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General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest

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Abstract: A severe outbreak of Lepidoptera followed the 1997–98 El Niño Southern Oscillation event, during which the climate in central Panama was unusually dry. The outbreak involved the larvae of at least 12 species of Lepidoptera and occurred at a seasonally dry, deciduous forest site, where extensive background data were available regarding climate, tree species and non-outbreak herbivory levels. Most Lepidoptera were associated with only one or two larval host plant species belonging to the same family, and the majority were monophagous during this study. During the outbreak, caterpillar densities for the major outbreak species averaged 1.6 larvae per young leaf and 0.18 larvae per leaf for leaves of all ages. For canopy trees and lianas, the mean level of leaf damage was 13.8%, ranging from 1–100%. Seven out of 20 tree species sustained most of the damage, with 21–37% of the leaf area consumed. Relative to non-outbreak years, damage levels increased by more than 250% during the outbreak. Single-species outbreaks were observed in other areas with a similar drought, but wetter forests in central Panama did not experience outbreaks during this period. Historically, fewer outbreaks have been reported from tropical forests than from temperate forests, however, similar El Niño-related outbreaks have occurred recently in several other locations throughout the tropics.

Key Words: canopy, defoliation, drought, El Niño Southern Oscillation, herbivory, Lepidoptera, outbreak, Panama, seasonally dry tropical forest

INTRODUCTION

Drought is sometimes associated with subsequent insect outbreaks in temperate and tropical mixed forests and monocultures (reviews by Gray 1972, Mattson & Haack 1987). Drought may have a direct effect on the physiology and behaviour of defoliators, or may indirectly alter interactions between the defoliator and its host and/or between the defoliator and its natural enemies. For example, foliage may become more palatable to herbivores during a drought (White 1969, 1976, 1984) or defoliators may be released from parasitoid pressure (Berryman 1987, Faeth 1987).

Droughts are associated with El Niño Southern Oscillation (ENSO) events in some parts of the tropics (Holmgren *et al.* 2001). A severe dry season in central Panama was associated with the 1997–98 El Niño Southern Oscillation (ENSO). Following this dry season, we observed a dramatic defoliation event in a Pacific coastal forest near Panama City, Panama. This defoliation can be classified as a pulse gradient outbreak, because it followed a change in environmental conditions and did not spread from an epicentre to cover large areas (Berryman 1987). The outbreak occurred at a site where extensive data had been collected concerning the climate, the tree species and their levels of herbivory in years preceding the outbreak. We used a tower crane to access the forest canopy, where the outbreak was most severe. We documented herbivore densities, identities and defoliation levels, in order to ask the following questions. First, how did herbivore densities and damage levels compare with non-outbreak years? Second, how similar was this outbreak to outbreaks reported from temperate and tropical forests? Finally, we consider the implications of the outbreak's association with an ENSO event, given that such events are predicted to increase in frequency and intensity (Timmermann *et al.* 1999).

METHODS

Parque Natural Metropolitano (PNM) is a dry, semi-deciduous forest near the Pacific coast (8°59′N 79°33′W)

Table 1. Plant species and sampling effort for caterpillar censuses.

