herbivore feeding behavior. Although hairs on leaves may deter some herbivores, many insects may be small enough, or conversely large enough, that hairs do not affect their feeding behavior. Along with pubescence, the thickness of leaves did not affect the amount of herbivory damage experienced by these plants.

Older leaves were significantly more damaged by herbivores than young leaves. This is probably explained by the fact that we sampled herbivory at a point of time instead of an herbivory rate over a period of time. Thus older leaves have a greater chance of being eaten due to their longer exposure to herbivory.

Most importantly, the amount of leaf area damage differed significantly among species. Younger leaves of all species showed similar amounts of herbivory while the older leaves showed different amounts of herbivore damage. Our findings agree with Coley's (1983) observations for young leaves and old leaves of pioneer and persistent tree species. It appears that mature leaves have more developed defensive characteristics. With respect to morphology, both young and old leaves of a species share common features of serration and venation, characteristics that did not change with leaf age. Yet young and old leaves experience different levels of herbivory damage, indicating that other changes in nutritive value, chemical compounds, and structural composition occur as leaves age.

Of all the leaf characteristics we examined, leaf age had the most significant affect on leaf area damage. However, this does not imply that leaf morphology has no influence on herbivory among plant species. We did find that serration and venation patterns accounted for some of the differential herbivory observed.

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THE RECOVERY OF QUEBRADA GUACIMAL

NICOLE D. POULIOT, AMY V. BARNHORST, VANESSA R. LEVESQUE AND JENNIFER L. MITCHELL

Abstract. (NDP) From 1954 to 1993, Productores Monteverde dumped dairy waste into Quebrada Guacimal, altering the downstream invertebrate communities. To determine if the stream had recovered from this dumping, we investigated the present diversity and composition of the invertebrate community at the site of the former discharge as well as upstream and downstream from it. The former point of discharge now contains pollution-sensitive invertebrates and higher diversity than in 1991 indicating the stream is recovering. A second downstream effluent of unknown origin, however, may still be polluting the stream, as indicated by lower invertebrate diversity and fewer pollution-sensitive invertebrates.

INTRODUCTION (VRL)

Productores Monteverde in Monteverde, Costa Rica dumped their by-products, mostly whey, into the Quebrada Guacimal from 1954 to 1993 (Hidalgo, personal com.). The whey is metabolized by bacteria, severely depleting oxygen in the stream. Since many invertebrate larvae that inhabit the stream are unable to survive in oxygen-poor water, stream pollution levels can be assessed by determining the presence or absence of invertebrate indicator species. For example, Ephemeroptera and Plecoptera are intolerant of pollution whereas Diptera are usually tolerant (Stoney 1991). Stream quality can also be assessed by examining invertebrate diversity. In polluted waters, tolerant invertebrates, such as Dipterans, outcompete the less tolerant invertebrates, thereby decreasing the invertebrate diversity of the stream.

Prior to 1993, the invertebrate community at the effluent point was characterized by low diversity and high Dipteran abundances (Stoney 1991). Spokesmen from the dairy claim there is currently no dairy waste entering the stream and the stream has recovered entirely since the termination of dumping in 1993 (Hidalgo, pers. comm.). However, we did notice effluent of unknown origin and composition leaking from a pipe 10 m downstream from the original discharge site.

Our purpose was to determine if Quebrada Guacimal has recovered from the past pollution by comparing the current conditions at the former discharge site with an upstream site and also by comparing our data to a 1991 study. In addition, we tested the stream at the new effluent site to see if it shows signs of pollution affecting the invertebrate community.

METHODS (JLM)

We sampled three sites along the Quebrada Guacimal, adjacent to Productores Monteverde, in the community of Monteverde, Puntarenas Province, Costa Rica. Site 1 (3.6 m stream width) was 25 m upstream from the location of previous discharge, site 2 (1.4 m stream width) was at the location of previous discharge, and site 3 (3.0 m stream width) was 13.5 m downstream from site 2 (2 m below current discharge). We reduced between-site physical variation by controlling for stream depth and substrate. Canopy cover was greater at site 1 because we were unable to find a suitable upstream site with low canopy cover. At each site, we took four independent kicknet samples, for one minute each. We combined the four samples at each site for analysis, and classified all organisms to order.

