THE ECOLOGICAL ROLE OF BAMBOO (CHUSQUEA SPP.)
IN THE OLD-GROWTH QUERCUS FORESTS OF THE
CORDILLERA DE TALAMANCA, COSTA RICA

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presented by

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1999
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INTRODUCTION

What is a bamboo? In response to this question, most people in Europe would think of the tall, stately grasses which decorate gardens and parks (Chapman, 1997). However, for many people in China, Japan and Southeast Asia the answer would be the enormously versatile woody plants which they use as their most important building material, for food, furniture and paper-making, and many other applications in everyday life (baskets, brushes, traps for fish and crabs, electricity poles, toys, jewellery, chopsticks, buttons, etc.; Liese, 1985).

For the plant taxonomist, bamboos comprise a subfamily, Bambusoideae, which is viewed as 'a heterogeneous group of rhizomatous, broadleaved, forest grasses with arm and fusoid cells in the chlorenchyma, bracteate inflorescences and trimerous flowers' (Clark, 1997b). There are approximately 116 genera and 1300 species of Bambusoideae (Clark, 1995). They have a wide range of distribution, from latitudes as far north as 46° and as far south as 47°, but occur mainly within the band circumscribed by the Tropics of Cancer and Capricorn. Bambusoid grasses are divided into the woody bambusoid grasses (or bamboos) and the herbaceous bambusoid grasses. Herbaceous bambusoid grasses are confined to warm and humid environments at lower elevations in the tropics, mainly within the forest under rather shaded conditions. In contrast, bamboos occur over a much larger latitudinal and altitudinal range, and exhibit a greater diversity in their habitats (Soderstrom & Calderón, 1979).

The rhizomes of herbaceous bambusoid grasses are less robust than those of bamboos and, in most cases, the internodes are extremely short, resulting in a caespitose growth form. In bamboos, there are basically two major types of rhizome: leptomorph and pachymorph (McClure, 1966). Bamboos with leptomorph rhizomes (or monopodial type) form groves or extensive tracts of rather evenly-spaced culms, and are common in temperate and cold regions (eg. Arundinaria, Phyllostachys, Sasa). The culms of bamboos with pachymorph rhizomes (or sympodial type) are usually close together and form discrete clumps; most are plants of warm, tropical regions (eg. Bambusa, Dendrocalamus, Gigantochloa).
Most of the herbaceous bambusoid grasses are diploid while the woody bamboos are polyploid (usually tetraploid, sometimes hexaploid), with $x = 12$ as the basic number (Soderstrom, 1981). According to Soderstrom (1981) and Tzvelev (1989), bamboos must have evolved from herbaceous ancestors. The large woody habit may have been a response to competition with trees, which represent the major growth form of the forest. As well as an increase in the chromosome number (polyploidization), the process of 'grandization' involved an increase in the number of internodes in the culms, elongation of the internodes by means of intercalary meristems, development of complex branching at the nodes, and a great increase in lignification. At the same time, the increased emphasis on vegetative growth, in the form of greater longevity of the individual culm and an increase in size by branching, was accompanied by a decrease in flowering. Not only was flowering frequency diminished, but there appears to have been less active inflorescence evolution, with the consequence that most bamboos show a 'primitive type' of inflorescence (Soderstrom, 1981).

For various reasons, the systematics of the bamboo grasses is in a state of flux. In the first place, there is a lack of flowering material of many species due to their unpredictable flowering at long intervals (Tzvelev, 1989). Secondly, many new genera and species are still being discovered and described, especially in the Neotropics (Calderón & Soderstrom, 1980; Clark, 1995). Thirdly, our understanding of the evolutionary relationships amongst the bamboos has been affected by the new insights into the grass family Poaceae as a whole, gained from the use of modern molecular and cladistic methods. The taxonomy of herbaceous bamboos is relatively complete, but woody bamboos are less well known taxonomically, due to the greater number of species, their complex morphology, and the difficulties of collecting them (Clark, 1995). The rate at which new bamboo species are still being discovered in the New World is well illustrated with the example of *Chusquea*: in 1989, 115 species were known to exist including 15 undescribed species (Clark, 1989); in 1992 the number was put at 150 (30 undescribed) (Clark, pers. comm.), in 1995 at 180 (55 undescribed) (Clark, 1995), and in 1997 at approximately 200 (70 undescribed) (Clark, 1997a).