Species*	Code	Family	No. indiv. plants†	No. census times	No. young leaves	No. mature leaves
Acalypha sp.	ACAS	Euphorbiaceae	8	1	99	263
Amphilophium paniculatum	AMPP	Bignoniaceae	8	3	307	1818
Anacardium excelsum	ANAE	Anacardiaceae	3	4	221	7199
Annona spraguei	ANNS	Annonaceae	5	2	203	1349
Aristolochia tonduzii	ARIT	Aristolochiaceae	9	3	63	730
Aristolochia inflata	ARII	Aristolochiaceae	8	1	51	248
Arrabidaea candicans	ARRC	Bignoniaceae	6	1	0	153
Arrabidaea patellifera	ARRP	Bignoniaceae	9	2	8	581
Bonamia maripoides	BONM	Convolvulaceae	8	3	172	637
Castilla elastica	CASE	Moraceae	6	3	591	3348
Cecropia longipes	CECL	Cecropiaceae	4	3	52	313
Cecropia obtusifolia	CECO	Cecropiaceae	1	3	22	150
Cecropia peltata	CECP	Cecropiaceae	4	3	64	364
Chlorophora tinctoria	CHLT	Moraceae	1	2	87	601
Chrysophyllum cainito	CHRC	Sapotaceae	2	1	138	1182
Cissus sp.	CISS	Vitaceae	6	2	67	208
Combretum fruticosum	COMF	Combretaceae	8	2	0	672
Cordia alliodora	CORA	Boraginaceae	4	3	766	5740
Doliocarpus major	DOLM	Dilleniaceae	8	1	21	191
Ficus insipida	FICI	Moraceae	4	4	406	3963
Genipa americana	GENA	Rubiaceae	1	2	0	277
Gouania lupuloides	GOUL	Rhamnaceae	7	1	253	43
Luehea seemannii	LUES	Tiliaceae	0‡	0‡	–	–
Mikania leiostachya	MIKL	Asteraceae	0‡	0‡	–	–
Nectandra cuspidata	NECC	Lauraceae	1	3	315	1742
Passiflora vitifolia	PASV	Passifloraceae	8	2	29	228
Philodendron sagittifolium	PHIS	Araceae	8	1	3	100
Phoebe cinnamomifolia	PHOC	Lauraceae	4	3	0	2959
Phryganocydia corymbosa	PHRC	Bignoniaceae	9	2	5	412
Pittoniotis trichantha	PITT	Rubiaceae	5	3	401	1754
Pseudobombax septenatum	PSES	Bombacaceae	1	1	0	158
Schefflera morototoni	SCHM	Araliaceae	1	1	2	88
Serjania mexicana	SERM	Sapindaceae	8	3	15	298
Spondias mombin	SPOM	Anacardiaceae	4	2	161	680
Stigmaphyllon hypargyreum	STIH	Malpighiaceae	4	2	43	378
Stizophyllum riparium	STIR	Bignoniaceae	7	2	27	321
Trichostigma octandrum	TRIO	Bignoniaceae	0‡	0‡	–	–
Urera caracasana	UREC	Urticaceae	4	2	99	291
Vitis tiliifolia	VITT	Vitaceae	8	2	178	438
Zuelania guidonia	ZUEG	Flacourtiaceae	1	1	0	180

* Plant species and authors follow Correa *et al.* 2004.
† Each individual tree had an average of four counting stations at each census; each individual liana had one counting station at each census.
‡ Plant species with zero values indicate that we measured herbivory only, and did not count larvae. See Methods for herbivory sample sizes.

in the Republic of Panama. A canopy crane, consisting of a 42-m tower and 52-m boom, provided three-dimensional access to approximately 0.7 ha of forest in the PNM. The seasonally dry, lowland tropical forest is secondary growth, approximately 90 y old, with canopy heights averaging 20–35 m. More than 50 tree and canopy liana species occur in the forest area under the crane boom. Tree species common in the area include *Anacardium excelsum*, *Luehea seemannii*, *Castilla elastica* and *Annona spraguei* (Table 1). Further details of the site can be found in Parker *et al.* (1992).

At PNM, a wet season (May to December) alternates with a dry season (January to April). In non-outbreak years, annual rainfall averages 1850 mm, with an average of 340 mm falling during the dry season (Figure 1). During the 1997–98 ENSO event, the dry season began 1 mo early, and only 4.2 mm of precipitation was recorded at the PNM during the first 4 dry months. Then in April 1998, rain fell on only 4 d (total of 68 mm) (Figure 1). We first observed the outbreak in the forest canopy of PNM on 14 August 1998, by which time severe defoliation already had occurred. Data collection began on 17 August 1998, when the outbreak was already past its peak, and continued until 30 September 1998 when caterpillar numbers had returned to normal levels. That the outbreak was past its peak was apparent, because of the severe defoliation and the presence of larval exuviae that littered the canopy and dropped to the forest floor.

