September 1999

Culm density of a bamboo (Chusquea pohlii) and its effect on species richness

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ABSTRACT

Limitation of nutrients can greatly reduce the success of plants. Such stresses can be caused by invasive species that can outcompete other plant species trying to establish themselves in the vicinity. This can lead to reduced species richness. This study investigates the relationship between *Chusquea pohlii* culm density and species richness around the clumps. Clump area, number of species within and immediately around each clump was recorded and analyzed by regressing culm density on species density around the clumps ($p = < .0001$, $R^2 = .493$). Results showed that increasing culm density reduced species richness in and around the clumps suggesting that *C. pohlii* may be an invasive species that reduces species richness in the forest. Observations also showed that certain hemiepiphytic and herbaceous species occurred more often than other species.

RESUMEN

El límite de nutritivos es algo que afecta mucho la salud de las plantas. Estos límites pueden ser causados por especies invasoras que impiden el establecimiento de otras especies cerca de ellos. Efectos como estos pueden resultar en poca variedad de especies. Este estudio investiga la relación entre la densidad de culmos en las macollas de *Chusquea pohlii* y la cantidad de especies que viven alrededor. Los datos se analizaron usando una regresión polynomial ($p = < 0.0001$, $R^2 = .493$). Lo que se descubrió fue que con alta densidad de culmos en las macollas, baja la cantidad de otras especies al dentro y alrededor de las macollas. Estos resultados sugieren que *C. pohlii* puede ser una especie invasora que esta afectando la cantidad de especies que se encuentran en el bosque. Observaciones sobre las especies presentes enseñan que unas especies de hierbas y hemiepífitas son mas común alrededor de *C. pohlii*.

INTRODUCTION

Chusquea sp. (Poaceae: Bambusoidea) is native to the Americas ranging from Mexico to Central Chile and has an altitudinal range of 800-3800m (sub-montane to Páramo) (Stern et al. 1999). It is the largest genus of Neotropical high elevation bamboo and is distinct in that it has branching woody culms (stems). *Chusquea* is known to grow vegetatively with a genetically fixed cycle of approximately 15 years. Mast fruiting occurs upon which the plant then flower, seed and die. *Chusquea sp.* is also known to send out horizontal rhizomes through the leaf litter which give rise to clones as far as 30m from its original location. Although these clones are eventually shaded out by canopy species, the clones do relatively well in disturbed habitats such as burned areas, tree fall gaps, edges of landslides and other naturally open areas (Janzen, 1983). A plant with a similar biology to *Chusquea sp.* is Pteridium aquilinum which also grows by rhizomes and is sun tolerant (Young 1991). These characteristics, as well as others, have been shown to make P. aquilinum capable of restricting growth of other plant species (Young 1991). Because Chusquea sp. shares these invasive qualities it may also influence the number of species living immediately around and within its culm basal area. If Chusquea sp. with its inhibitory effect on other plants is competing with the surrounding *non-Chusquea* plant species for resources such as nutrients and water one might expect that in a *Chusquea sp.* clump with high culm density (# of culms/culm basal area), stress on the surrounding plants might be unusually high. This stress may reduce the success of the surrounding plant species, causing them to occur less frequently and therefore reducing species richness in and around the *Chusquea sp.* clumps. *Chusquea pohlii* is a relatively unstudied species found in the mid elevation cloud forest surrounding the Monteverde area. The purpose of this study is to determine how culm density within a clump affects species richness in and around the clump. I hypothesize that greater culm density will result in lower species richness within the C *pohlii* clumps.

METHODS

Study site

This study was conducted from October 23 through November 16, 1999 on a Pacific slope primary cloud forest just above the small town of Santa “Elena in the Cordillera de Tilarán in Puntarenas Costa Rica. The site is at an elevation of 1570 m and receives an average of approximately 2.5 m to 3 m of rainfall yearly.

Experimental Method

I first designated clumps as two or more culms within 50 cm of each-other and only culms showing new growth were considered. At each clump I recorded the number of C. *pohlii* culms present and measured the width and length of the basal area in order to calculate the culm density (# of culms/m^2). Elliptical area ($A=lw\pi$) was calculated for this formula because the vast majority of clumps best approximated an elliptical basal shape. At each clump I also recorded species identities and total number of different plant species rooted inside and within 6 inches around the basal area of the clump. This was done by compiling a morphological species log and comparing the log to each new plant found. After data collection the morphological species log was taken to local botanists for identification. I analyzed these data with a polynomial regression between culm density within the basal area and species density of the total area sampled at the clump. I also looked more carefully at the species that make up the top 30% of most frequently encountered species to find special relationships or possibilities for their high occurrence.