Until recently, it was widely supposed that the Bambusoideae contain the most primitive members of the Poaceae, though the exact taxonomic
status of the group was uncertain. Recently, Clark (1997b) has shown that three tribes which were formerly regarded as herbaceous bamboos (the Anomochloeae, Streptochaeteae, and Phareae) represent the most ancient grass lineages. On the other hand, the woody bamboos, Bambuseae, together with two other tribes of herbaceous bamboos (Olyreae and Buergersiochloeae) 'form a monophyletic clade of "true bamboos" that evolved later'.

Chusquea is the largest and most diverse genus in the subfamily Bambusoideae, and it has the greatest latitudinal and altitudinal ranges of any bamboo genus (Clark, 1997a). It is a woody clump-forming bamboo generally with pachymorph rhizome; 'solid culms becoming fistulose with age; multiple, dimorphic buds in linear or constellate insertion per node; determinate, paniculate inflorescences; spikelets consisting of two glumes, two sterile lemmas, and one fertile floret with no rachilla extension' (Clark, 1989). The Andes is the region with the greatest diversity of Chusquea (49 species); second comes south-eastern South America including the Brazilian Atlantic forests (37 species), and Central America and Mexico is the third most diverse region (33 species). Of the species within each of these phytogeographic region, 91-100% are endemic to that region (Clark, 1997a). Species of Chusquea are mostly understory plants of montane forests in the Neotropics, but due to widespread deforestation, they have also become very successful in secondary vegetation. In Costa Rica a few species occur in lowland rain forests (Chusquea simpliciflora Munro ex Hemsley, C. serpens L.G. Clark), and one species occurs above the forest limit in the páramo vegetation (C. subtessellata Hitchcock). Most of the montane forest Chusquea species have a semelparous life cycle with a more or less regular flowering cycle at long intervals, and synchronization of the flowering event within a population. Chusquea shows a general tetraploid chromosomal pattern and the base chromosome number is \( x = 10 \) (Clark, 1989).

This dissertation describes aspects of the taxonomy and ecology of bamboos of the genus Chusquea in montane forests in Costa Rica. The original reason for the study arose from the fact that foresters working at the Silviculture of Natural Forests Project at CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) in Costa Rica considered Chusquea bamboos in the oak forests to be weeds which must be controlled. When the forest is disturbed, for example by felling trees, the
structure of the vegetation is changed, and many open habitats are created. This often leads to a rapid increase in the abundance of *Chusquea* bamboos, which grow so vigorously that they turn the forest into an impenetrable thicket. Furthermore, the swathes of bamboo which cover the forest floor prevent tree regeneration and so the forest becomes a secondary scrub which is of no economic value either for timber and other forest products, or for grazing.

The initial aim was to investigate the ecology of *Chusquea* in the high-mountain forests, and especially to study the regeneration dynamics of the forest-bamboo system in the absence of human intervention. An understanding of these processes would be useful to foresters wanting to manage the forest in a sustainable way and without incurring the high costs involved in clearing bamboo. With this aim in mind, I selected plots with different *Chusquea* species and different canopy closures in order to compare the species composition of the vegetation, the abundance of trees and the performance of bamboos.

As often happens with field research in the tropics, unpredictable events soon modified the course of the study. Early in the field work I realized that the two most abundant species in the study area had not been described, and I was confronted with the problem of having no names for the dominant species in my plots. It was therefore necessary to contact the *Chusquea*-specialist, Dr. Lynn G. Clark, and collect taxonomic data. The unexpected event which made the systematic description of these species possible was that they began to flower. Flowering started in 1987 with a few scattered plants of both species. In the following years (1988-1990) there was mass flowering of the species in the entire region, followed by the death of whole populations and regeneration from seed. The event provided a rare opportunity to examine the flowering phenology of bamboo species, and allowed us to describe new species which had only been seen in their vegetative state. We made a good collection of specimens during Lynn Clark’s visit to Costa Rica in 1989 and subsequently described three new species of *Chusquea*.

These events meant that the original conception, which had been more directed to the practical value and management of *Chusquea*, was greatly altered. As it developed, the study had four main objectives:
Table 1. List of the studies on the ecology of Chusquea species including the works presented in this thesis.