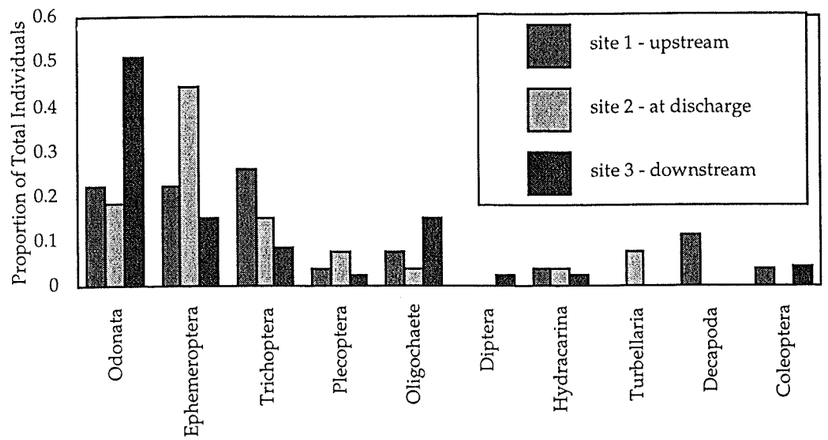

FIG 1. Proportion of individuals in invertebrate taxa from three sites on the Quebrada Guacimal.

RESULTS (AVB)

Taxa richness was comparable across all three sites (Table 1). Diversity, as calculated by the Shannon-Weiner diversity index, was highest at site 1 (H=2.0) and the same at both sites 2 and 3 (H=1.7). Sites 1 and 2 had similar proportions of each pollution-sensitive taxa; however site 2 had twice as many Ephemeroptera as site 1 (Fig. 1). At both sites, other taxa accounted for about 40% of all individuals. Site 3 had the lowest proportions of Ephemeroptera and Plecoptera and was the only site with Dipterans.

TABLE 1. Total number of individuals per taxa from three sites* on the Quebrada Guacimal.

Taxa	Site 1	Site 2	Site 3
Odonota	6	5	24
Ephemeroptera	6	12	7
Trichoptera	7	4	4
Plecoptera	1	2	1
Oligochaete	2	1	7
Diptera	0	0	1
Hydracarina	1	1	1
Turbellaria	0	2	0
Decapoda	3	0	0
Coleoptera	1	0	2
Total Individuals	27	27	47
Number of Taxa Present	8	7	8
Shannon Diversity Index	2.0	1.7	1.7

*Site 1: 25m upstream from previous discharge; Site 2: at previous point of discharge; Site 3: at point of current discharge.

DISCUSSION (NDP)

Our results suggest the conditions of the stream at the former discharge site have indeed improved since 1991 but full recovery has not yet been reached. Ephemeropterans and Plecopterans, which Πare indicative of high quality streams, comprised 55% of all invertebrates at site 2. The remaining 45% of invertebrates were mostly Odonates and Trichopterans which are considered moderately tolerant taxa and are found in both clean and polluted waters. The upstream site contained similar proportions of Plecopterans, Odonates, and Trichopterans but fewer Ephemeropterans. We found no Dipterans, which are considered indicators of pollution, at either site. This similarity between the types of invertebrate pollution indicators at both sites suggests that the former discharge site is returning to predisturbance conditions characteristic of the upstream site.

Currently the numbers of taxa represented at both the discharge and the upstream sites are comparable. However,

the diversity index at the former discharge site was 1.7 whereas the upstream site had an index of 2.0. This lower diversity at the former discharge site may indicate that while many types of taxa have returned to the site, their abundances have yet to reach pre-pollution levels. Perhaps some pollution residues persist in the stream substrate. Further study of the chemical composition of the sediment is needed to determine the amount of any such residue.

In 1991, Stoney found a Shannon diversity index of 1.0 at the former discharge site, which is lower than our value of 1.7. In addition, Dipterans comprised 80% of total individuals at the site in 1991. Our observed increase in diversity, coupled with the increase in pollution-sensitive invertebrates and the decrease in pollution-tolerant ones indicates that the stream is recovering.

The site of current discharge has a diversity index of 1.7, the same as the previous discharge site. The majority of the invertebrate community at this site was composed of Odonates, one of the moderately tolerant taxa. We also found low proportions of Ephemeroptera there. This suggests that this downstream site, like the former discharge site we examined, had been effected by the pre-1993 dumping and is also now recovering. Another possible explanation is that the unknown discharge we discovered at this site is affecting the area by lowering the invertebrate diversity. Further study should identify this pollutant entering the stream to determine the effects it is having on the invertebrate community.