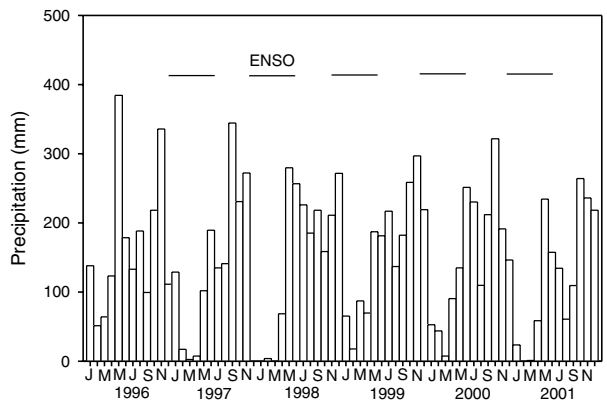

Figure 1. Monthly precipitation for 1996–1999 at the Parque Natural Metropolitano, Panama. The 1997–98 El Niño Southern Oscillation (ENSO) was accompanied by a drought throughout Central Panama. Horizontal lines indicate the dry seasons (January–April).

Insect density and identification

To count and collect larvae, we created 185 census stations in the canopy (Table 1). Individual lianas had one station each, whereas individual trees had 4–5 stations each. A counting station consisted of the area of foliage in front of the parked gondola (approximately 2 m^2). We assigned caterpillar morphospecies numbers in the field to facilitate counts. During a visit to a station, counts included the number of young leaves, the number of mature leaves, and the number of larvae per morphospecies. Young leaves were defined as those that were still expanding, were noticeably paler in colour and/or softer than mature leaves. We include a summary of sampling effort for larval counts in Table 1. We visited as many active census stations as possible within a 4-h period. Census stations became inactive once the leaves and/or caterpillars disappeared. From 17–31 August, the censuses took place 4 h d^{-1}, 5 d wk^{-1}. From 2–30 September, censuses were reduced to 3–4 d wk^{-1}.

We collected and reared several specimens of each larval morphospecies. All larvae were reared in clean, plastic bags. Many larvae died before we could identify them, and in some of these cases we report only families. Final identifications were made by Vitor Becker (University of Brasilia), Michael Pogue, Alma Solis (U.S. Dept. of Agriculture) and Annette Aiello. We caution that it was often difficult to distinguish morphospecies in the field, and a couple of closely related species were lumped into one morphospecies during our counts (see footnotes of Table 2). Some caterpillars may have been wandering in search of palatable food or places to pupate, and therefore were not necessarily associated with the plant species they were collected on. Therefore, we report only caterpillar–host plant associations for which the larva fed on the plant for $\geq$ 5 d and then pupated successfully. In addition, we used past rearing data to confirm caterpillar–host associations (Aiello, unpubl. data).

Herbivory

We estimated levels of herbivory for 20 tree species and 19 liana species that we could reach easily from the crane. We defined herbivory as the percentage of leaf area missing due to chewing or scraping; leaf miner and fungal damage were not included. For each plant species, we measured herbivory once on four randomly chosen focal branches. We estimated herbivory levels for 10–40 leaves per branch using a 10-mm clear, plastic grid to measure total leaf area and a 3-mm grid to measure leaf area missing. During the outbreak, we estimated herbivory levels for 2293 leaves. The measured leaves were of various ages: approximately 10% young (soft and pale coloured) and 90% mature (fully lignified). We compared herbivory levels during the outbreak year (1998) with herbivory levels during non-outbreak years (1992–97) for 24 tree and liana species for which we had past measurements (Wright & Samaniego, unpubl. data). We estimated herbivory levels using identical field methods during outbreak and non-outbreak years. In the 1992–97 dataset, herbivory measurements were performed on 10–40 leaves of 3–12 branches per species. The leaves measured in the 1992–97 dataset were 1 mo (58%), 4 mo (35%) and 9 mo old (7%).

Our herbivory measurements were a one-time estimate of standing crop damage; therefore, the measurements likely underestimate the damage due to the outbreak. Because we did not follow the fates of individual leaves, we would have missed leaves that were completely eaten before the census, which may have led to an underestimate of up to 50% (Coley & Barone 1996, Lowman 1984).

RESULTS

Outbreak Lepidoptera and herbivory

The larvae of at least 12 species reached outbreak proportions in the local area; 10 had counts of 50 or more individuals per species and two showed evidence of an earlier outbreak generation (hundreds of larval exuviae) (Table 2). In addition, we documented 21 lepidopteran-host associations and counts for species reared during the outbreak (Table 2).

