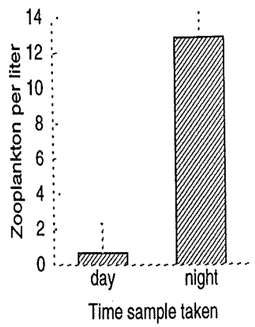

FIG. 1. Mean (± S.E.) abundance of zooplankton in open water habitats of the Río Tempisque marsh during the day (n=10) and at night (n=9).

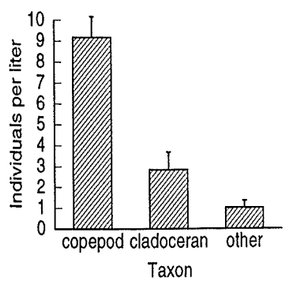

FIG. 2. Mean (± S.E.) abundance of zooplankton taxon at night in the open water of the Río Tempisque marsh. Nine samples were taken from 0.5 meters below the surface.

DISCUSSION

We found a marked difference in the abundance of zooplankton between night and day within the open water micro-habitats of the Río Tempisque marsh. Pennak (1978) has shown that various species of copepods and cladocerans exhibit daily vertical migrations in lakes throughout the world; rising at dusk and returning to the bottom at dawn. Pennak (1978) suggested that this behavior is an evolved mechanism to avoid visual predators such as fish, although on a proximal level the migration may be a reaction to changing light conditions within the water column.

Within the Río Tempisque marsh, Carson et al. (1995) reported that zooplankton were more abundant under the vegetation than in the open water during the day. We also sampled (n=2) under vegetation during the day and found a high abundance of zooplankton present (unpubl. data). These observations, coupled with our findings of more zooplankton in the open water at night, suggest a horizontal migration hypothesis, i.e., that zooplankton may retreat horizontally to the dark conditions under the vegetation during the day and then move out again into the open water at night. This could be related ultimately to selective pressures from visually-feeding fish, with zooplankton avoiding high light areas to escape predation, or more proximally, to local removal of zooplankton from these areas during the day by fish, and then movement of zooplankton out from the vegetation to the open water at night. However, because the vegetation mat is so expansive relative to the open water patches, it is unlikely that a large scale migration of all zooplankton under the vegetation to the open water occurs. This migration may occur on a local level with those zooplankton near the open water patches migrating, and those further from open water remaining under the vegetation.

To test the fish predation hypothesis further, it might be possible to design an experiment using a barrier in the open water through which zooplankton, but not fish, could pass. By sampling for zooplankton within this barrier during the day the extent of control in zooplankton abundance by fish predators could be determined.

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EFFECTS OF ELEVATION AND CANOPY COVER ON THE DISTRIBUTION OF *HELICONIA* IN A MONTANE CLOUD FOREST

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Abstract. In the cloud forest of Estación Biológica Monteverde, Costa Rica, the broad-leafed monocot, *Heliconia*, increases in abundance at higher elevations. Many factors may affect vegetation distribution change along an elevational gradient, including canopy cover. Because *Heliconia* is a shade-intolerant plant, we predicted (1) that its distribution would be related to changes in canopy cover along the elevational gradient, and (2) that the distribution of *Heliconia* at low elevations would be related to the occurrence of gaps and other openings in the forest canopy. We found that openness of the canopy did increase with elevation, as did the abundance of *Heliconia*. Likewise, *Heliconia* also occurred under canopy openings at low elevations. Our findings suggest that *Heliconia* grow at all elevations, provided that the canopy is at least 12 % open.

Key Words: abundance, canopy, elevational gradient

INTRODUCTION

The Heliconiaceae are shade-intolerant, broad-leafed monocots common throughout the tropics at nearly all altitudes (Kress and Barry 1991, Haber 1975). Our investigation was concerned with the distribution of the high altitude species of *Heliconia* along an elevational gradient in a tropical cloud forest. Preliminary observations indicated that *Heliconia* was patchy in distribution at lower elevations, but that it increased in abundance at higher elevations. Because it is highly shade-intolerant, we hypothesized that the distribution of *Heliconia*, particularly its increased abundance at high elevations, may be due to a more open canopy cover. We also hypothesized that the occurrence of *Heliconia* at low elevations would be related to substantial forest canopy openings, such as those that result from tree fall gaps.