<table>
<thead>
<tr>
<th>Chusquea species</th>
<th>Forest type (Region/Country)</th>
<th>Altitude (m asl.)</th>
<th>Position in vegetation</th>
<th>Ecological subject studied</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. abietifolia</td>
<td>Tropical lower montane forest (Jamaica)</td>
<td>800-2000</td>
<td>Forest understory and secondary vegetation</td>
<td>Flowering, Forest structure</td>
<td>Seifriz 1920, 1950, Grubb &amp; Tanner 1976</td>
</tr>
<tr>
<td>C. longifolia</td>
<td>Tropical lower montane forest (Costa Rica)</td>
<td>2000-2100</td>
<td>Quercus forest understory</td>
<td>Flowering</td>
<td>Widmer 1994</td>
</tr>
<tr>
<td>C. patens</td>
<td>Tropical lower and upper montane forest (Costa Rica)</td>
<td>2400-2750</td>
<td>Quercus forest understory and secondary vegetation</td>
<td>Flowering</td>
<td>Widmer 1994</td>
</tr>
<tr>
<td>C. foliosa</td>
<td>Tropical lower and upper montane forest (Costa Rica)</td>
<td>2200-3100</td>
<td>Quercus forest understory and secondary vegetation</td>
<td>Flowering, Morphology and population dynamics, Soil-plant relationships</td>
<td>Widmer 1994, 1998a</td>
</tr>
<tr>
<td>C. subtilis</td>
<td>Tropical upper montane forest (Costa Rica)</td>
<td>2550-2800</td>
<td>Quercus forest understory</td>
<td>Flowering</td>
<td>Widmer 1994, 1998b</td>
</tr>
<tr>
<td>C. talamancensis</td>
<td>Tropical upper montane forest (Costa Rica)</td>
<td>2600-3200</td>
<td>Quercus forest understory and secondary vegetation</td>
<td>Flowering, Morphology and population dynamics, Soil-plant relationships</td>
<td>Widmer 1994, 1998a</td>
</tr>
<tr>
<td>C. tomentosa</td>
<td>Tropical upper montane forest (Costa Rica)</td>
<td>2500-3000</td>
<td>Quercus forest understory and secondary vegetation</td>
<td>Flowering, Morphology and population dynamics, Soil-plant relationships</td>
<td>Widmer 1994, 1998b</td>
</tr>
<tr>
<td>C. scandens</td>
<td>Tropical lower and upper montane forest (Ecuador)</td>
<td>2800-3800</td>
<td>Mixed forest understory and secondary vegetation</td>
<td>Distribution, Performance, Morphology, population structure and forest dynamics</td>
<td>Veblen 1982, Schlegel 1991, Veblen et al. 1980</td>
</tr>
<tr>
<td></td>
<td>Tropical timberline forest (Peru)</td>
<td>3400-3600</td>
<td>Mixed forest understory</td>
<td>Performance, Morphology, population structure and forest dynamics</td>
<td>Veblen 1982, Schlegel 1991, Veblen et al. 1980</td>
</tr>
<tr>
<td>C. culeou</td>
<td>Temperate rain forest (Chile &amp; Argentina)</td>
<td>500-900</td>
<td>Nothofagus forest understory secondary vegetation</td>
<td>Morphology, growth, population structure</td>
<td>Veblen 1982, Schlegel 1991, Veblen et al. 1980</td>
</tr>
<tr>
<td></td>
<td>Subalpine forest (Chile &amp; Argentina)</td>
<td>900-1200</td>
<td>Nothofagus forest understory</td>
<td>Morphology, growth, population structure</td>
<td>Veblen 1982, Schlegel 1991, Veblen et al. 1980</td>
</tr>
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</table>
• To describe three new species of bamboo on the basis of flowering material which became available as a result of the mass flowering (Chapter 1);
• To characterize the vegetation and soils in the study area in which the Chusquea species occur (Chapters 2 and 3);
• To investigate aspects of the population structure of Chusquea in relation to the cover of the forest canopy (Chapter 4).
• To describe the flowering phenology of selected species and the distribution of Chusquea species in the northwestern Talamancan range (Chapters 5 and 6).

The final chapter presents a discussion of the life cycle of Chusquea species and shows how these bamboos influence the regeneration dynamics of the Quercus forests in which they grow.