RESULTS

Average basal area was 1.138 m^2 (min=.001, max=7.069). Average culm density was 82.530 culms/m^2 (min=.849, max=1414.710, sd=224.372). Average species density per clump was 6.708 species/m^2 (min=.588, max=24.308). A total of 86 clumps were examined and 96 species of plants were found. The polynomial regression showed a negative relationship between culm density and species density which was found to be significant (p=<.0001, $R^\wedge 2$=.493) (Figure 1). The top 30% of the most frequently occurring species were *(Syngonium sp.* (Araceae) (E), *Philodendron sp.* (Araceae) (A); *Pilea ptericlada* (Urticaceae) (C); *Peperomia hernandipholia;* (B) (Piperaceae) and an herbaceous species of Apiaceae (D). Figure 2 shows the frequency of these five species. The frequency distribution (Figure 3) showed that low species density was exhibited by the majority of the clumps.

DISCUSSION

Species density data was used for statistical analysis to eliminate the effect of uneven sampling size due to varying basal areas of each clump. If only species richness in and around the clump was taken into account, greater sampling area in a clump regardless of culm density might result in greater species richness, according to MacArthur and Wilson's (1967) Island Biogeography theory. Often applied to mainland fragments, Island Biogeography theory associates greater species richness with greater area. Species density however is a function of species richness and can be used to compare species richness. Also, all clumps sampled contained culms of approximately the same diameter (3-4 cm) to insure that culm density in each clump was proportionate to all other clumps. As I had expected, greater culm density resulted in lower species richness in and around the *Chusquea* clumps (Figure 1). The trend in the graph showing an increase in species density then a decrease, suggests that once culm density reaches a certain height, species density and in turn species richness is possibly affected by *C. pohlii" s* inhibitory effects and begins to decrease. Something similar to this occurred in a study done on Cerro Cuerici by Widmer (1993), where the oak seedlings studied suffered higher mortality rates where Bamboo density was high. One possible reason for this is as previously stated, C. *pohlii's* rhizome growth. Most *Chusquea* species have been known to have pachymorphic (short and thick) roots. (Stern *et al.* 1999) examined dead pachymorphic rhizomes and found that aboveground vegetation closely approximated the underground rhizomes. Therefore we can infer that where culm density is high, rhizome density is also high leaving little unoccupied soil for the establishment of other plant species. It has also been suggested in the past that some rhizomes survive flowering and culm death, making it hard for non-bamboo species to succeed well after culm death (Sterne et *al* 1999). One factor may be that these rhizomes from current or past generations make soil space unavailable to other plant species simply because of their presence. The space that their rhizomes occupy is space that other plant species cannot utilize for establishment. Rhizomes may also have an effect due to the fact that they by definition absorb nutrients and water for the bamboo possibly reducing the amount of resources available to *non-Chusquea* species. These factors would certainly have damaging effects on species richness under the clumps by limiting the establishment of other plant species.

In another study, Widmer (1998) concludes that in pristine forest it is not the clonal rhizome spread that makes *Chusquea spp.* invasive; but instead *Chusquea's* morphological plasticity allow it to optimize light use efficiency. She also finds that under closed canopy, *Chusquea tomentosa* changes morphology to developing more branches as foraging structures in order to exploit the favorable light patches. *C. pohlii* clumps considered in this study were also found in closed canopy locations due to the difficulty of reaching gap clumps. Although I did not test light availability, it is likely that *C. pohlii* exhibits a similar response. Thus, *C. pohlii* could become better adapted to the available sunlight, increasing its fitness and possibly making it a better competitor for resources than surrounding plant species. Again, this advantage could allow *C. pohlii* to reduce the success of surrounding plant species, thereby lowering species richness.

Another possibility is allelopathy whereby some plants use leaves, roots or decaying litter to release chemical compounds into the environment that inhibit or kill competing species. If the plant can reduce the growth of nearby plants by releasing these chemicals, it may increase its access to light, water and nutrients and thus its fitness making it a better competitor (Taiz 1991). Although *Chusquea* is not commonly known for this, it does seem a possible explanation considering that it has shown to have some type of negative effect on species density around it. Also while in the field, I noticed that often times there were high amounts of C. *pohlii* leaf litter on the ground below it. If C. *pohlii* is in fact allelopathic it is possible that it releases its chemicals through its leaves and this may be affecting those *non-Chusquea* species living below.

Interestingly, Figure 1 shows an increase in species density with lower values of increasing culm density however this trend may be due to the possibility that at low culm densities, C. pohlii's inhibitory affects are not strong enough to affect the surrounding plants.