Caterpillar densities for the major outbreak species (part I of Table 2) averaged 1.6 larvae per young leaf and 0.18 larvae per leaf for leaves of all ages. By comparison, in 2000, a non-outbreak year, caterpillar densities were censused on six randomly chosen branches

Table 2. Host–caterpillar associations and caterpillar counts at the Parque Natural Metropolitano during the 1998 outbreak.

Lepidopteran	Host plant code	No. indiv.	Average larvae per young leaf	Average larvae per leaf*
I. Observed outbreak species				
Arctiidae				
Eucereon tesselatum Schaus	FICI	53	0.32	0.02
Munona iridescens Schaus	CORA	109	0.40	0.03
Epiplemidae				
Syngria druidaria Guenée	AMPP	144	1.09	0.10
Lasiocampidae				
Euglyphis rivulosa & E. fibra†(Moesch., Schaus)	NECC	273	1.54	0.18
Euglyphis rivulosa & E. fibra†(Moesch., Schaus)	PHOC	50	–	0.06
Noctuidae				
Dyops dotata (Walker)	CECO	61	5.07	0.73
Notodontidae				
Rifargia distinguenda (Walker)	ANAE	105	–	0.33
Malocampa albolineata & M. satis† Druce	CASE	397	1.27	0.15
Pyralidae				
Deuterollyta nigripunctata (H. Sch.)	PHOC	72	–	0.05
II. Evidence of previous outbreak				
Limacodidae				
Phobetron hipparchia Cramer	ANAE	11	–	–
Pyralidae				
sp.	UREC	29	0.52	0.16
III. Additional species reared during the outbreak				
Apatelodidae				
Olceclostera maya Schaus	AMPP	3	–	–
Olceclostera maya Schaus	PHRC	5	–	0.08
Arctiidae				
Aclytia heber Cramer	ANNS	17	0.51	0.07
Halysidota schausi Rothschild	CASE	2	0.22	0.02
Bombycidae				
Colla rhodope (Drury)	FICI	17	0.27	0.02
Elachistidae				
sp.	ANNS	25	0.76	0.09
Limacodidae				
Phobetron hipparchia Cramer	CHLT	2	0.32	0.02
Phobetron hipparchia Cramer	SPOM	2	0.17	0.04
Noctuidae				
Dyops dotata (Walker)	CECL	21	5.16	0.69
Cropia philosopha Schaus	CORA	3	–	0.028
Notodontidae				
Nystalea nigritorquata (Dognin)	ANAE	9	–	0.21
Nymphalidae				
Adelpha iphiclus (L.)	PITT	17	0.16	0.03
Callicore pitheas (Latreille)	SERM	7	1.00	0.08
Eueides lineata Schaus	PASV	2	0.20	0.05
Papilionidae				
Parides eurimedes (Cramer)	ARIT	3	–	0.04
Pyralidae				
Conchylodes salamisalis Druce	CORA	4	0.09	0.01
Paridnea holophaealis Ragonot	CORA	5	0.14	0.04
Phostria trucatalis (Hampson)	GENA	4	–	0.06
Saturniidae				
Hylesia sp.	ANNS	21	0.50	0.68
Periphoba arcaei (Druce)	ANAE	19	–	–

* The average number of caterpillars per leaf with young and mature leaves combined.

† The larvae of *Malocampa albolineata* and *M. satis* were difficult to distinguish in the field, so count data represent the sum of larvae counted for both species on this host. Also difficult to distinguish were *Euglyphis* species on *Nectandra cuspidata* and *Phoebe cinnamomifolia.*

each of *Castilla elastica* and *Anacardium excelsum* using comparable census methods, at which time the average number of caterpillars per leaf was 0.041 for *C. elastica* and 0.009 for *A. excelsum* (Van Bael, unpubl. data). In the 1998 outbreak, those numbers were 0.147 and 0.333, respectively (Table 2).