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VARIATION IN SEEDLING AND SAPLING DENSITY, RICHNESS AND DIVERSITY RESULTING FROM TREE FALL GAPS

JASON H. BRADY AND CARTER D. WRAY

Abstract. (JHB) Because tree fall gaps are a common disturbance in most mature forests, understanding their role as a mechanism for sustaining diversity is important. We hypothesized that there would be a decrease in diversity, richness and density of tree seedlings and saplings across a gradient from no cover to full canopy and that this gradient of microhabitats would result in an increase in overall diversity. We tested this hypothesis in a tropical cloud forest at Monteverde. We found significantly higher seedling and sapling diversity and species richness in edge areas as opposed to gaps or under the canopy. There were no significant differences in density, however, among these zones. These findings support the idea of disturbance as a mechanism for sustaining species diversity in tropical forests.

INTRODUCTION (CDW)

Tree falls in primary forest generate gaps that strongly affect the microhabitats within and surrounding them. Variation in microhabitat from open gap to edge of the gap to adjacent intact forest with complete canopy cover should lead to a higher overall number of potential niches available and therefore overall diversity, as compared to undisturbed forest.

In his study of tropical forests, Brokaw (1985) found two types of saplings: those that occurred only in gaps and those that were distributed in both gaps and the understory of mature forest. Since both types occur in gaps, species richness in gaps should be higher than in undisturbed forest. Habitats along gap edges have intermediate light availability and thus should support an intermediate number of species.

Seedling establishment and survival are both higher in gaps than under full canopy (Augspurger 1984), which should cause densities of seedlings to be highest in gaps, intermediate in edge areas, and lowest under full canopy.

Since diversity is a function of both species richness and density, it should be highest in gaps. We hypothesized that there would be a decrease in species diversity, species richness and density of tree seedlings across a gradient from no cover to full canopy cover, and this gradient should cause overall diversity to be higher in forests with tree fall gaps than in forests with a totally undisturbed canopy.

METHODS (JHB)

We sampled three tree fall gaps in roughly the same successional state on the trails near the Monteverde Biological Station in Monteverde, Costa Rica. All gaps were at an elevation of 1500-1600 m in cloud forest habitat. We categorized the areas immediately surrounding the disturbance as (1) gap center defined as the area in the center of the tree fall with no canopy cover immediately above; (2) gap edge, the area underneath the canopy of trees immediately surrounding the gap and (3) under intact canopy in the surrounding forest. The latter was far enough removed from the gap to be isolated from the increase in light, and therefore was expected to be unaffected by the gap.

We measured the distance across the smallest gap which was not under any cover (4.5 m); this was the gap center area. We considered the next 4.5 m into the forest, from the edge of the gap into the surrounding forest, to be the gap edge. The next 4.5 m was considered to be intract forest. We sampled a consistent area in treefalls of different sizes to correct for differential effects of different gap sizes. We laid a similar transect across the larger gaps but used only the center 4.5 m of the gap area. We classified the first 4.5 m of the transect which fell under canopy to be the gap edge. The canopy zone for the larger gaps lay on the same transect, and was an equal distance further into the forest from the gap edge as the gap center zone was from the gap edge.

Once these plots were determined, we counted and took leaf samples from all free-standing woody plants < 2 m tall in a 91 cm wide belt plot along each 4.5 m transect. By comparing samples we determined the number of individuals and of distinct morphospecies. We then calculated Shannon diversity indices for each transect, and tabulated which species were unique to each area. Statistical comparisons were done with a two-way ANOVA with Bonferroni comparison of means.

RESULTS (CDW)

We counted 222 individuals representing 88 distinct morphospecies. Of these morphospecies, 15 occurred only in the center of gaps, 46 only in edge areas, and 20 only under a full canopy. In total, 81 of 88 morphospecies were found to be unique to one particular habitat in our sample and only one species was found in all three habitats. However, only two morphospecies occurred in more than one gap (N=21), three in more than one edge site (N=51), and one morphospecies in more than one full canopy cover site (N=25).

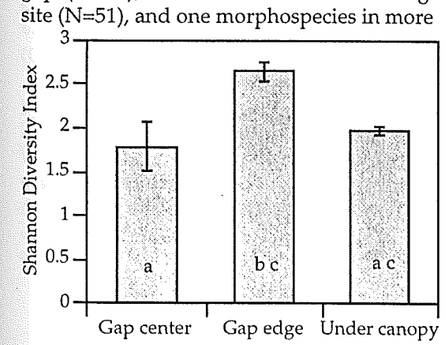

Fig 1: Morphospecies diversity of tree seedlings and saplings in three habitats associated with tree falls in Monteverde, Costa Rica (means ± 1 SE, N=3 for each). Letters indicate significant difference.

