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ABSTRACT

Daphnopsis americana (Thymelaeaceae) is a medium-sized tree found in Monteverde, Costa Rica, that is often completely defoliated by moth caterpillars during the beginning of the rainy season. Herbivory on this tree occurs mainly in adult trees. This study determined if herbivory was greater in open and edge habitats than in interior forest habitats. This study also determined if herbivory on adult *D. americana* trees was related to tree diameter and distance to nearest conspecific neighbor. Herbivory was estimated as a percentage of the total tree foliage consumed. These data were compared using simple regression and ANOVA tests. Trees found in edge and open habitats had significantly more herbivory than those in forest habitats. Some of this difference may be explained by lower conspecific densities in forest habitats. Forest fragmentation, leading to the creation of more edge habitats, may have detrimental effects on the fitness of populations of *D. americana* since they suffer more herbivory in these habitats.

RESUMEN

Daphnopsis americana (Thymelaeaceae) es un árbol de tamaño mediano que se encuentra en Monteverde, Costa Rica, y que frequentemente es devorado completamente por orugas de polillas al principio de la estación lluviosa. La mayor parte de la herbivoría en este árbol ocurre principalmente en los árboles adultos. Este estudio determinó si la herbivoría era más frecuente en hábitats abiertos y a la orilla que en los habitats del interior del bosque. Este estudio también determinó si la herbivoría en los árboles *D. americana* adultos estaba relacionada con los diámetros de los árboles y la distancia al vecino más cercano. Se estimó la herbivoría como el porcentaje del follaje total del árbol consumido. Estos datos fueron comparados usando pruebas de regresión simple y ANOVA. Los árboles localizados en los hábitats abiertos y de borde presentaron una herbivoría más significativa que los árboles en los hábitats del bosque. La fragmentación del bosques, que conlleva a la creación de más hábitats de borde, puede tener efectos prejudiciales en las adaptaciones de las poblaciones de *D. americana* si éstas sufren más herbivoría en estos hábitats.

INTRODUCTION

Herbivory may impact the succession of secondary forests from previously deforested pastures or the biodiversity of forest fragments by affecting certain plant species' growth and reproductive capabilities (Coley and Barone 1996). In general, herbivory occurs at higher rates in the understory than in the canopy because canopy leaves tend to be smaller and tougher, and the hotter, windier environment of the canopy is less favorable to small herbivores. Plants in forest edges and open pastures may suffer more insect herbivory than less exposed canopy trees. Herbivory in more open habitats may also be higher because of greater primary productivity due to increased light availability (Sagers and Coley 1995). Herbivory also affects young leaves more than it

affects old leaves of mature trees due to their greater nutritional content (Coley and Barone 1996).

Daphnopsis americana (Thymelaeaceae) is a medium-sized, dioecious tree that occurs from 1300-1600 m above sea level in Monteverde, Costa Rica and is common in old pastures, forest edges and old light gaps in mature forests (Haber et al. 2000). The species is common from Mexico through South America, and occurs on both slopes in Costa Rica (Quesada et al. 1997). Adult trees are often severely defoliated by herbivory from moth caterpillars during the beginning of the rainy season in Monteverde. Not much is known about the biology of these moth larvae, as they have not even been identified (Haber, personal communication). Herbivory tends to be greater on adult *D. americana* trees than on seedlings and saplings, which is contrary to general trends of herbivory on trees in the tropics. Complete defoliation of this tree may have impacts on its reproductive capabilities (Price et al. 1991). Rates of herbivory on *D. americana* may be affected by conspecific density. Studies have found that other tree species experienced decreased growth and higher mortality when a tree's nearest neighbor was of the same species and when there was a higher conspecific density (Coley and Barone 1996). Open and edge habitats tend to have lower species richness and therefore have higher conspecific densities. If *D. americana* experiences higher densities in more open habitats, then it may also experience greater herbivory in these habitats. Fragmentation of forests leads to the creation of more edge habitats, which could in turn increase herbivory on trees and decrease the reproductive and growth capabilities of these trees.

