Table 1: Differences in the mean (± SE) number of individuals observed per sampling event in closed and open forest at five sites in Costa Rica. *=P<0.005.

Site	Closed	Open	t	df	P
Palo Verde	2.13±0.58	7.73±1.65	3.19	28	0.004*
Monteverde	1.07±0.37	1.33±0.39	0.49	28	0.63
Cerro	4.80±1.30	9.20±0.94	2.74	28	0.011*
Corcovado	1.47±0.62	4.13±2.68	0.97	28	0.34
La Selva	1.47±0.45	2.93±0.58	1.53	28	0.14
All Sites	2.19±0.36	5.07±0.75	3.47	148	0.0007*

Table 1: Differences in the mean (± SE) number of taxa observed per sampling event in closed and open forest at five sites in Costa Rica. *=P<0.005.

Site	Closed	Open	t	df	P
Palo Verde	1.47±0.34	3.27±0.55	2.80	28	0.009*
Monteverde	0.66±0.19	1.07±0.30	1.13	28	0.27
Cerro	2.80±0.66	3.73±0.33	1.27	28	0.21
Corcovado	0.93±0.39	1.67±0.72	0.89	28	0.38
La Selva	1.00±0.28	1.93±0.48	1.68	28	0.10
All Sites	1.37±0.19	1.93±0.48	3.04	148	0.003*

RATES OF HERBIVORY ON UNDERSTORY LEAVES IN FIVE COSTA RICAN FORESTS

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Abstract. We measured understory leaf biomass lost to herbivory at five types of tropical forests in Costa Rica. Herbivory was greatest on leaves in the tropical dry forest (27.5%) while it ranged from 13.9% to 17.0% in the other four sites, for an overall average of 17.3%. This was similar to most previous reports for tropical forests. We found no difference in herbivory rate in young versus old leaves. Orthoptera were responsible for the greatest percent of leaf tissue lost at all sites (21.8% of biomass), followed by Lepidoptera (18.3%). No relationship was found between % herbivory and leaf toughness. Our findings indicate that herbivory is a major factor in tropical forests that varies greatly among habitats.

Key Words: Coleoptera, *leaf loss,* Lepidoptera, *plant defenses, toughness*

INTRODUCTION

Herbivory is an important animal-plant interaction influencing both plant growth rate and survival. It has been reported that there is greater herbivory in the tropics even though tropical plants have more defenses, like leaf toughness (Coley and Aide 1991). In this study, we examined how herbivory rates differed among five forest types in Costa Rica: tropical dry forest, cloud forest, montane forest, Pacific slope lowland tropical rainforest, and Atlantic slope lowland tropical rainforest. We predicted that leaf toughness would be greatest in areas where the leaves live longer (in wet forests). Also, because old leaves usually have more plant defenses, old leaves should be tougher than young leaves (Coley and Aide 1991). We hypothesized that with increasing leaf toughness, herbivory rates should decline because tougher leaves are considered less digestible. In addition, we expected herbivory on leaves in a dry forest to be greater than in a wet forest. This is based on the assumption that plants in a dry forest may invest less in defense because leaves there abscise after the wet season and the tree must produce new leaves every season. In deciduous forests expensive leaf defenses would be lost each time leaves are dropped.

METHODS

All 16 members of the 1997 Biology FSP gathered herbivory data during one day of our stay at each of five sites: the OTS station at Parque Nacional Palo Verde, Monteverde Biological Station at Monteverde, Estación Cuerici near Cerro de la Muerte, Estación Sirena at Parque Nacional Corcovado, and the OTS station at La Selva.

