Patterns in Reproductive Litterfall along an Elevation Gradient in a Tropical Forest

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Abstract The ecological impacts of global climate change have become increasingly well-documented recently. Tropical ecosystems may be particularly sensitive to small climatic changes due to their relatively constant, aseasonal climates. This study sought to investigate the effects of climate change on reproductive litterfall production in a tropical forest. The study site was situated along a 330 m elevation gradient in a humid Puerto Rican forest. The elevation gradient and the corresponding 1°C temperature gradient were used as a proxy for potential climate change. Litterfall was collected for eight years at 12 sites along the elevation gradient spanning four distinct forest types. The litter was then sorted into four fractions, dried, weighed for mass, and analyzed for carbon and nutrient content. This study focuses on the fraction of the litter containing reproductive structures including fruits, flowers, and seeds. Differences in magnitude as well as temporal patterns of reproductive litterfall support the classification of the cloud forests as distinct forest types. Overall, the forests displayed a significant negative relationship between elevation and reproductive litterfall mass. Reproductive litterfall production decreased significantly during the course of the study in all of the forest types, but the temporal patterns in each forest type varied dramatically. These results suggest that small climatic changes may significantly alter reproductive patterns in tropical forests. Changes in reproduction are likely to have significant impacts on ecosystem function. It is likely that any climatic changes that do occur will differentially affect the forest types described in this study.

Introduction

The vast majority of climate change research has focused on mid and high latitudes where warming is predicted to be the greatest (Walther *et al.* 2002). However, recent modeling studies suggest that humid, tropical ecosystems may be particularly sensitive to even very small changes in climate because of their current lack of significant drought stress and near constant temperatures throughout the year (Loope and Giambelluca 1998, Wang *et al.* 2003). These small climatic changes have the potential to alter carbon and nutrient allocation patterns (Silver 1998).

Using elevation gradients to investigate the effects of differences in microclimate is a common approach, especially in conjunction with litterfall measurements (Reiners and Lang 1987, Waide *et al.* 1998). There are a number of well-established relationships between temperature, elevation, litterfall production, and litterfall nutrient content. Litterfall production is positively correlated with temperature (Silver 1998). In the tropics, litterfall production tends to be negatively correlated with elevation, which follows from the previous correlation since elevation and temperature are negatively correlated (Waide *et al.* 1998). Litterfall nitrogen concentrations are also positively correlated with temperature (Vitousek and Sanford 1986).

Allocation of carbon and nutrients in plants has been the subject of extensive research, but the vast majority of work has focused on carbon allocation to vegetative structures and has neglected reproductive structures as carbon and nutrient sinks. The small amount of work that has focused on reproductive allocation has investigated the effects of elevated carbon dioxide levels (He and Bazzaz 2003). Research into the reproductive allocation of wild species has remained especially limited (Amthor 2001, Saxe *et al.* 2001). Reproduction is critical to ecosystem function and deserves much more attention than it has received.

Island tropical montane cloud forests, like my study site in Puerto Rico, are especially valuable for investigating the effects of climate change due to their extreme sensitivity to climatic variation (Loope and Giambelluca 1998). My research focuses on how carbon and nutrient allocation to reproduction in a mixed tropical forest vary along an elevation gradient. I hypothesize that differences in elevation, and consequently climate, will lead to differences in resource allocation, specifically carbon and nutrient allocation to reproductive structures. This question and hypothesis reflect the broader goal of the project, which is to develop a more complete understanding of the ecological impacts of climate change.

Methods

Study Site The study sites were located along a 330 m elevation gradient (635-968 meters above sea level) in the upper elevations of the Luquillo Experimental Forest (LEF), Puerto Rico (18° 19' N 65° 45'W). A network of twelve 30 m x 10 m permanent plots were used along the gradient where all trees ≥ 2.5 cm diameter at breast height (dbh) were tagged and identified to species. The forest type changes along the elevation gradient with colorado forest at 500-750 meters above sea level (masl), palm forest at 500-1000 masl, and cloud forest at 750-1050 masl. A significant difference in tree height and a small difference in tree species composition were noted between the short and tall cloud forests. Mean annual rainfall at all sites is approximately 3700 mm, and temperatures decrease from 20^{o}C in the lower elevation sites to 19^{o}C in the upper elevations. Cloud water deposition adds an estimated 500 mm/yr in precipitation (Brown *et al*. 1986, Weaver 1995).