This study determined if herbivory on *D. americana* was related to habitat, nearest conspecific neighbor distance, and tree size by comparing the percentage of defoliation of various sized trees in open pasture, edge and forest interior habitats. It was hypothesized that *D. americana* trees would have greater herbivory in open and edge habitats as compared to interior forest habitats.

METHODS AND MATERIALS

Study sites

Data were collected on the Pacific slope in Monteverde, Puntarenas, Costa Rica between 1300-1500 m above sea level (Figure 1). Study sites included secondary growth forests, forest fragments, regenerating pastures, and some continuous old-growth forests near the Estación Biológica de Monteverde. Pastures, fragments, and edges were also located along the road between La Estación Biológica de Monteverde and the southern edge of Monteverde (Figure 1). Data were collected between July 16th and July 28th, 2005.

Data collection

Daphnopsis americana trees were located and identified with the aid of binoculars to inspect leaf morphology and branching patterns. Only trees with a diameter at breast height (DBH) greater than 10 cm were included. Once an adult tree was located and the DBH measured using a regular tape measure, amount of herbivory was estimated

as the percentage of crown defoliation. The total crown was scanned for remaining leaves. Many trees were observed initially to establish a consistent quantification of percent herbivory. This estimate was made one time for each tree. Habitat was characterized and recorded as pasture, edge, or forest. A tree was recorded as in the forest if none of its branches were exposed to the edge. Distance to the nearest neighbor *D. americana* tree was measured as a measure of conspecific density. In order to maintain independent data, the nearest neighbor measurement was recorded only for the first tree seen and not for the neighbor so that the nearest neighbor distance data was not repeated for the same pair of neighbors. Thus, the sample size for the nearest neighbor measurement was half the sample size of other data measured. After the nearest neighbor measurement was recorded, a new tree was found that was not the nearest neighbor to either of the previous two trees.

RESULTS

Of the 118 *D. americana* trees studied, 16 trees were in pastures, 58 were on edges, and 44 were in forests. Nearest neighbor measurements were only recorded for the first tree seen of a pair of neighbors, and sometimes the nearest neighbor was in a different habitat than the first tree. Therefore, for nearest neighbor data, 8 trees were in pastures, 34 were in edges, and 17 were in forests.

Percent herbivory data were normalized using a standard arc sine of the square root transformation (Zar 1984). The transformed values were used when doing all tests with percent herbivory data. Herbivory increased significantly with DBH (Simple regression, $R^2 = 0.112$, $p < 0.0001$)(Figure 2). Edge trees had the greatest mean percent herbivory (82.6% $\pm$ 14.1), followed by pasture trees (81.9% $\pm$ 17.4) and forest trees (47.9% $\pm$ 24.4). Herbivory was significantly different in the tree habitats (One-way ANOVA, $F = 9.826$, $P = 0.0001$). Forest trees had significantly less herbivory than either edge (FPLSD, $p < 0.0001$) or pasture trees (FPLSD, $p = 0.0055$) (Figure 3). There was no significant difference between herbivory in edge and pasture trees.

Pasture trees had the largest mean DBH (0.591 m $\pm$ 0.178), followed by edge trees (0.412 m $\pm$ 0.202), and forest trees (0.385 m $\pm$ 0.191). The diameters differed significantly between habitats (One-way ANOVA, $F = 6.835$, $p = 0.0016$). Pasture trees had significantly greater DBHs than edge trees (FPLSD, $p = 0.0015$) as well as forest trees (FPLSD, $p = 0.0005$) (Figure 4). No significant difference was found between the DBHs of edge and forest trees (One-way ANOVA, $p = 0.5019$).

Forest trees had the greatest mean nearest neighbor distance (48.1 m $\pm$ 87.9), followed by trees in the pasture (16.9 m $\pm$ 12.9), and trees in the edge (12.9 m $\pm$ 12.3). Nearest neighbor distances were significantly different in the three habitats (One-way ANOVA, $F = 3.112$, $P = 0.050$) with the forest having a significantly greater nearest neighbor distance than the edge (FPLSD, $p = 0.0171$) (Figure 5). There was no significant difference between nearest neighbor distance of the forest to the pasture (FPLSD, $p = 0.1362$) or between the pasture and the edge (FPLSD, $p = 0.8353$).

