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Bamboo and gaps in the oak forests of the Cordillera de Talamanca, Costa Rica

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Synopsis

Chusquea talamancensis und *Chusquea tomentosa* sind die häufigsten Bambusarten des Unterholzes von Eichenwäldern (Wolkenwälder) der Cordillera de Talamanca in der Höhenlage zwischen 2600 bis 3100 m.ü.M. Der Oberstand dieser Wälder weist eine Dominanz der Baumarten der Gattung *Quercus* auf: *Q. costaricensis* und *Q. copeyensis*. Die meisten Eichenwälder befinden sich in der Alters- und Zerfallsphase nach LEIBUNDGUT (1982) und die Bestandslücken entstehen durch einfachen oder mehrfachen Baumsturz. Aufnahmeflächen von 500 m^2 wurden in den Bestandslücken und unter geschlossenem Kronendach des *Quercus*-Altbestandes ausgewählt. Der mittlere Deckungsgrad von Bambus beträgt in den Bestandslücken 87%, unter geschlossenem Kronendach 32%. Die morphologischen Merkmale von Bambus zeigen einen signifikanten Unterschied zwischen denn beiden Kronenschlußtypen. *Chusquea tomentosa* weist stärkere intraspezifische Konkurrenz auf als *C. talamancensis*. Die Dominanz von Bambus in den Beständen hat einen negativen Einfluß auf die Verjüngung von *Quercus costaricensis*.

Chusquea spp., bamboo, oak forests, deforestation, gaps, closed canopy, Quercus regeneration, competition

1. Introduction

The importance of treefall gaps in tropical forest dynamics has been extensively discussed in literature (HARTSHORN 1978, BROKAW 1982, PICKETT 1983, HUBBEL & FOSTER 1986). The influence of bamboo undergrowth on tree regeneration has been studied in *Fagus* and *Fagus-Abies* forests (NAKASHIZUKA 1988, TANAKA 1988), *Abies-Betula* forests (TAYLOR & QIN 1988, TAYLOR & QIN 1992) and in *Nothofagus*-forests (VEBLEN 1982, VEBLEN & al. 1977, VEBLEN & al. 1979). It has been generally shown, that bamboo presence affects tree regeneration. However, YOUNG (1991) did not observe this negative effect in a species-rich tropical montane forest in Peru.

Quercus forests with *Chusquea*-bamboo understory are found above 2000 m.a.s.l. (BLASER 1987) in the mountains of Costa Rica (KAPPELLE & al. 1990) south to Colombia (VEGA 1966). Recently, much interest has been directed to the oak-bamboo forests of the Cordillera de Talamanca, the largest area of primary forest (17% of entire country, SADER & JOYCE 1988) remaining in Costa Rica. Due to the approaching depletion of lowland forests and increasing pressure on the high-elevation forests, much national and international effort has been concentrated in developing a plan for sustainable natural forest management of the oak forests at the Cordillera de Talamanca. Studies on phytosociology (KAPPELLE & al. 1989), structure and composition (BLASER & CAMACHO 1991, OROZCO 1991) and the effects of slope on forest dynamics (BERNER 1992) provided basic information for this task.

Disturbance in the *Quercus*-forests like clearcutting and selective logging caused by past human activity led to secondary vegetation dominated by *Chusquea*-bamboos. It has been observed, that the bamboo character of big canopy gaps in the virgin forest can be compared to deforested sites. A big gap in the oak-bamboo forest is defined as a patch in the overstory canopy caused by multiple tree fall and delimited by old-growth oak trees. The study of big treefall gaps in an undisturbed oak-bamboo forest aims to understand the autoecology of *Chusquea spp.* in their natural environment and the reaction of vegetation to the bamboo understory canopy. This article deals with the spatial and morphological features of bamboos under different canopy closure types and the effect of bamboo cover on *Quercus costaricensis*-regeneration.

2. Materials and methods

This study was conducted between 1988 and 1989 in an area of 12 km^2 on the Cerro Cuericí and Cerro Abarca along the Cordillera de Talamanca, near the hamlet Villa Mills (9°33' N, 83°43' E). Compulsory criteria for site selection was the absence of human impact which was found at an elevation of 2800 to 3100 m.a.s.l. (the forest limit is at 3200 m.a.s.l.). *Quercus costaricensis* Liebm. and *Q. copeyensis* C.H. Müller are the dominant tree species at this altitudinal range. The bamboo species studied are of the neotropical genus *Chusquea*: *C. talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark and *C. foliosa* Clark, the first two are the most abundant in the study area and have been recently described (WIDMER & CLARK 1991). They are woody, medium-sized (3-7 m height) and clump forming, distributed in certain areas and excluding each other. Since these *Chusquea*-species show gregarious and monocarpic flowering (WIDMER, in prep.) it can be assumed that all individuals of a species colonized the site at the same time, i.e they are all even-aged.