Another aspect that must be considered is the species that were most often in the Chusquea clumps (between 14 and 20% of clumps) (Figure 2), two of which are hemiepiphytic climbers and three herbaceous species. These plants showed the highest occurrence among clumps and may simply be because they are common forest understory plants (W. Zuchowski, pers. comm.), but it may also be related to their physiological nutrient requirements. Since hemiepiphytes, like epiphytes use, other plants for their structural support, it is possible that they expend less energy on the production of support structures. If less energy is needed for these structures, it is also conceivable that they may not need as many nutrients and water as a similar plant that must produce its own support structures. This reduced need for nutrient absorption may make them better adapted to areas of low nutrient availability - characteristic of the soil in and around the *Chusquea* clumps in which they were found.

A similar argument could be made for the herbaceous species found, which although must produce their own support structures still exhibit less biomass than plants such as trees. One could conceivably infer that because herbs in general produce less biomass (less leaves, shorter stems) they too could establish themselves and be successful with a lower minimum requirement of nutrients and water. The greater occurrence of herbaceous species could also be explained by studies done in disturbed or reduced nutrients areas. In these habitats when disturbance is chronic, species with short life cycles such as grasses and herbs are favored (Jordan 1985). The fifteen year lifespan of a *Chusquea* clump could be considered to have the same effect as a chronic disturbance for a plant living below it. Nutrient availability would be low throughout the life cycle and special adaptations would have to be made for this constant stress allowing them to persist in these areas.

The presence of these five common species found living below the *Chusquea* may also be attributed to the mast fruiting and die off of *Chusquea*. During periods after the culms have died assuming that the rhizomes have also died, opportunities arise for non-*Chusquea* plant species to enter. Nutrients and water are then made more available to these plant species. These plants may have established themselves during these periods of die off and later adapted to the presence of *C. pohlii* plants.

Of the 96 species found living in and around the clumps, no more than 7 were tree species and in a past study light demanding tree species were the ones affected by the bamboos growing in the forest (Young 1991). The species found most frequently in this study are understory shade tolerant plants not light demanding species which may also explain their common occurrence.

Chusquea pohlii has shown to be an invasive species of bamboo, reducing species richness when culm density is high. This is something that should be of great concern considering that *Chusquea* species are prevalent in disturbed areas. As Figure 3 shows, a large number of clumps exhibited low species density while few showed high species density. *C. pohlii*'s effect on species richness and its inclination to occur in disturbed areas indicate that it may be preventing successional growth from occurring in these disturbed areas that need to be regenerated. For example, the fact that it seems to have an effect on tree establishment poses problems for the regeneration of such an important part of the forest - the canopy, in these areas which *C. pohlii* occupies. This study supports the theory that disturbances in the forest lower species richness because *C. pohlii* is inclined to establish itself in disturbed areas and has shown to lower species richness when more culms are present.

ACKNOWLEDGMENTS

I would like to thank *mi hermana* Seidy Maria Torres for helping make the arrangements, the crew at Sky Walk for allowing me to use their site and for the *cafesito* on rainy days. Also to the Torres Leiton family for all their support, José Manuel for his help with keying out and Doña Elsi for keeping me clean and the boys for being interested. I would also like to thank my advisor Mauricio Garcia for his help and most of all for his encouragement. He has no idea how encouraging a smile is. Karen Masters for her "opinion", Justin Calabrese and Andrew Rodstrom for their life-saving help with graphs, Alan Masters and Eben Broadbent for their smiles, hugs and occasional backrubs during this entire process, Bill and Willow for identifying my moldy plants and the whole CIEE Fall 1999 crew for all the LOVE, support and good times at La Taberna. Oh and of course, to the Monteverde Electric Company for turning the power back on.

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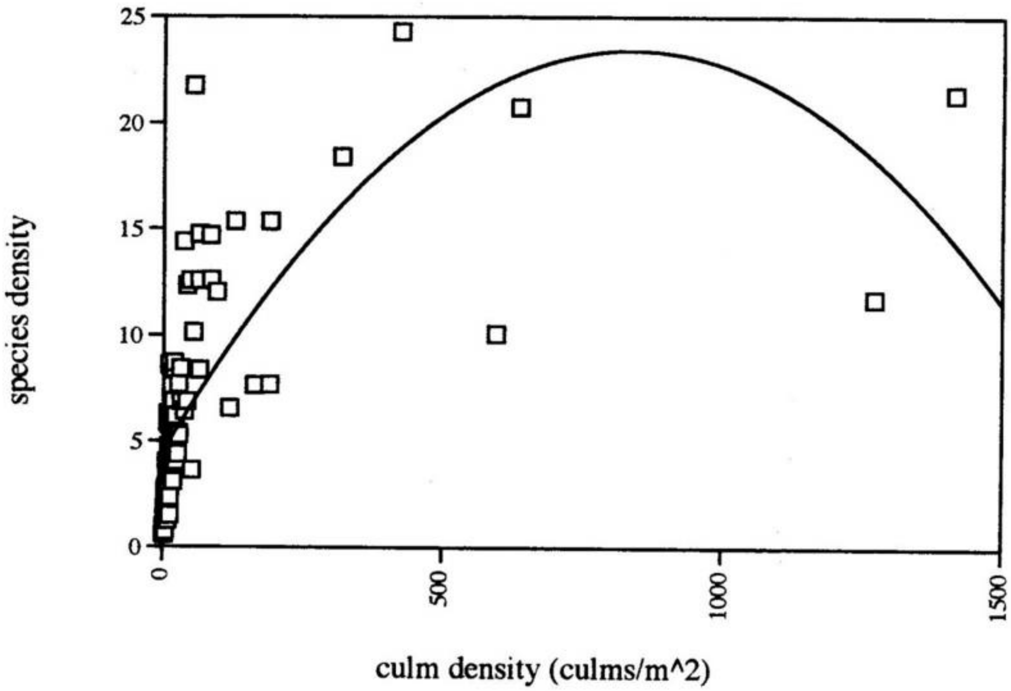