Litterfall Collection and Analyses Litterfall was sampled every two weeks from 1994 to 2004 from five, perforated plastic, mesh-lined baskets (0.14 or 0.17 m^2) per plot, distributed in a stratified random manner to assure plot coverage. Baskets were suspended above the ground on short (approximately 50 cm) PVC poles to facilitate drainage. Litter was dried at 65^{o}C and sorted into fruits and flowers, wood (< 10 cm diameter), leaves, and miscellaneous material. The fruits and flowers fraction contains all reproductive structures including fruits, flowers, seeds, and buds. The wood fraction contains small twigs, bark and woody stems. The leaf fraction contains all leaves except palm fronds and ferns; because palm and fern fragments and leaflets could not be identified with confidence they were included in the miscellaneous (unrecognizable organic matter) fraction. After sorting, samples were redried at 65^{o}C and weighed to determine mass. Samples were then bulked by litter fraction, forest type, and month and ground in a Wiley mill to pass through a forty-mesh screen. Ground litter was analyzed for total C and N content on a CE Instruments NC2500 C and N analyzer. Additional subsamples were digested in HNO_3 (Luh Huang and Schulte 1985) and analyzed for total Al, CA, Fe, K, Mg, Mn, and P on a DCP Spectrascan V spectrophotometer at the IITF/USDA Forest Service Laboratory in Rio Piedras, Puerto Rico.

Statistical Methods Data were analyzed using Systat 10 (Wilkinson 2000). Analysis of variance (ANOVA) and regression techniques were used to examine patterns in litterfall with elevation, forest type, and over time. Similar analyses were performed to explore patterns in litter chemical characteristics. Data were log transformed where necessary to meet the assumptions for ANOVA. A Least Significant Differences (LSD) protocol was used to determine where significant differences occurred. Statistical significance was determined at $p \leq 0.05$ unless otherwise noted.

Results

Mean annual reproductive litterfall varies significantly among forest types (ANOVA, $F=64.3$, $p<.001$) (Fig. 1). LSD analysis reveals significant differences between the short and tall cloud forests ($p<.001$), as well as between the cloud forests and the palm and colorado forests ($p<.001$) (Fig. 1).

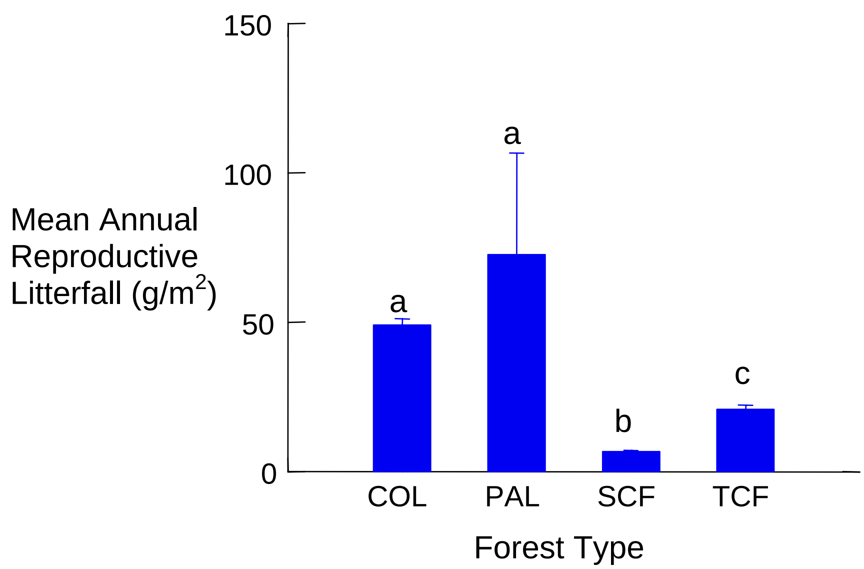

Figure 1. Mean annual reproductive litterfall among forest types. Lowercase letters denote significant ($p<.05$) differences. Error bars indicate +1 SE.