As the outbreak declined, some tree species flushed new leaves. This leaf flush did not match usual phenological

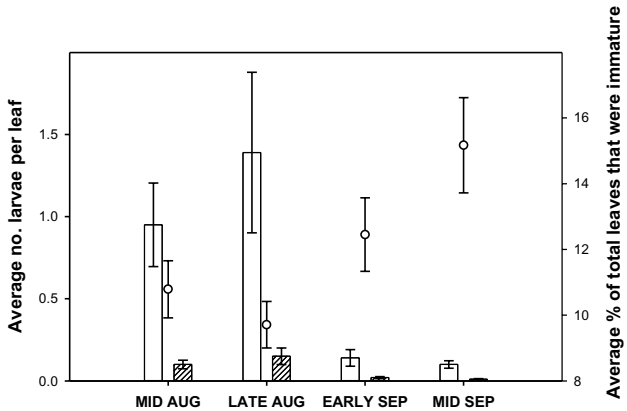

Figure 2. Average number of larvae on immature leaves (open bars) and on mature leaves (shaded bars) and the average percentage of leaves that were immature (open circles). All error bars represent 1 SE. The number of active census stations for each time period was: mid-August (n = 55), late August (n = 98), early September (n = 101) and mid-September (n = 73).

patterns with respect to timing (Wright, unpubl. data) and appeared to replace damaged and abscised leaves. Caterpillar densities decreased despite this increase in young leaves (Figure 2). At the counting stations, the average percentage of young leaves (out of all leaves) increased as the caterpillar densities decreased (Figure 2).

Most Lepidoptera were associated with only one or two larval host plant species belonging to the same family, and the majority were monophagous during this study (Table 2). We caution, however, that monophagy is difficult to determine conclusively without long-term natural history work. Only one species, *Phobetron hipparchia* Cramer (Limacodidae), fed on several unrelated host plants during the study (Table 2). *Phobetron* is a known generalist in Panama (A. Aiello, *pers. obs.*).

Herbivory levels were significantly greater in the outbreak year (1998) than in non-outbreak years (1992–97) for 20 out of 24 species (Table 3, Sign test, $P < 0.001$, $df = 23$). The absolute increase in leaf damage from 1992–97 to 1998 averaged 9.1%, reflecting a relative increase of more than 250% (Table 3). Seven tree species and a liana received the highest amount of damage, with herbivory levels greater than 20% during the outbreak (Table 3). For these seven species, average herbivory levels ranged from 21.6% to 37.0%, and the mean of the difference from 1992–97 to 1998 was 21.7%. Across all tree and liana species, the average leaf area missing was 13.8% (range 1.3–100%, Table 3).

Our estimates of caterpillar densities and herbivore damage probably are underestimates. For example, when the outbreak was first discovered, all individuals of one liana species, *Trichostigma octandrum*, had been 100% defoliated (Table 3), and the defoliator was no longer present. Thus, it could not be reared, counted or even identified. In addition, *Anacardium excelsum* had been defoliated severely, with evidence (larval exuviae and characteristic leaf damage) of an outbreak by the previous generation of *Phobetron hipparchia* (Table 2, Figure 3). Soon after herbivory on *A. excelsum* was estimated, the trees abscised 100% of their leaves and grew a completely new set. Hence, our herbivory measurements greatly underestimate the total impact of the outbreak for this tree species.

Table 3. Canopy herbivory levels during the 1998 outbreak compared with herbivory levels in non-outbreak years.

Species	Average % herbivore outbreak	Average % herbivore non-outbreak	Difference
Aristolochia inflata	3.20		
Arrabidaea candicans	4.50	0.08	4.42
Arrabidaea patellifera	11.73	2.12	9.61
Bonamia maripoides	7.52	5.12	2.40
Castilla elastica	36.96	3.38	33.58
Cecropia longipes	21.59	1.98	19.61
Cecropia obtusifolia	17.55	0.54	17.01
Cecropia peltata	8.48	0.68	7.79
Chlorophora tinctoria	1.11		
Chrysophyllum cainito	14.06	16.52	– 2.47
Cissus sp.	8.16		
Combretum fruticosum	7.17		
Cordia alliodora	31.73	2.67	29.05
Doliocarpus major	2.38	1.04	1.34
Ficus insipida	7.68	0.30	7.38
Genipa americana	7.80		
Gouania lupuloides	7.20	8.96	– 1.76
Luehea seemannii	6.77	5.15	1.62
Mikania leiostachya	4.13	0.86	3.26
Nectandra cuspidata	34.32		
Passiflora vitifolia	4.24		
Phoebe cinnamomifolia	12.83	8.05	4.78
Phryganocydia corymbosa	6.25	0.40	5.85
Pseudobombax septenatum	6.54		
Schefflera morototoni	2.61		
Serjania mexicana	10.99		
Stigmaphyllon hypargyreum	0.89	4.10	– 3.21
Stizophyllum riparium	10.90		
Trichostigma octandrum	100.0		
Urera caracasana	32.26	6.15	26.12
Vitis tiliifolia	3.69	1.59	2.10
Zuelania guidonia	7.85		
Minimum % herbivory	1.27	0.30	
Maximum % herbivory	100.0	16.52	
Average % herbivory	13.75	3.86	9.14