We therefore predicted that the shade-intolerant *Heliconia* will increase at higher elevations as canopy cover decreases and that *Heliconia* at lower elevations would occur mostly in canopy gaps and under other openings in the forest canopy.

METHODS

This research was conducted at Estación Biológica Monteverde, Costa Rica on 21-22 January 1997. We sampled *Heliconia* abundance and the distribution of canopy cover along three randomly selected 10 by 100 m transects at three elevations - low (1520 m), mid (1650 m), and high (1782 m). We determined a random number between 0-60 using a stopwatch, and began our transect at that distance (in m) from the trail. We counted the total number of individuals of *Heliconia* contained within each transect. We used a spherical densitiometer to determine the percentage of open canopy at 10 m intervals so that 10 measures of canopy coverage were obtained for each transect. Percent open canopy was defined as the percentage of open area directly above the 10 m points, taken as an average of four readings at each of the cardinal directions. With this design we examined changes in canopy coverage and the occurrence of *Heliconia* across the three elevations.

We also sampled the percentage of open canopy above systematically selected individuals within the same altitudinal range. To do this, we moved along the trail, measuring every individual plant found between 2- 50 m from the trail. We used the spherical densitiometer to determine the percentage of open canopy directly above each *Heliconia* individual.

With these two sampling methods, we obtained canopy cover data at each of the 10 points in the three transects as well as above each individual *Heliconia* plant. We combined these data into three categories of elevation (1510-1590, 1591-1691, and 1692-1782 m), and examined the percent open canopy at points in the transect and above individual *Heliconia* plants. With this design we examined changes in canopy coverage and distribution of *Heliconia* across the three elevations.

Results

At low and mid- elevations, most of the systematically selected transect points were under dense canopy cover, i.e., had low % open canopy values, ranging from 6-15 % (Fig. 1). At high elevations, the canopy was more open, with % openness ranging from 12-30 % (Fig. 1). Thus the canopy was more open at higher elevations.

At low and mid elevation sites, Heliconia occurred only where canopies were >12 % open (Fig. 1). A similar trend was seen at high elevations, as only one Heliconia was found in a site with < 12 % open canopy. These data suggest a minimum % open canopy level (roughly 12%), below which Heliconia does not occur.

Because of problems with our sampling design we were not able to test these results statistically.

Discussion

Heliconia is a fast growing, pioneer species that thrives in well-lit areas. In this study at Monteverde, we found that Heliconia grows at all elevations between 1500 and 1800 m, provided that the canopy was at least 12 % open. The fact that Heliconia is widespread at all elevations if given adequate light supports our hypothesis that available light is a crucial factor limiting Heliconia distribution along the elevational gradient.

At the low and medium elevation transects, the available light in the understory in most places was below the minimum Heliconia tolerance. As a result, Heliconia only grew in canopy gaps at these lower elevation sites. Canopy gaps at lower elevations are most often created by disturbances such as fallen trees. Thus it seems that at lower elevations, Heliconia relies upon periodic disturbances to open the canopy and provide enough light for colonization. An increase in canopy-opening disturbances as a result of natural or anthropogenic causes would result in an increase in Heliconia distribution at lower elevations.

At the high elevation transect, the mean canopy density was low enough to permit adequate light for Heliconia to thrive over most of the area. Thus Heliconia was widely distributed at high elevation. In addition, during our study, we observed many other species of plants at high elevation that were not present at lower elevations. This suggests that the relatively open canopy at higher elevations may represent an opportunity for other shade-intolerant species to persist as well, resulting in different communities, both in terms of species richness and abundance, along the elevational gradient.