There is a significant negative correlation between mean annual reproductive litterfall and elevation ($p<.001$), although elevation explains only 24% percent of the variation (Fig. 2). Removing the palm forests from the regression analysis increases the r^2 to 0.291.

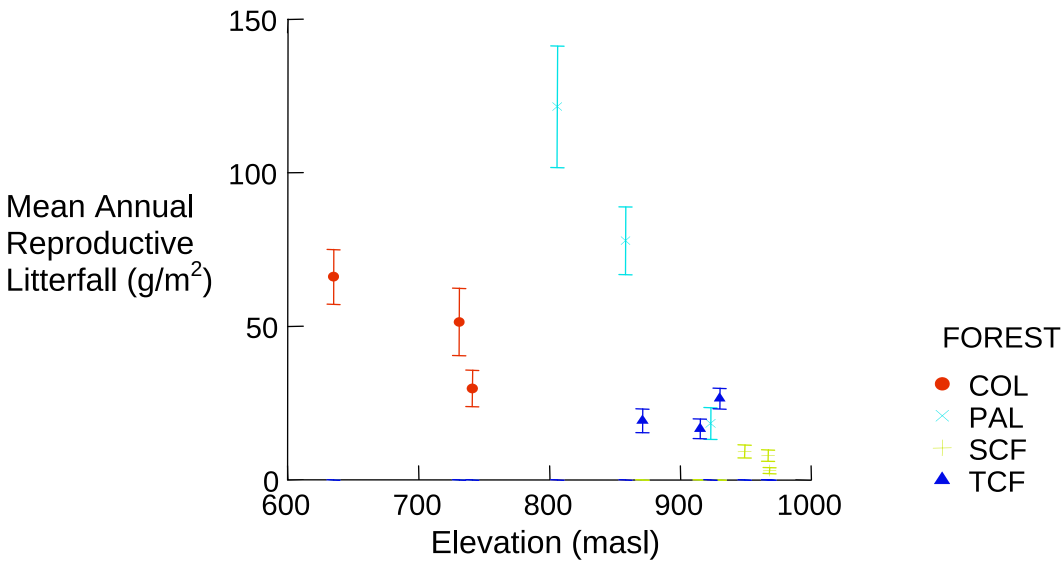

Figure 2. Mean annual reproductive litterfall along a gradient in elevation. Error bars indicate ±1 SE.

Reproductive litterfall for the study site as a whole has decreased significantly a number of times while displaying no significant increases (Fig. 3). The most significant ($p<.001$) decrease occurred from year one to year two. There was also a significant ($p=.048$) decrease from year

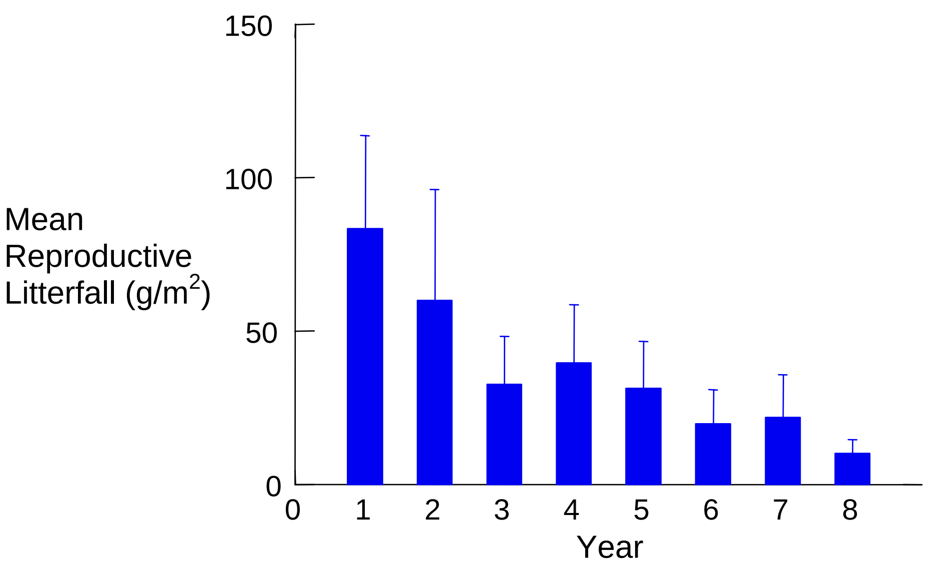

Figure 3. Mean annual reproductive litterfall for all forest types. Year on x-axis refers to the number of years since litterfall sampling began in June of 1994. Error bars indicate +1 SE.

five to year six. The observed decrease from year seven to year eight approached significance (p=.083).