Fifty-four plots of 500 m^2 were selected on the criteria of canopy closure, i.e. placing them in gaps or under closed canopy. The sites, whose canopy closure could not be classified in one of the two types were defined as intermediate gap and intermediate canopy. This plot size was used to estimate the cover (%) for bamboo and for the upper tree layer. Besides, the number of large trees (> 51 cm diameter at breast height/ DBH) was recorded. In the center of these plots, subplots of 100 m^2 were placed to sample data on bamboo: total number of clumps, total number of culms per clump, diameter of randomly selected adult culms (one per clump) and young culms (one per clump, when present). This area was also used to record the total number of saplings (> 1.50 m height - 10 cm DBH). Five subplots of 4 m2 each were put in the center and in the corners of the 100 m^2 subplot to register data on number and height of seedlings (< 1.50 m height). Besides the altitude, different slope expositions and inclinations were considered in plot selection. Two factor (gap vs. closed canopy, *Chusquea talamancensis* vs. *C. tomentosa*) unbalanced analysis of variance was performed for 30 plots and regression analysis for the total plot number (54). Hereby some preliminary results are presented.

3. Results and discussion

Canopy closure and bamboo development

As the first step all three *Chusquea* species (*C. talamancensis*, *C. tomentosa*, *C. foliosa*) were analysed together. A higher cover of bamboo is found when the upper tree layer has low cover values. In a gap the mean cover of the upper tree layer is 10 times lower than in closed canopy. As shown in Fig. 1 there is a negative linear relationship between the number of large trees (DBH > 51 cm) and the cover of bamboo.

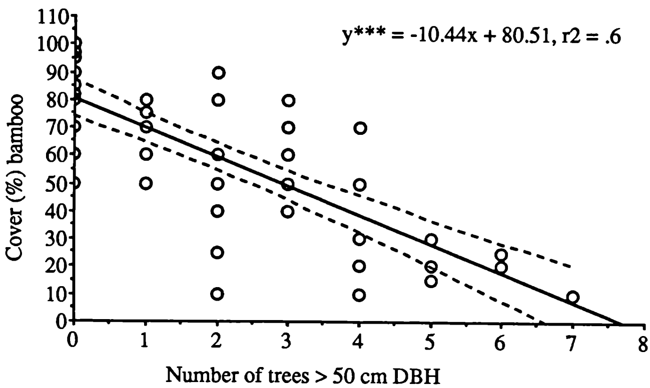

Fig. 1: Relationship between the number of large trees (DBH > 51 cm) and the cover (%) of bamboos (significance level: *** = 0.001).

In the range of 2 to 4 trees there is a great variability in the cover of bamboo which can be due to the variable degrees of crown cover of the large trees themselves, the position and the spatial arrangement of the trees in the plot, and the cover degree of the middle tree layer. Thus, the *Chusquea*-bamboos studied are sensitive to changes in canopy closure. One factor analysis of variance of bamboo cover (all three species) shows significant difference between gap (87.4%) and closed canopy (32.1%).

Nevertheless, differences between species can be recognized in the reaction to canopy closure (Tab. 1). *Chusquea tomentosa* has one fourth of the clumps in gaps compared to closed canopy, whereas *C. talamancensis* clumps are reduced to half. Meanwhile, the average number of culms per clump of *Chusquea tomentosa* is 4.6 times higher in gaps than in closed canopy, while for *C. talamancensis* it is only 2.1 times. The diameter of adult and young culms is higher in gaps than under closed canopy for both species, whereby each species has specific morphological limits for culm growth. The mean diameter increasing factor between gap and closed canopy is similar for the adult culms of both species: *Chusquea tomentosa* has a factor of 1.47 and *C. talamancensis* of 1.54. The lower increasing factor for young culms of *Chusquea talamancensis* (1.40) compared to *C. tomentosa* (1.76) may be explained by the fact that the first had a reduced vitality because of monocarpic and gregarious flowering from 1988 on (WIDMER, in prep.). *Chusquea foliosa* shows similar results as *C. tomentosa*.