At each site, data were collected along two randomly selected, 30 m transects in closed forest (primary or mature secondary growth), and two in edges (gaps or forest within 0-35 m of an edge). Measurements were taken on seedlings of woody plants <1.5 m tall that crossed the drag line. Each new morphotype was recorded and its leaves were counted, classed as young or old, and inspected for leaf damage. After an initial period of calibration using a graph paper technique to estimate leaf loss, we visually estimated the percent of leaf area lost to herbivory for up to five young and five old leaves on each plant. We identified the type of insect herbivore by using a key to insect-damaged leaves (Hill 1983). Several physical attributes were measured for one representative young and old leaf on each sampled plant. Leaf length and width were measured with a ruler and leaf thickness with calipers. Toughness was measured with a ChantillonTM penetrometer and a hand lens was used to determine the presence or absence of pubescence on the leaf surface. Only the first seedling of each morphotype along the transect was sampled. All other seedlings of that morphotype were scored but no further data were collected on them. Distance covered along the transect was determined by a 30 min. time limit. Percent canopy cover along each transect was estimated using a spherical densiometer.

The physical data measurements were used to calculate the total leaf biomass at each site. Individual leaf volume was calculated by multiplying length by width by thickness. This leaf volume was then multiplied by the number of leaves per plant, weighted by size and age of leaf. This was then multiplied by the number of plants of that morphotype per transect in order to obtain a value for leaf biomass of that morphotype for that transect. Biomass values of each morphotype were added up for each transect and

the subsequent values for each transect were added together to come up with a total leaf biomass estimate for that site.

RESULTS

Overall, 17.3 % of understory leaf tissue was lost to herbivory across the five sites in Costa Rica, 15.4% on young leaves and 17.5% on mature leaves. Thus, overall, there was no difference in leaf-biomass loss by leaf age (t-test, t=0.88, df=208, P>0.38).

This overall herbivory rate is similar to the 10% average reported by Coley and Aide (1991) for various tropical sites (t-test, t=1, df=28, P=0.05; Table 1). Among our five sites, the total leaf loss varied significantly (one-way Anova, F=4.035, df=195, P=0.003). Leaf loss at Palo Verde was 27.5%, significantly greater than that at Monteverde, La Selva or Corcovado (Tukey-Kramer, n=17, P<0.05; Fig. 1). At the four wetter sites, the leaf loss estimates were lower than previously reported by Stanton (1975), whose data were also collected in Costa Rica (statistical comparison not possible because no variance was provided by Stanton; Table 1). The 27.5% leaf loss at Palo Verde was similar to the 30% reported by Stanton.

We found an average herbivory rate on young leaves of 15.4% (Fig. 2), which is less than half that found in a previous study in Panama (Coley and Aide 1991). Leaf damage at our studied sites was caused by many types of herbivores, including leaf mining Lepidoptera and Diptera, gall-forming or leaf-curling Hymenoptera and Diptera, sap-sucking Hemiptera, Homoptera and Thysanoptera, as well as leaf-chewing Coleoptera, Orthoptera and Lepidoptera. For purposes of analysis, we lumped the types of herbivores into three classes (Orthoptera, Lepidoptera and others) based on their frequency of occurrence. Leaf-biomass loss due to Orthoptera (21.8%) was greater than that due to either Lepidoptera (18.3%) or other herbivores(12.5%; Tukey-Kramer, n=69, P<0.05). There was considerable variation in the dominant herbivore agent between sites. At Palo Verde, Monteverde, and Corcovado, Orthopterans removed the highest fraction of biomass. Only at La Selva were Lepidopterans the dominate number of herbivore. At Cerro de la Muerte, sucking insects of order Hemiptera removed most of the biomass lost to herbivores (Fig. 3).

We found no relationship between leaf loss and leaf age (Fig. 4). Although more mature leaves were tougher than young leaves (t-test, t=3.47, df=286, P<0.001) there was no relationships between leaf loss and leaf age (t-test, t=0.829, df=208, P<0.38). Leaf toughness commonly found to be the physical character of leaves that most strongly predicts herbivory (Coley and Aide 1991) appears unrelated to leaf tissue loss in our study (Fig. 4). To test for relationships between leaf toughness and the leaf loss within more homogenous groups of plants, we performed 16 different regressions with different combinations of young leaves, old leaves, leaves in edge forest, leaves in closed canopy forest, leaves at each site, leaves consumed by Orthopterans alone or by Lepidopterans alone. Leaf toughness failed to explain more than 1% of the variation in the proportion of leaf loss.