The pattern of decreasing reproductive litterfall varies widely among forest types. The cloud forests show similar patterns except that the tall cloud forest produces approximately twice as much reproductive litterfall as the short cloud forest (Fig. 4 and 5). The short cloud forest displays the most extreme decrease, almost six fold, in reproductive litterfall from year one to year two of all the forest types (Fig. 4). The only other significant changes are between year five and year eight (p=.006) and between year six and year eight (p=.024). There was also a noticeable, albeit insignificant (p=.092), increase in reproductive litterfall from year four to year five.

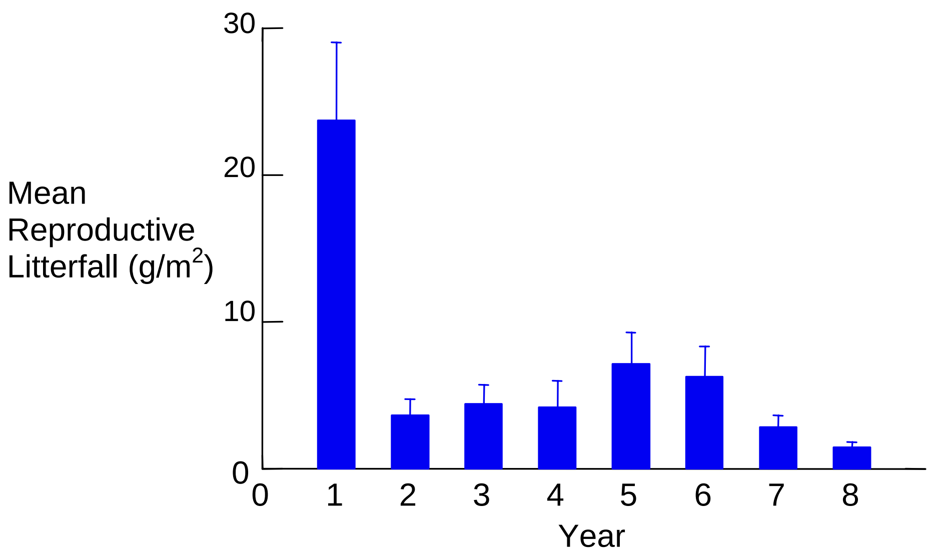

Figure 4. Mean annual reproductive litterfall for the short cloud forest. Year on x-axis refers to the number of years since litterfall sampling began in June of 1994.Error bars indicate +1 SE.

The tall cloud forest displays a decrease similar to that observed in the short cloud forest from year one to year two (Fig. 5). For the remaining years the tall cloud forest displays a pattern very similar to that of the short cloud forest except that the observed increase in reproductive litterfall occurs one year earlier, from year three to year four.