Our data support our prediction that the increase in Heliconia abundance along this elevational gradient may be due to an increase in available light. At high elevations, cloud moisture and wind stress are much greater than at lower elevations. That Heliconia was so widely distributed in well-lit areas at all elevations suggests that light is the critical factor limiting Heliconia distribution. Heliconia plants are often resistant to desiccation, herbivory, and temperature stresses (Janzen 1983). Further, the abundance of Heliconia in all forest gaps suggests that it is competitively dominant to other understory species if given adequate light. Further study, however, is necessary to accurately assess the role of other factors, including competition between Heliconia and other understory species, that might also influence their distributions. whether tree health determines ant colonization preferences or whether distribution of ant species determines tree health.

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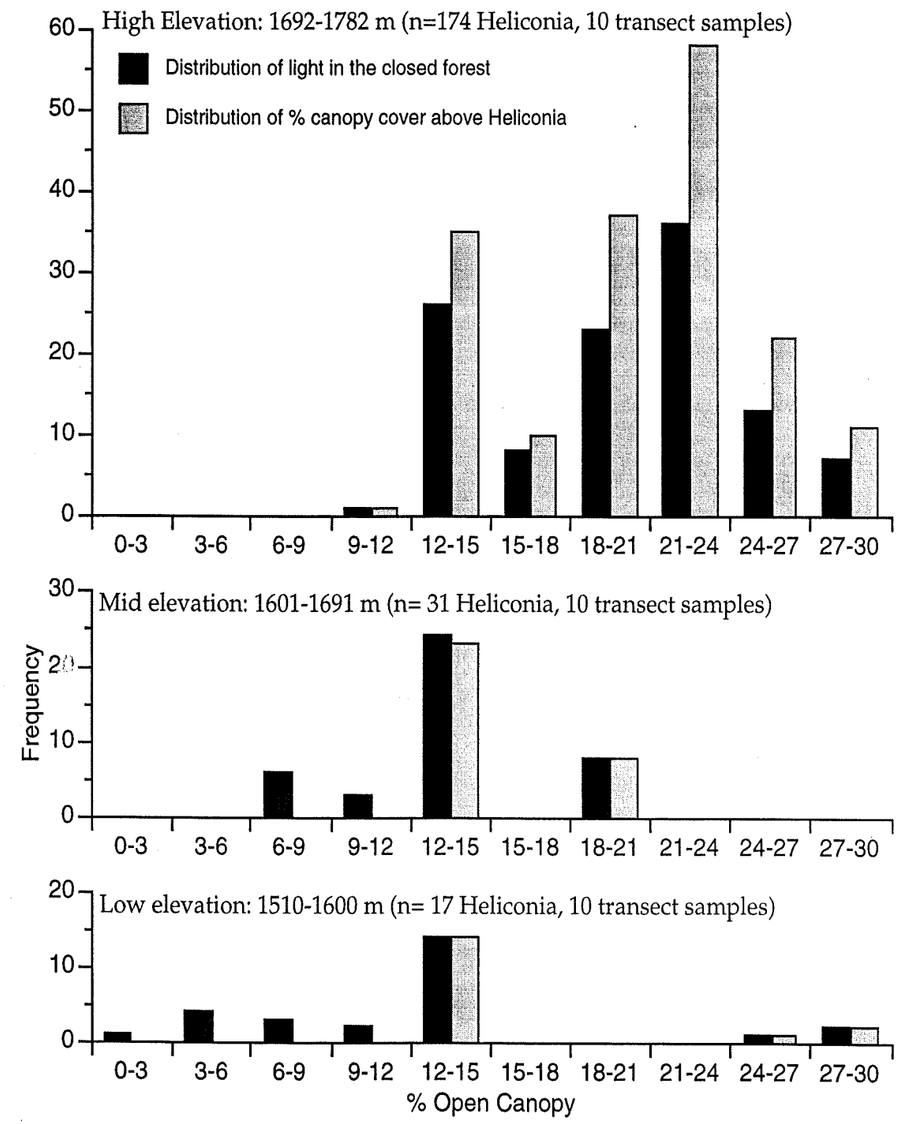

Fig. 1. Distribution of open canopy (%) in the forest in general at each elevation and the distribution of open canopy (%) above individual Heliconia plants.