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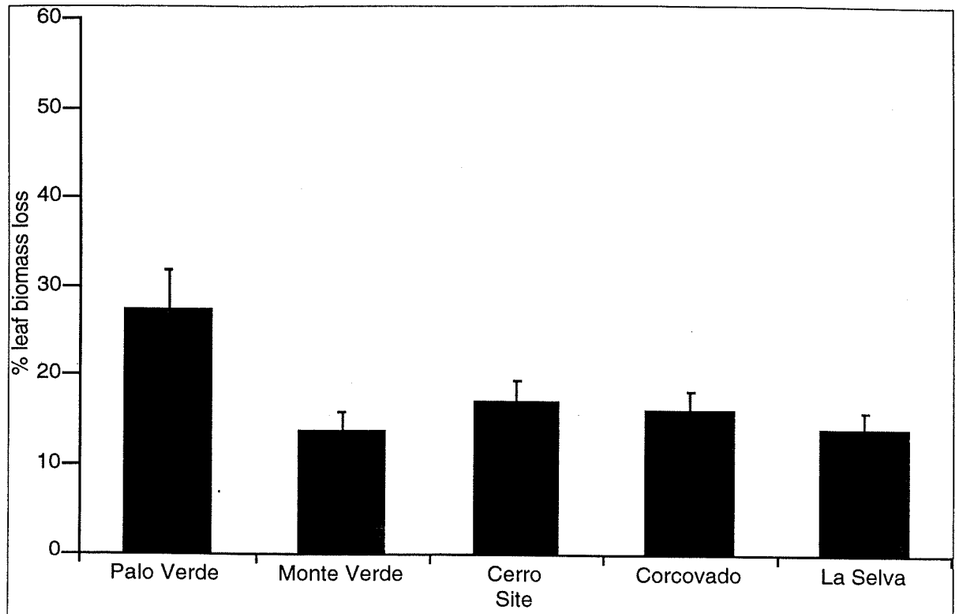

FIG. 1. Mean (±S.E.) % leaf biomass loss in five tropical forests.

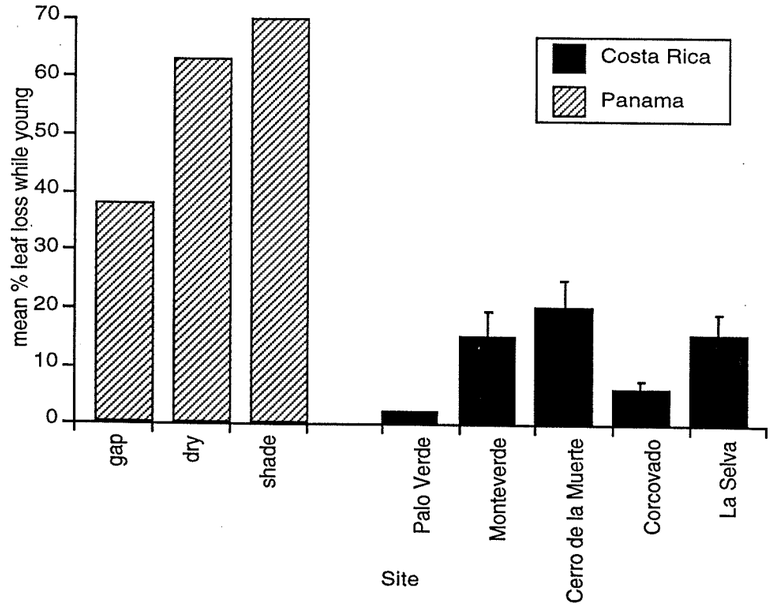

FIG. 2. Mean (± S.E.) %leaf loss while young in Panama (gap, dry, and shade forest estimates from Coley and Aide 1991) and in Costa Rica sit e (this study).