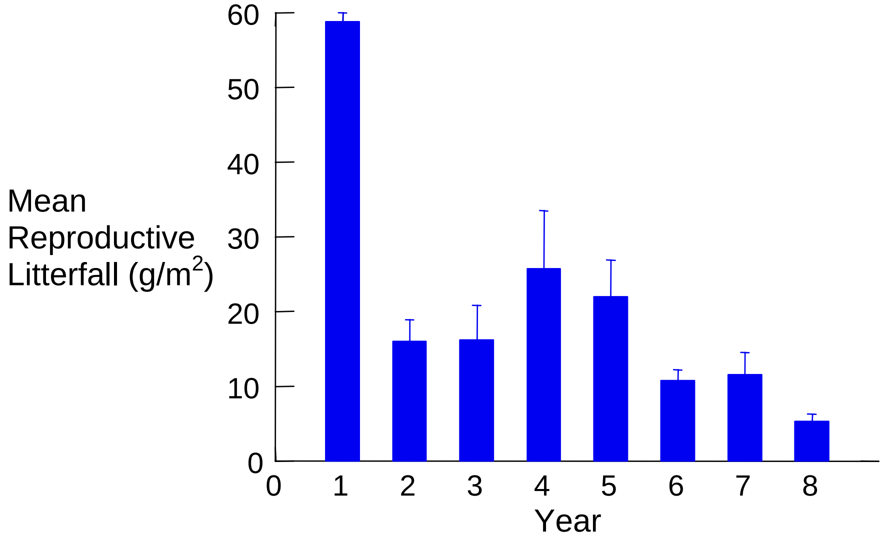

Figure 5. Mean annual reproductive litterfall for the tall cloud forest. Year on x-axis refers to the number of years since litterfall sampling began in June of 1994. Error bars indicate +1 SE.

The palm forest displays the highest levels of reproductive litterfall of all the forest types. The decrease observed in the other forest types from year one to year two occurs one year later in the palm forest (Fig. 6). From year three to year seven there are no significant changes in

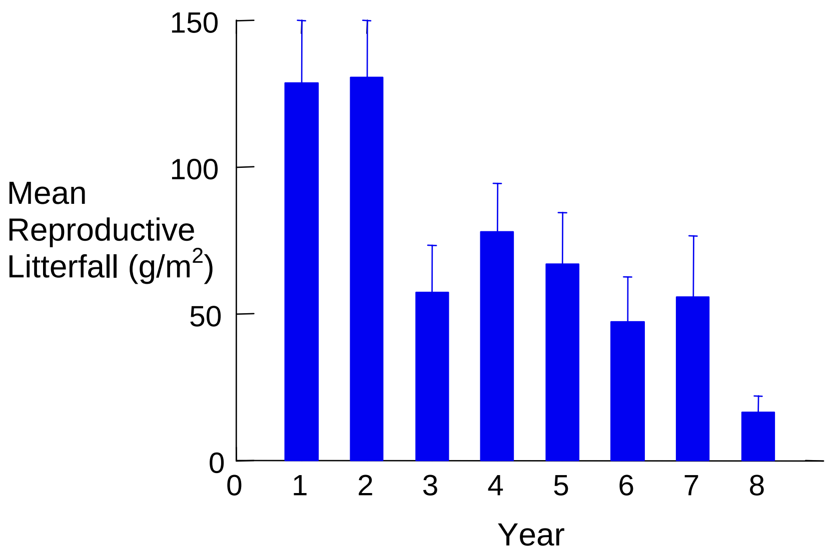

Figure 6. Mean annual reproductive litterfall for the palm forest. Year on x-axis refers to the number of years since litterfall sampling began in June of 1994. Error bars indicate +1 SE.

reproductive litterfall production in the palm forest. The observed decrease from year seven to year eight is nearly significant (p=.063).

The colorado forest follows the most consistent pattern of decreasing reproductive litterfall throughout the course of the study (Fig. 7). There is a noticeable, but not significant (p=.144), decrease from year one to year two followed by a significant (p=.029) decrease from year two to year three. After remaining relatively constant during years three and four reproductive litterfall decreases from year four to year five sufficiently to approach significance (p=.092). Year four is significantly different from years six, seven, and eight (p=.005, .001, .003 respectively).