Table 1 summarizes the literature on the ecology of Chusquea until 1998. The first paper was published in 1920 and describes observations by Seifriz of mass flowering of Chusquea abietifolia in Jamaica. Veblen and co-workers investigated the population structure of Chusquea culeou and C. tenuiflora in the Nothofagus forests in Chile in the 1980's. Several more papers have been published in the 1990's, but there remains a great deal more to do, especially concerning the population structure and dynamics of these most interesting plants.

References


CHAPTER 1

New species of Chusquea (Poaceae: Bambusoideae) from Costa Rica

Yvonne Widmer and Lynn G. Clark


Abstract

Three new species of Chusquea from the upper montane forests of the Cordillera de Talamanca in Costa Rica are described and illustrated. Chusquea tomentosa and C. subtilis belong to Chusquea sect. Longifoliae L. G. Clark and are closely related to C. foliosa L. G. Clark. The third species, C. talamancensis, is a member of Chusquea sect. Swallenochloa (McClure) L. G. Clark and shows similarities to both C. tonduzii Hackel and C. vulcanalis (Soderstrom & C. Calderón) L. G. Clark. Revised keys to the species of sect. Longifoliae and sect. Swallenochloa in Costa Rica are provided.

Keywords: Chusquea, Bambusoideae, bamboo, Longifoliae, Swallenochloa, Costa Rica, new species

Introduction

Species of the woody bamboo genus Chusquea Kunth are often important components of montane forests in the New World (Veblen et al., 1977; Clark, 1989), but little ecological data relating to Chusquea is available. In Costa Rica, the upper montane forests along the Cordillera de Talamanca and volcanoes of the Cordillera Volcánica Central (northern slopes) are dominated by species of Quercus L., with a number of species
of *Chusquea* found as elements in the understory or along the forest margins.

A Swiss Forestry Project, in association with the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica, is developing a management plan for these forests.

As part of this project, the ecology of two species of *Chusquea* in these forests was studied (Widmer, 1998). When the two species began to flower in 1987-1989, we were able to confirm that they were both undescribed. Material of a third undescribed species in flower was also collected during the ecological study.

In this paper, we describe and illustrate the three new species, *C. tomentosa, C. subtilis,* and *C. talamancensis.* The first two species are members of *Chusquea* sect. *Longifoliae,* and the third belongs to *Chusquea* sect. *Swallenochloa.* Revised keys to the species of these two sections in Costa Rica are included.

*Key to the species of Chusquea Sect. Longifoliae in Costa Rica (based on vegetative specimens)*

1 a. Thin, curly leafless fibrillar branchlets interspersed with the normal, leafy subsidiary branches; internodes scabrous; foliage leaf blades with the base rounded to rounded-truncate ....................................................*C. scabra*

1 b. Fibrillar branchlets absent; internodes usually smooth, rarely scabrous just below the nodes; foliage leaf blades with the base attenuate to rounded attenuate.

2a. Foliage leaf blades 0.6-1.3 cm wide; subsidiary branches 18-30 per node; culm leaf sheaths 0.7-3 times as long as blades..........*C. longifolia*

2b. Foliage leaf blades 0.3-0.9(-1.1) cm wide; subsidiary branches 24-80(-150) per node, culm leaf sheaths 1.5-10.5(-14) times as long as blades.

3a. Culm leaf sheaths abaxially scabrous to pilose, or sometimes glabrous; subsidiary branches 24-65 per node; inner ligules of foliage leaves 0.5-4 mm long; foliage leaf blades 0.4-0.9 cm wide......................................................*C. patens*

3b. Culm leaf sheaths abaxially glabrous to pilose at the base; subsidiary branches 50-80(-150) per node; inner ligules of foliage leaves to 1.5 mm long; foliage leaf blades 0.3-0.7(-1.1) cm wide.
4a. Foliage leaf blades abaxially tomentose; fimbriae at the apex of foliage leaf sheaths straight few per tuft. C. tomentosa
4b. Foliage leaf blades abaxially glabrous to sparsely pilose with scattered hairs; fimbriae at the apex of foliage leaf sheaths often curly, several to many per tuft.
5a. Foliage leaf blades with the base attenuate, L:W = (26-)30-48(-54); culm leaf sheaths 4.4-6.6 times as long as the blades. C. subtilis
5b. Foliage leaf blades with the base rounded-attenuate, L:W = 20-40(-45); culm leaf sheaths 1.5-5.4 times as long as the blades. C. foliosa