Tab. 1: Differences in cover (%) and morphological features of the bamboos *Chusquea talamancensis* and *C. tomentosa* between gap and closed canopy (significance level: *** = 0.001, ** = 0.01).

Types of canopy closure	Gap		Closed canopy	
	x̄	SD	x̄	SD
Cover (%) * **				
Chusquea talamancensis	85	9.1	31.7	20.3
Chusquea tomentosa	87.2	7.8	32.5	17.8
Number clumps /100 m2 * **				
Chusquea talamancensis	11.7	3.1	20.9	5.1
Chusquea tomentosa	4.5	0.6	17	6.9
Number culms/clump * **				
Chusquea talamancensis	19.3	8.2	9	4.3
Chusquea tomentosa	30.2	6.8	6.5	3.8
Diameter adult culms (cm)* **				
Chusquea talamancensis	2.22	0.20	1.44	0.43
Chusquea tomentosa	3.18	0.27	2.16	0.50
**Diameter young culms (cm) ** **				
Chusquea talamancensis	1.79	0.12	1.27	0.48
Chusquea tomentosa	3.54	0.53	2.01	0.75

x : mean, SD : standard deviation

Bamboo cover and *Quercus costaricensis*-regeneration

Bamboo cover has a negative effect on seedling density of *Quercus costaricensis* (Fig. 2). Obviously, other factors as number, distance and seed productivity of parent trees, seed dispersal mechanisms and predation have an influence on the recruitment of oaks, too. Bamboo cover and *Quercus costaricensis*-sapling density was weakly correlated (r = 0.21, p = 0.001). Nevertheless, a bamboo cover over 50% seems to affect the survival of juvenile oaks, regardless of other factors which could influence the success of *Quercus costaricensis* at this developmental stage. The effect of soil nutrient status was considered in the ongoing study, but no significant difference between soils in gaps and closed canopy has been found.

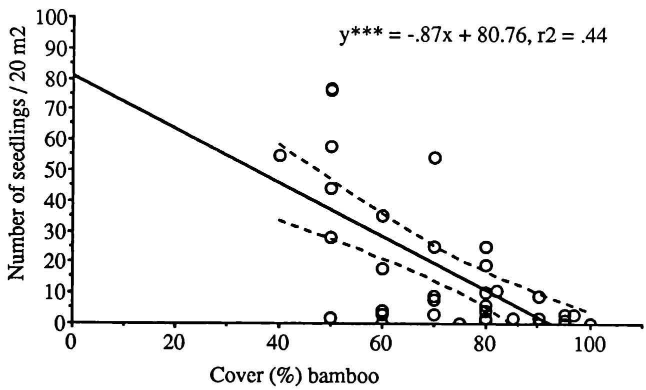

Fig. 2: Relationship between the cover (%) of bamboo and the seedling density of *Quercus costaricensis* in 20 m^2 (significance level: ** = 0.01).

4. Conclusions

Chusquea-bamboo development is controlled by the degree of cover of the overstory of the old-growth oaks. Bamboo culm production and diameter growth is enhanced in gaps compared to closed canopy. *Chusquea tomentosa* has larger and fewer clumps in gaps than *C. talamancensis*, which may suggest that intraspecific competition is more pronounced for the first bamboo. The difference in clump density and size between species is not as considerable under closed canopy, i.e. when the cover of the upper tree layer is over 60%. Thus, a large opening in the canopy of the *Quercus spp.*-overstory causes a physiognomic change in the bamboo-dominated understory, con-

verting the open area in a bamboo stand.
Survival of *Quercus costaricensis*-seedlings seems to be dependent on the cover of *Chusquea*-bamboos. The > 1.50 m height sapling density of *Quercus costaricensis* (trees > 1.50 m height - 10 cm DBH), may also be affected by the cover degree of the *Chusquea*-species studied. If we consider the large time scale of this virgin tropical high mountain forest ecosystem and the effect of gregarious monocarpic bamboo-flowering on the forest dynamics (i.e. recovery of tree species), then *Chusquea* may not be such a problem. But, since silvicultural treatments are planned and carried out, in order to favour natural tree regeneration, it is strongly recommended to avoid clearcutting over large areas, especially during the rainy season.

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