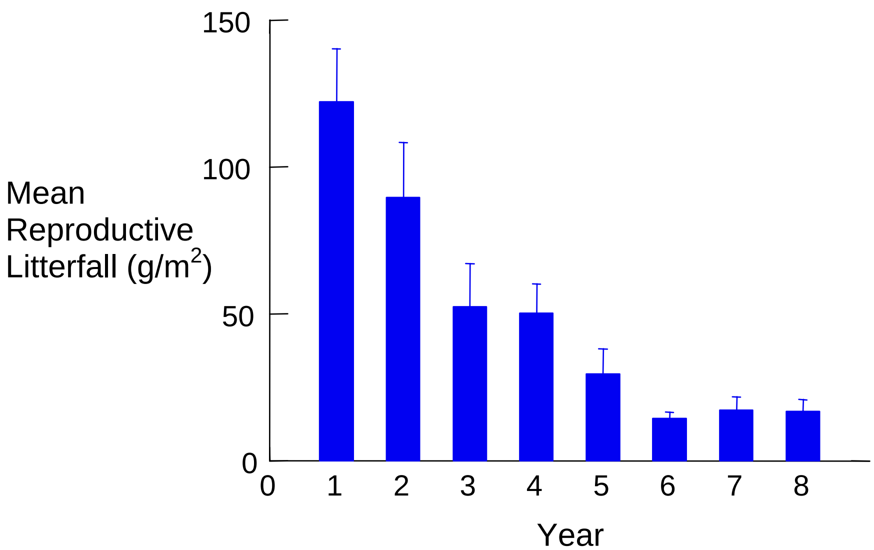

Figure 7. Mean annual reproductive litterfall for the colorado forest. Year on x-axis refers to the number of years since litterfall sampling began in June of 1994. Error bars indicate +1 SE.

Discussion

The significant differences in reproductive litterfall between the short and tall cloud forests support the initial classification of these forests as distinct forest types. The forests differ not only in magnitude, but also in their patterns of reproductive litterfall through time. These differences are most likely the result of differences in elevation and the associated variations in climate (Silver 1998).

The results of this study show that the palm forests exhibit significantly greater reproductive litterfall production than the other forest types. Many studies have produced similar results

(Waide *et al.* 1998). The high productivity of the palm forest has been explained in the past by palms specific adaptations to the floodplains they inhabit, such as high rates of retranslocation of nutrients (Waide *et al.* 1998). Another possible explanation, specific to reproductive productivity, is the morphology of the palms reproduction. Palms produce seeds that are much larger and denser than the lightweight flowers and small seeds produced by the other forest types (pers. observ.). Due to the palm forests inherently larger allocation to reproduction it seems reasonable to consider them outliers and to remove them from the regression analysis.

The significant negative relationships between elevation and reproductive litterfall production suggest that small changes in temperature may result in significant changes in reproductive allocation. Increased allocation to reproduction may have negative impacts on other functions such as root and leaf growth by depleting stores of carbon and nutrients (Chapin *et al.* 1990). If climate change does cause montane forests to move to higher elevations as predicted by many researchers, they may experience significant decreases in reproductive allocation which could decrease their productivity in the future (Saxe *et al.* 2001).

The overall decrease in reproductive litterfall production over the course of the study may be explained by two periodic environmental events which occurred during the study. First, the apparent decrease may not be as dramatic as it seems because of an unusually productive year at the beginning of the study. The largest decreases in all of the forest types occur from year one to year two. Luquillo Forest experienced a drought during the first year of the study which may have increased oxygen levels in the normally anoxic soils (Waide *et al.* 1998). If the drought did result in abnormally high reproductive production then the subsequent decrease would only be a return to normal levels of productivity. The forests may be less productive in the subsequent years because they used allocated large portions of their stores of carbon and nutrients to reproduction in order to take advantage of the favorable soil oxygen conditions during the drought year. A second explanation of the decreases, pertaining to the latter years of the study, focuses on the effects of Hurricane Georges which struck the forest early in the fifth year of the study. Hurricanes are generally recognized as decreasing the productivity of forests, especially cloud forests, for years after they strike (Waide *et al.* 1998, Lugo and Scatena 1996). The results of this study show that the cloud forests may still be experiencing the effects of the hurricane disturbance years later. The lower elevation colorado forest seems to be recovering much more quickly. This disparity may be due to ecological differences or simply because hurricanes tend to be more intense near the tops of mountains.

Tropical montane forests are some of the world's most diverse ecosystems, but they may also be some of the most vulnerable to the effects of potential climate change (Loope and Giambelluca 1998). The results of this study reinforce this assertion and also show how these potential effects may differ dramatically across relatively small spatial scales. This study also shows how natural disturbances, such as drought and hurricanes, may have long lasting effects on these ecosystems. Further research should be conducted in order to identify the mechanisms driving the changes observed in this study.

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