Key to the species of Chusquea Sect. Longifoliae in Costa Rica (based on flowering specimens)

la. Primary branches of panicle strongly spreading.................C. patens
lb. Primary branches of panicles appressed or ascending.
2a. Sterile lemma II 3/4-7/8 the spikelet length; thin, curly, leafless fibrillar branchlets interspersed with the normal, leafy subsidiary branches; internodes scabrous.......................C. scabra
2b. Sterile lemma II equalling or nearly equalling the spikelet length; fibrillar branchlets absent; internodes usually smooth, rarely scabrous just below the nodes.
3a. Spikelets 10.4-20.6 mm long; foliage leaf blades 0.6-1.3 cm wide; subsidiary branches 18-30 per node; culm leaf sheaths 0.7-3 times as long as the blades.........................C. longifolia
3b. Spikelets 8.4-15 mm long; foliage leaf blades 0.3-0.7(-1.1) cm wide; subsidiary branches 50-80(-150) per node; culm leaf sheaths 1.5-10.5(-14) times as long as the blades.
4a. Spikelets 11.5-15 mm long; sterile lemma I 5/8-2/3 the spikelet length; foliage leaf blades abaxially tomentose .........................................C. tomentosa
4b. Spikelets 8.4-11.8 mm long; sterile lemma I 2/3-3/4 the spikelet length; foliage leaf blades abaxially glabrous to sparsely pilose with scattered hairs.
5a. Spikelets 8.4-11.2 mm long, fertile lemma subulate; foliage leaf blades with the base rounded attenuate, L:W=20-40(-45)...............................C. foliosa
5b. Spikelets 9.8-11.8 mm long; fertile lemma aristate; foliage leaf blades with the base attenuate; L:W = (26-)30-48(-54)..............C. subtilis

**Chusquea tomentosa** Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Villa Mills, road to Piedra Alta, 2880 m asl, 30 May 1989 (fl), Clark, Widmer & Stein 500 (holotype, CR; isotypes, ISC, MO, NY, US). Figure 1 A-E.

Culmi 1.3-4 cm diam., 6-9 m alti. Folia culnorum 20.8-29 cm longa; vaginae 11.8-25.4 cm longae, 4-10.5(-14) plo longior quam laminae, abaxiales glabrae; laminae 1.4-5.4 cm longae, erectae, adaxiales pubescentes, abaxiales glabrae. Ramificatio infravaginalis. Vaginae foliorum fimbriatae, fimbriae paucae 1-2 mm longae, rectae; laminae foliorum 15-27 cm longae, 0.3-0.7(-1.1) cm latae, L: W = 25-40, abaxiales tomentosae, non tessellatae. Paniculae 8-16 cm longae, angustae; rami laxe adpressi. Spiculae 11.5-15 mm longae, scaberulae. Glumae 2, squamiformes. Lemmata sterilia 2, subulata; lemma sterile 17.2-9.7 mm longum; lemma sterile II 11.7-14 mm longum. Lemma fertile 11.5 - 13.5 mm longum, subulatum. Palea 9.5-12.1 mm longa, sulcata.