FIGURE 1 . Relationship between culm density and species density (species /total area). As culm density increasses, species density increases to a point then begins to decrease ($p=<.0001$, $R^2=.493$).

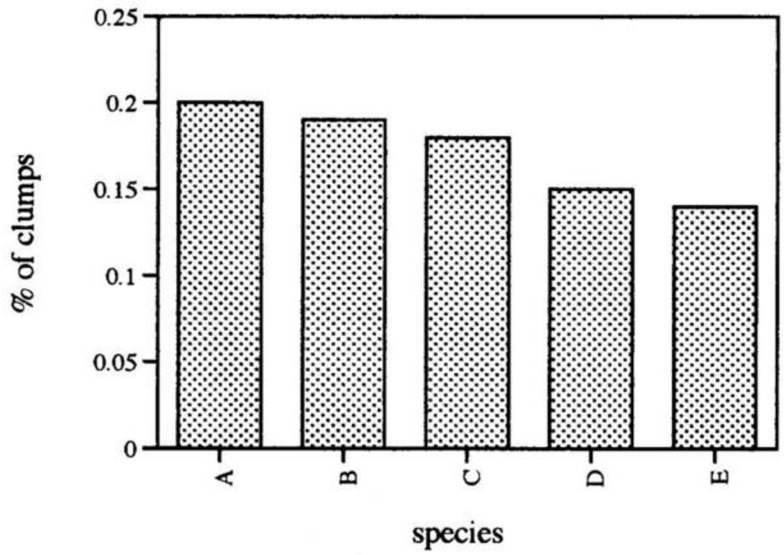

FIGURE 2 . Frequency distribution of the five most commonly occuring species. ***Philodendron sp.*** (Araceae) (A); ***Peperomia hernandifolia***(Piperaceae) (B); ***Pilea ptericlada***(Erticaceae) (C); (Apiaceae) (D);***Syngonium sp*** . (Araceae) (E).

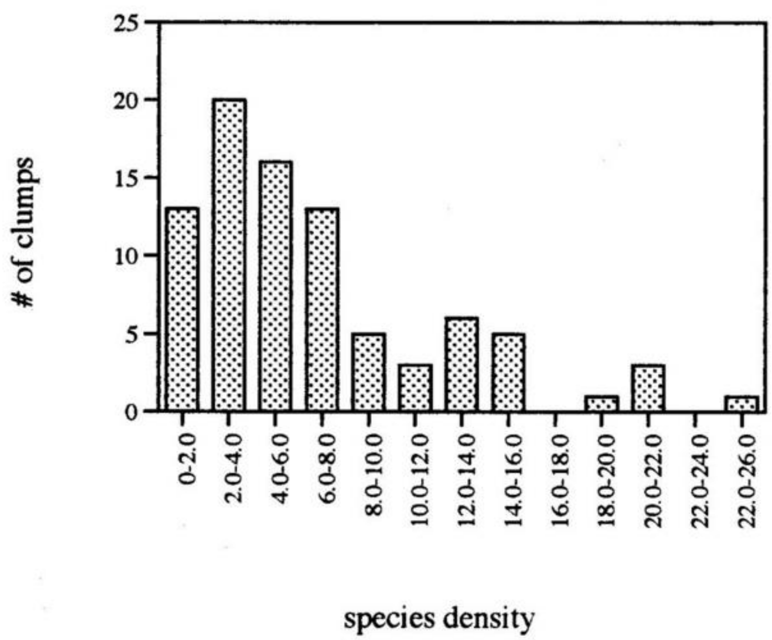

FIGURE 3. Frequency distribtion of species densities. High species density can be seen only in few of the *Chusquea pohlii* clumps whereas most clumps exhibit less than 8.0-10.0 species/m^2.