Natural enemies and predators

Parasitoids were present in 16% (8/50) of a subsample of caterpillars (eight Lepidoptera species) collected on 14 August 1998. In this sample, seven of the eight parasitoids were dipteran (Tachinidae), and the remaining was an unidentified wasp. Moreover, large numbers of

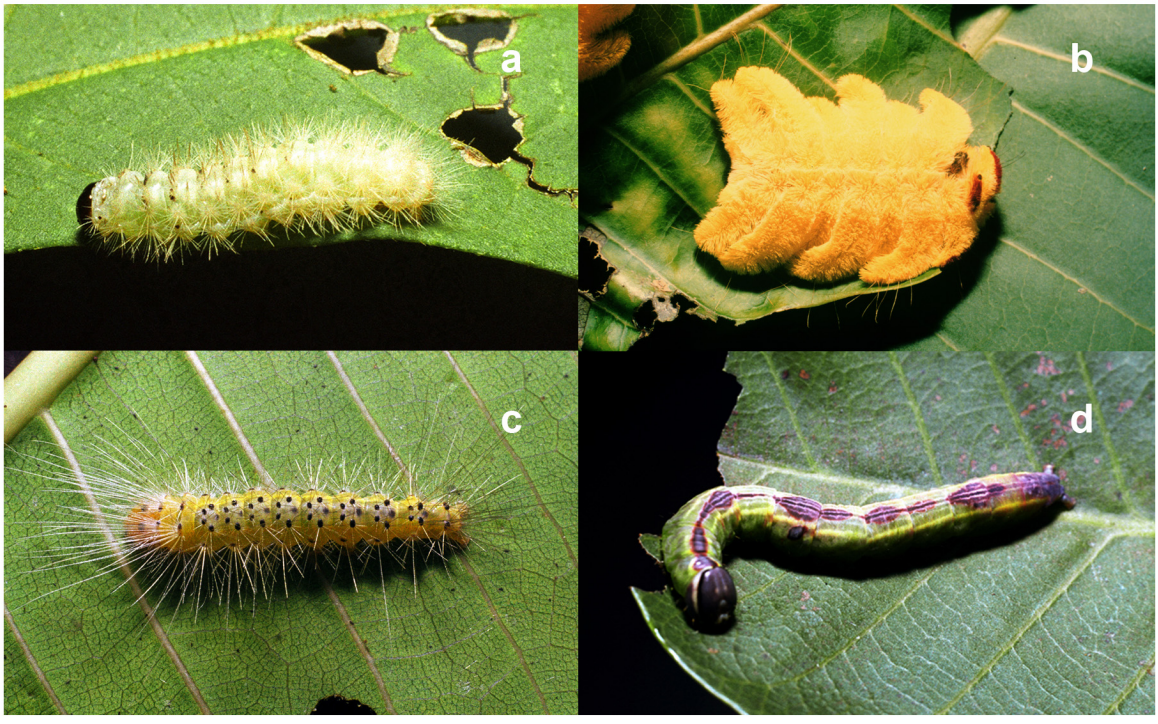

Figure 3. Larvae of four Lepidoptera species that were observed at outbreak levels. (a) *Munona iridescens* (penultimate instar), (b) *Phobetron hipparchia* (final instar), (c) *Eucereon tesselatum* (penultimate instar), (d) *Rifargia distinguenda* (final instar). Photographs by A. Aiello.

caterpillars died in the canopy and in the laboratory, apparently from bacterial, viral and/or fungal infections.