The diversity indicies of the edge habitats (2.64 ± 0.119, N=3) were higher than those of the gap (1.78 ± 0.278, N=3; F=6.427; df=2,6; P=0.042), but did not differ from those under the canopy (1.98 ± 0.048, N=3; F=6.427; df=2,6; P=0.118). The diversity indicies of seedlings in the gap did not differ from those under the canopy (F=6.427; df=2,6; P=1.000; Fig. 1).

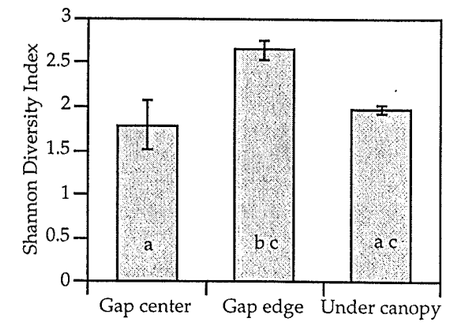

Fig 2. Morphospecies richness in three habitats associated with tree falls in Monteverde, Costa Rica (means ± 1 SE, N=3 for each)). Letters indicate significant difference.

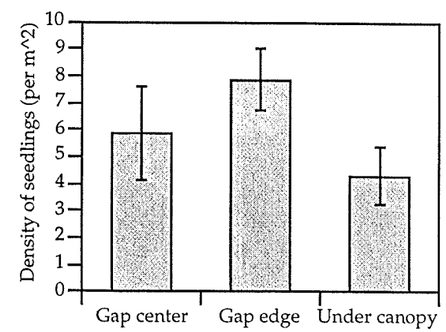

Fig 3. Density of all woody seedlings and saplings < 2 m tall in three habitats associated with tree falls in Monteverde, Costa Rica (means ± 1 SE, N=3 for each)

Morphospecies richness in the edge habitats (18.3 ± 1.33) were also higher than those of the gap (8.0 ± 0.58; F=28.29; df=2,6; P=0.001) as well as those under canopy (9.0 ± 1.16; F=28.29; df=2,6; P=0.001). Morphospecies richness in gaps

was not different from that under the canopy (F=28.29; df=2,6; P=1.000; Fig. 2)

Tree seedling densities did not differ significantly between gap (5.9 ± 1.77) and edge (7.9 ± 1.16; F=1.694; df=2,6; P=1.000), gap and under canopy (4.31± 1.07; F=1.694; df=2,6; P=1.000), or edge and under intact canopy (F=1.694; df=2,6; P=1.000; Fig. 3)

DISCUSSION (JHB)

The high number of morphospecies unique to each of the three habitats supports our hypothesis that the variation in microhabitat in and around gaps contributes to higher species diversity. However, the significantly higher diversity and richness in the gap edge zones as opposed to other habitats and the lack of significant difference in density across the three zones did not substantiate our hypothesis that richness and diversity should be highest in the gap center. Higher diversity and richness in the gap edge area may have resulted from many species existing both in an intermediate environment, as well as in a gap center or canopy zone. However, because 81 of 88 morphospecies were unique to a particular zone, it does not seem to be the case that the edge zone is an "intermediate" environment in which species exist.

Furthermore, in the gap edge zone, where we expected to see a high number of shared species, or those that exist in at least two habitats, 46 of 51 species were found to be specific to that zone. Despite the greater diversity in the gap edge rather than the predicted gap center, the idea that variation in microhabitat from gap to canopy increase diversity and richness is supported by our data .

However, because so few species were shared among replicate treefalls within each habitat, the high number of species found in only one microhabitat type may not be representative. Our small sample size greatly limits the relevance of our statistical tests. To relate each species to a particular habitat, we would need a much larger sample to confirm that the high numbers of distinct species we found in each sampling area were in fact truly unique and not shared with other habitats. Further research is also needed to quantify life-history strategies of each plant species along the gradient from gap center to intact forest, and how these strategies affect their distribution.

In conclusion, our results show that microhabitat variation over the space of a few meters could have a profound impact on species composition and diversity of tree seedlings and saplings of tropical cloud forests. These results support the idea advanced by Connell (1978) that disturbance, as evidenced here by tree fall dynamics, is an important mechanism for the maintenance of diversity and richness. Without disturbance and the corresponding creation of new habitats, species diversity would have been lower.

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