DISCUSSION

The results of this study upheld the hypothesis that *D. americana* trees in edge and open habitats would have greater herbivory than those in forest habitats. Although herbivory was significantly positively related to tree size, it only explained 11.2% of the observed herbivory. Other factors must be contributing to the herbivory of *D. americana*. Trees in the edge and in the pasture had more herbivory than those in the forest. How much of this difference is due to size of the trees sampled? Trees found in pastures had the greatest average DBH. This means that high herbivory on pasture trees may be explained by size. Pasture trees may be larger than edge or forest trees because they receive more light and water and have to deal with less competition. The difference in DBH between edge trees and forest trees is not significant; therefore, higher herbivory on the edge can not be explained by size. *Daphnopsis americana* density was the lowest in the forest, which may partially explain the lower percent herbivory on forest trees (Coley and Barone 1996). From the statistical tests done, it is not possible to determine whether greater herbivory on edge trees is due to greater conspecific densities or to open edge effects. It is probable that it is due to a combination of the two effects.

Higher herbivory on *D. americana* trees in open and edge habitats could have ecological impacts for this tree in the community. Trees that were observed to be fruiting and exhibited heavy herbivory appeared to have reduced reproductive output – they only had fruit on some branches that had leaves remaining. This could have ecological repercussions for this population of trees in the future (Hochwender et al. 2003). If reproductive output is less in edge and open habitats, then eventually these populations of *D. americana* may decline due to a loss of competitive ability. More research needs to be done to see if there is a relationship between reproductive output and degree of herbivory in *D. americana*. Although reproductive output may be reduced, overall fitness of the trees did not seem to be significantly affected by the herbivory. After the data collection period, many *D. americana* trees were observed to be flushing new leaves on all branches. The trees were able to recover photosynthetic ability after complete defoliation.

One of the most interesting aspects of herbivory on *D. americana* is the observation that seedlings had little or no herbivory. This is interesting because it is contrary to the general pattern that young leaves have greater herbivory than mature leaves. The moth larvae that feed on *D. americana* could be avoiding seedling leaves because of secondary metabolites produced by young leaves such as alkaloids; however, more research should be done to determine if this is the case (Coley and Barone 1996). If the seedlings do not produce secondary metabolites, it is possible that the moths do not eat them because they are simply not large enough to build tents of silk around bunches of leaves (as the moths tend to do) or because the moths cannot easily see them. Trees located in edge habitats may have higher herbivory than forest interior trees, partially because moths can more easily locate them.

As fragmentation becomes more and more of a problem in the tropics, plants will have to adapt to more open habitats. This will bring challenges such as greater exposure to herbivory. *Daphnopsis americana* experiences greater herbivory when it occurs in edge habitats, and if *D. americana* cannot adapt to this increased herbivory, then its populations may decline.

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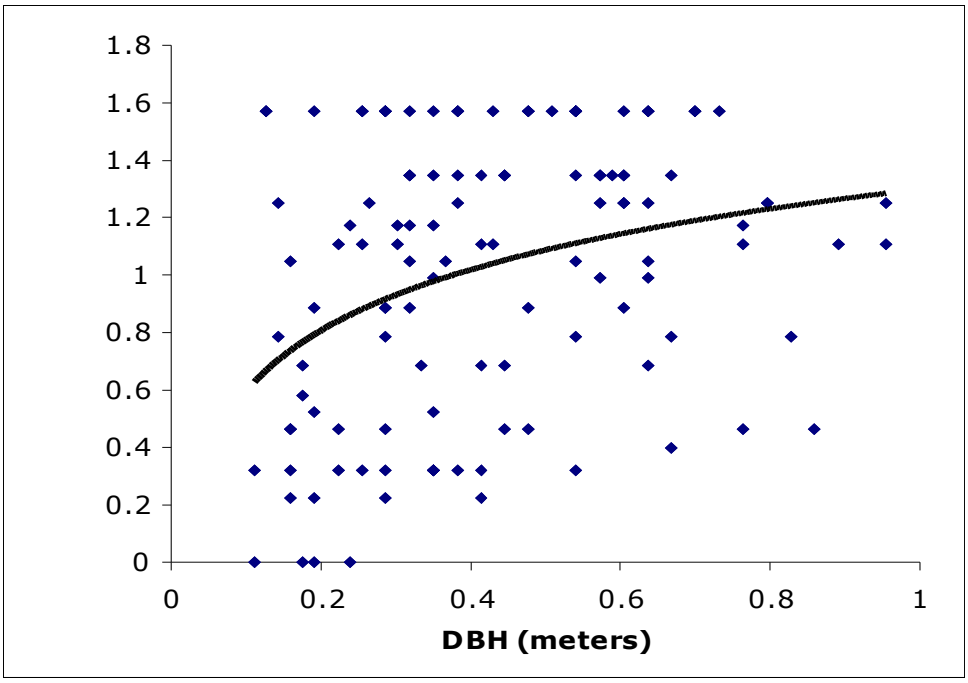