Flocks of 10–20 tropical kingbirds (*Tyrannus melancholichus*) and dusky-capped flycatchers (*Myiarchus tuberculifer*) were observed consuming caterpillars in the canopy. These species normally take flight when approached by the crane gondola. During the outbreak, the same species allowed the gondola to approach to within 1 m. Only when displaced repeatedly would birds gain altitude to escape, and even then their flight was clearly labored. Apparently the birds were heavily laden with ingested caterpillars. These flocks may have greatly reduced several caterpillar populations that were still at outbreak levels in September (J.Wright, *pers. obs.*).

Other outbreaks

Observations at other sites indicated that the geographic scale of the outbreak was limited to the drier Pacific coast of central Panama. Several smaller, localized outbreaks were observed in the vicinity of Panama City (Aiello, *pers. obs.*, Table 4). During the PNM outbreak, researchers searched for evidence of a similar event on Barro Colorado Island (BCI, 40 km N of PNM) and at the Fort Sherman crane site (70 km N of PNM). No evidence of an outbreak was observed in the canopy or understorey at either of these sites (Table 4). Both these sites received greater average levels of rainfall than PNM during normal years as well as during the 1997–98 ENSO event (Table 4). BCI and PNM share many of the same host plant species, but densities are lower on BCI. There is no tree species overlap between Fort Sherman and PNM.

DISCUSSION

Outbreaks and drought

The relationship between climate and fluctuating insect densities has been well established in the temperate literature (reviews by Mattson & Haack 1997, Myers 1998), especially with respect to global climate change (Bale *et al.* 2002). While temperature is most often described as the key variable driving insect population fluctuation in temperate forests, the direct impacts of precipitation have been neglected in recent research (Bale *et al.* 2002). Because temperature is more constant in tropical areas, changes in precipitation may play a larger role for tropical than temperate insect populations. Data from outbreaks in tropical forests are currently too few to outline broad patterns, but drought has long been thought to play an important role (Gray 1972).

The outbreak described above shares an important characteristic with earlier reports from forests in this and other tropical regions. Notably, the outbreak occurred

Table 4. Outbreaks and sites monitored in 1998.

Site	Coordinates	Defoliator	Host plant	Date 1998	Rainfall (mm)*
Parque Metropolitano	8°59′N 79°33′W	See Table 2	See Table 2	Aug–Sep	72.9
Naos Island	8°54′N 79°31′W	*Eudocima materna* (L.)† Noctuidae	*Odontocarya lamnoides* Menispermaceae	9 Jun	83.82
Arraiján	8°56′N 79°39′W	*Cerura dandon* Notodontidae	*Xylosma chlorantha* Flacourtiaceae	16 Sep	83.82
Ft. Kobbe	8°54′N 79°34′W	*Adelpha iphiclus* (L.) Nymphalidae	*Pittoniotis trichantha* Rubiaceae	22 Aug	83.82
Pipeline Rd.	9°9′N 79°44′W	*Adelpha iphiclus* (L.) Nymphalidae	*Pittoniotis trichantha* Rubiaceae	10 Aug	238.8
B.C. I.	9°10′N 79°51′W	No outbreaks observed			289.6
Ft. Sherman	9°17′N 79°58′W	No outbreaks observed			641.6

* Precipitation for December 1997–April 1998. For Naos, Arraiján, and Ft. Kobbe, ACP data for Balboa Heights (8°57′N, 79°33′W) were used. Daily rainfall records are available at www.stri.org/tesp
† Genus also known in the literature as *Othreis* and *Ophideres*.

during the rainy season that followed an ENSO-related drought. Similarly, Aiello (1992) noted a general outbreak of Lepidoptera in Panama after the extended dry season associated with the 1982–83 El Niño event. Several butterfly species were observed in large numbers on BCI and 40 km away in Panama City. In the same year as Aiello's observation, Janzen (1985) documented an outbreak of a moth, *Aellopos titan* (Sphingidae), in Costa Rica. Of the outbreak species noted during 1983, only one species, *Adelpha iphiclus* (Nymphalidae) overlapped with species that we noted at PNM in 1998. Outside of Central America, Lepidoptera outbreaks in natural systems have followed ENSO droughts in Indonesia (Whitten & Damanik 1986), tropical Australia (McKillup & McKillup 1997), and Borneo (Itioka & Yamauti 2004).

