plants of *S. eridania* larvae. Most of the food plants reported in the literature are garden or agricultural crops (Scriber 1986, Tietz 1972). Findings here confirm early suggestions that the genus *Phytolacca* is among the natural host plants of *S. eridania* (Crumb 1927). In temperate North America, *Phytolacca americana* is an acceptable host for the larvae of this moth; it is well digested and efficiently converted into body weight. Conversion is efficient because the larval period on this plant is short, resulting in a smaller energy expenditure for the maintenance of body functions (Soo & Fraenkel 1966a, b). *Cestrum macrophyllum* (Solanaceae) is probably another natural host. The range of *C. macrophyllum* includes Hispaniola and Puerto Rico, and it is found in the majority of forests in Puerto Rico. Elsewhere, *C. macrophyllum*

plants are grown as ornamentals (Little *et al.* 1974). The outbreak of *S. eridania* in Puerto Rico following Hurricane Hugo persisted in the highland forest until the end of June, and there was abundant *C. macrophyllum* as food in these areas.

Termination of the *S. eridania* outbreak appeared to be associated with a reduction of the highly acceptable larval food due to feeding activity, and to an apparent increase in parasitism by ichneumonid wasps. Contrary to Mitchell (1984), parasitism by braconids was not observed in Puerto Rico.

By August 1990, outbreaks of Lepidoptera other than *S. eridania* had ceased. Wild-caught larvae of those lepidopterans grown on their original host plants suffered intensive parasitism by tachinid flies, a factor that might have contributed to their decline. However, the causes of the collapse of these outbreaks remain an enigma. Another question that remains unanswered is the relative short duration of the outbreaks.

One of the drawbacks of the present study is a lack of control information on the status of the Lepidoptera in the Luquillo Mountains prior to the hurricane. However, insect outbreaks were not reported in other Puerto Rican forests which suffered only mild damage from the hurricane. This lends some support to the hypothesis that insect outbreaks were related to changes brought about by the hurricane. A revision of the book *Annotated food plant catalog of the insects of Puerto Rico* (Martorell 1976) does not indicate that the lepidopteran species discussed in this paper (with the exceptions of *Syllepte silicalis* and *Hypanartia paullus*) have caused extensive defoliation in the Luquillo Mountains before the passage of this hurricane. In addition, many of the host plants are the first records for these lepidopterans in Puerto Rico.

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