Figure 2: Relationship between DBH and normalized percent herbivory on *Daphnopsis americana* (Simple regression, R^2 = 0.112, p < 0.0001, N = 118).

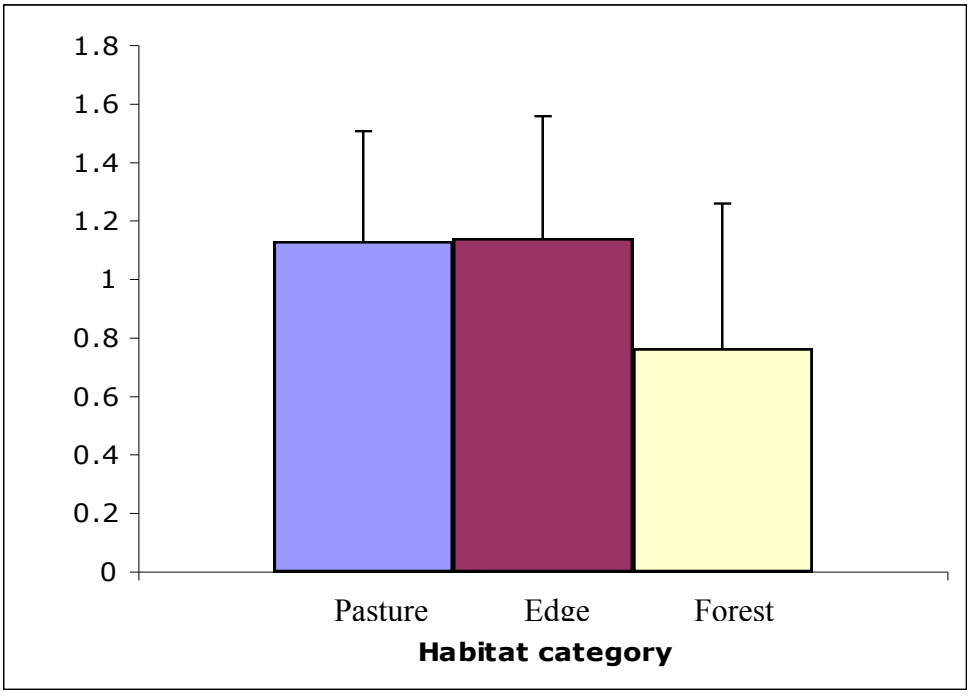

Figure 3: Mean normalized percent herbivory on *Daphnopsis americana* trees was significantly lower in forest habitats (x = 47.9% $\pm$ 24.4, N = 44) than in either edge (x = 82.6% $\pm$ 14.1, FPLSD, p < 0.0001, N = 58) or pasture habitats (x = 81.9% $\pm$ 17.4, FPLSD, p = 0.0055, N = 16).