Drought-like conditions, however, are not a necessary precursor for the initiation of a tropical forest outbreak. Reports of Lepidoptera outbreaks on Barro Colorado Island, *Zunacetha annulata* (Dioptidae) (Wolda & Foster 1978) and *Eulepidotis* spp. (Noctuidae) (Barone 2000, Wong *et al.* 1990) were not related to drought. Notably, neither of these lepidopteran species overlap with outbreak species that followed severe droughts (Aiello 1992, Janzen 1985, this study).

Whereas the association between drought and subsequent outbreaks is clear in some instances, the mechanism involved is debatable (Watt 1994). Drought may affect the parasitoid populations of Lepidoptera (Aiello 1992, Janzen 1985), it may affect the chemistry (i.e. palatability) of their food (White 1969, 1976, 1984), it may alter the leaf phenology and thus food availability for herbivores (Itioka & Yamauti 2004), or it may result in a combination of such effects. We speculate that the outbreak we observed was caused by low levels of parasitism in the outbreak generation of Lepidoptera. The drought preceding the wet season may have decreased parasitoid populations to levels below that of non-outbreak years (Aiello 1992, Janzen 1985). Hymenopteran parasitoids, especially, seemed to be unusually rare in our collections, until the outbreak was nearing the end. Unfortunately, we did not have measurements of parasitism and leaf quality before, during and after the outbreak to distinguish between the hypotheses of parasitoids versus leaf quality. We cannot rule out the possibility that changes in leaf phenology, and thus greater quantities of young, palatable leaves might have caused the outbreak (Itioka & Yamauti 2004). We did observe, however, that the quantity of young leaves in the canopy actually increased as the outbreak waned (Figure 2). This pattern may be due to trees producing young leaves that were less palatable as the season progressed, or because parasitoids and disease prevented the second generation of Lepidoptera from reaching outbreak proportions. Finally, although the precise mechanism for the outbreak was not clear, the observation that the 1998 outbreak in Panama clearly occurred in dry locations and not in wetter sites further strengthens the argument that drought was a key correlate.

Tropical versus temperate forest outbreaks

Historically, insect outbreaks have been viewed as phenomena restricted to temperate zone forests (Elton 1958, Voûte 1946). More recently, however, ecologists have suggested that insect outbreaks in the tropics are just as common as in temperate forests, but are less obvious because there are so many tree species, and thus are less frequently reported (Gray 1972, Janzen 1984, 1985; Wolda & Foster 1978). The most striking difference between temperate and tropical outbreaks is

that forest outbreaks in mixed tropical forests tend to be sudden and very short-lived, involving only one or two generations of larval herbivores (Aiello 1992, Janzen 1984, 1985; Wong *et al.* 1990). The outbreak observed here, over a 5–6-wk period, was extremely brief and apparently without an obvious build-up. In contrast, a short outbreak in a temperate forest may be of 3–4 y duration, while a longer outbreak may continue for 10–15 y (Berryman 1987). Such a difference in temporal scale may be due to a greater diversity and strength of density-dependent regulating agents such as disease or natural enemies in tropical forests. As the 1998 outbreak ended, we observed increased predation by birds and evidence of increased levels of disease (e.g. large numbers of dead, blackened caterpillars draped over twigs). In general, tropical entomologists have reported rapid control of defoliator outbreaks by viral disease (Janzen 1984), fungal disease (Wolda & Foster 1978), or by a rebound of parasitoid populations (Janzen 1985).

Implications

ENSO events can have strong impacts on the dynamics of terrestrial ecosystems (Holmgren *et al.* 2001). ENSO events occur every 3–6 y, but are predicted to occur with greater frequency and severity as global temperatures rise (Timmermann *et al.* 1999). One consequence of that scenario might be an increased frequency of outbreaks in tropical forests that experience drought. Repeated, severe defoliations would likely decrease the fitness (Marquis 1984, Rockwood 1973, Wong *et al.* 1990) and alter the community composition of tropical trees (Terborgh *et al.* 2001), especially because some tree species appear to be more vulnerable than others to outbreaks.

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