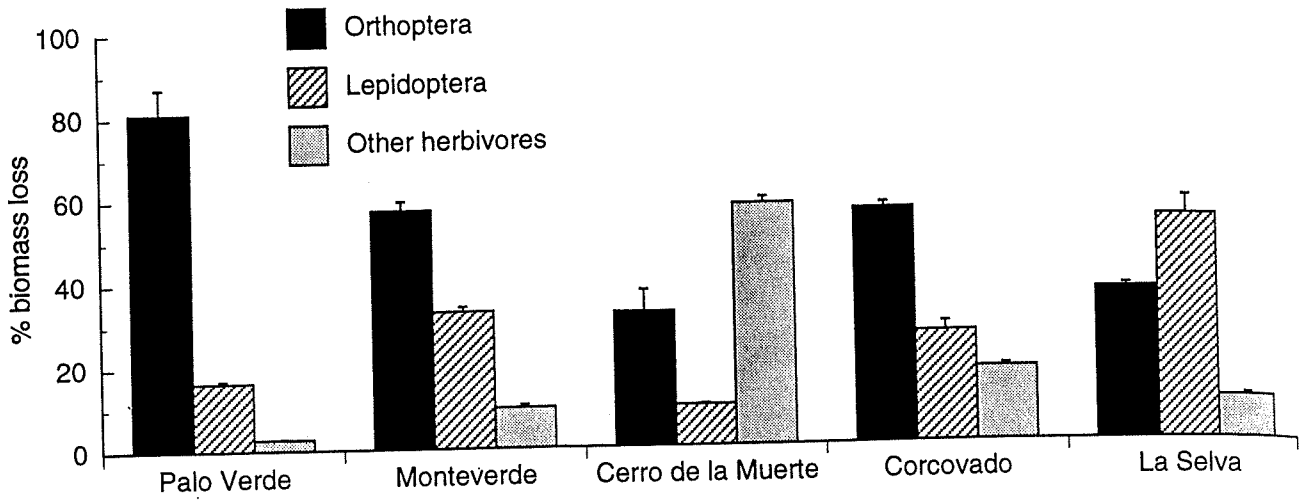

FIG. 3. Mean (≠ S.E) %proportion of leaf tissue lost to three herbivore groups at five sites in Costa Rica by herbivory agent.

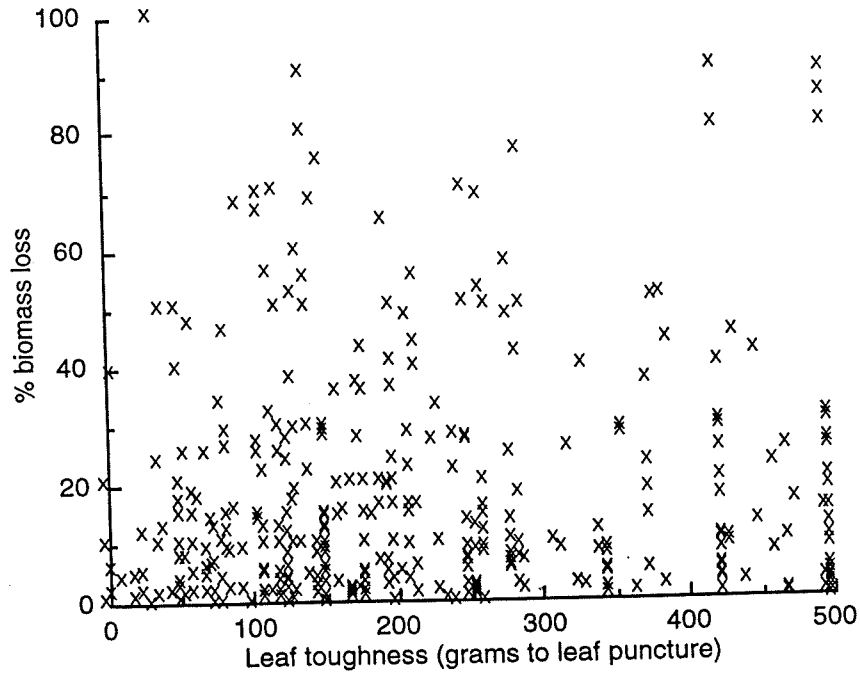

Fig. 4. Leaf tissue lost to herbivory is unrelated to the toughness of leaves at five Costa Rican forest sites. Each dot represents the mean %biomass lost and toughness of a single morphotype; n=162 morphotypes.