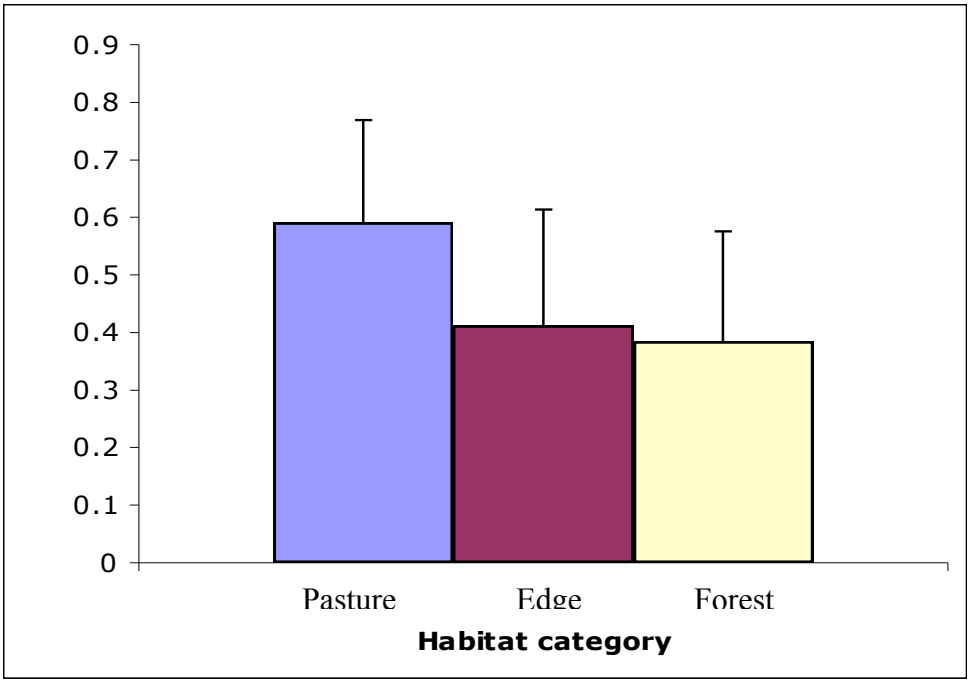

Figure 4: *Daphnopsis americana* trees were significantly larger in pasture habitats (x = 0.591 m ± 0.178, N = 16) than in either edge (x = 0.412 m ± 0.202, FPLSD, p = 0.0015, N = 58) or forest habitats (x = 0.385 m ± 0.191, FPLSD, p = 0.0005, N = 44).

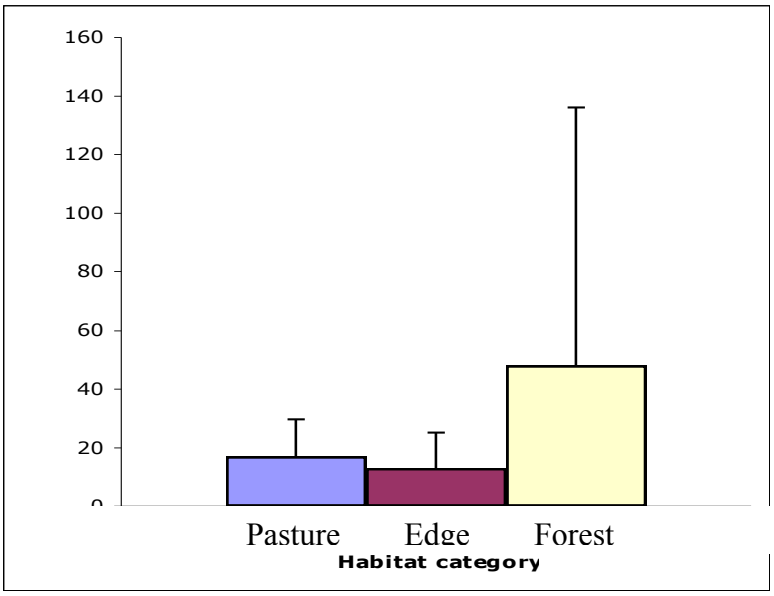

Figure 5: Mean nearest neighbor distance of *Daphnopsis americana* trees was significantly higher in forest habitats (x = 48.1 m ± 87.9, N = 17) than in edge habitats (x = 12.9 m ± 12.3, FPLSD, p = 0.0171, N = 34) but not compared to pasture habitats (x = 16.9 m ± 12.9, FPLSD, p = 0.1362, N = 8).