**Culms** 1.3-4 cm basal diam., 6-9 m tall, erect at the base, arching above and scandent. Internodes (11-14-)18-38(-51) cm long, more or less terete, shallowly sulcate above the central bud, usually smooth to scabrid below the node. Culm leaves 20.8-29 cm long, the juncture of the sheath and blade abaxially a ± horizontal and distinct line, sheaths 11.8-25.4 cm long, 4-10.5(-14) times as long as the blades, abaxially glabrous, the margins glabrous, one side occasionally minutely ciliate toward the apex; blades 1.4-5.4 cm long, triangular, erect, usually persistent, adaxially pubescent, abaxially glabrous, the apex subulate, the base narrower than the apex of the sheath; girdle 3-5 mm wide densely pubescent, inner ligule 1-4 mm long, apically ciliolate. Nodes with one triangular central bud subtended by 50-60 subsidiary buds; sheath scar dipping away markedly below the bud/branch complement. Branching infravaginal; central bud developing tardily at the middle and upper nodes; leafy subsidiary branches 18-32 cm long, frequently rebranching basally, 60-80(-150) in the mature complement. Foliage leaves 4-9 per complement; sheaths glabrous, the overlapping margin ciliate, the apex with a tuft of fimbriae on either side of the summit, the fimbriae few per tuft, 1-2 mm long, straight, eventually deciduous; blades 15-27 cm long, 0.3-0.7(-1.1) cm
wide, L : W = 25-40, adaxially glabrous, sometimes with some scattered hairs, abaxially tomentose and often glaucous, not tessellate, the apex short-setose, the base attenuate to rounded-attenuate; pseudopetiole 1-1.5 mm long; outer ligule an irregular, glabrous rim to 0.5 mm long; inner ligule to 1 mm long, truncate to rounded, pubescent. **Panicles** 8-16 cm long, narrow, the base often retained within the subtending sheath; rachis triquetrous, glabrous, the edges scabrid; branches loosely appressed, angular, scabrid, the lower ones 3-4 cm long; pedicels 2-6 mm long, angular, scabrid. **Spikelets** 11.5-15 mm long, scabrid. **Glumes** 2, scalelike, usually acute, nerves lacking or 1-nerved; glume I ca. 1/15 the spikelet length, 0.5-1.3 mm long; glume II ca. 1/10 the spikelet length, 0.7-1.5 mm long. **Sterile lemmas** 2, subulate, abaxially scabrid; sterile lemma I 5/8-2/3 the spikelet length, 7.2-9.7 mm long, 5- or 7-nerved; sterile lemma II extending the full spikelet length, 11.7-14 mm long, 5-, 7-, or 9-nerved. **Fertile lemma** 11.5-13.5 mm long, subulate, abaxially scabrid, 7-9-nerved. **Palea** 9.5-12.1 mm long, sulcate for most of the length, apiculate, scabrid, 6-8-nerved. **Stamens** 3; anthers 6-8 mm long. **Fruit** unknown.

**ADDITIONAL SPECIMENS EXAMINED.**— COSTA RICA. CARTAGO: S slope of Volcán Turrialba, 1-2 km E of Hacienda Central, *Pohl & Davidse 10867B* (ISC); Villa Mills, at Quebrada Voltea, *Widmer 500* (CR, ISC), 501 (CR, ISC); on the path to Cerros Cuericí, *Widmer 502, 503, 504, 506 & s.n.* (CR, ISC), La Esperanza del Guarco, Km 61.8 on the Carretera Interamericana, 4 km NE, 19 Jan. 1990 (fl), *Widmer 505* (CR, ISC). SAN JOSE: along the Carretera Interamericana between Km 77 & 78, *Clark & Clark 274* (ISC, MO, US); Cordillera de Talamanca, Km post 107, ca. 20 km N of San Isidro del General along the Carretera Interamericana, *Davidse 761* (ISC); Trinidad de Dota, Km 62.5 along the Carretera Interamericana, 6 Feb. 1990 (fl), *Widmer 507* (CR, ISC).

**Chusquea tomentosa** is characterized by the abaxially tomentose foliage leaf blades and the scabrid spikelets 11.5-15 mm long. This species occurs in the Cordillera de Talamanca in montane forests at elevations of 2500 to 3000 m asl. It grows on slightly drier sites with southern to southeastern exposures.

Vegetative specimens of *C. tomentosa* were previously assigned to *C. foliosa* L. G. Clark (Clark, 1989). With the advent of flowering in 1989, *C. tomentosa* could be clearly distinguished from *C. foliosa* based on the
large spikelets. Vegetatively, the two species are very similar in overall aspect, but may be differentiated by the abaxially tomentose foliage leaf blades and the few, straight fimbriae at the apex of the foliage leaf sheaths of *C. tomentosa*. In *C. foliosa*, the foliage leaf blades are abaxially glabrous to sparsely pilose with scattered hairs, and the fimbriae are more numerous and usually curly. *Chusquea foliosa, C. tomentosa*, and *C. subtilis* form a complex of closely related species within sect. *Longifoliae*; a comparison of the three species is presented in Table 1.

**Table 1. A morphological comparison of Chusquea foliosa, C. subtilis, and C. tomentosa.**

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. foliosa</em></th>
<th><em>C. subtilis</em></th>
<th><em>C. tomentosa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Culm leaf sheath blade</td>
<td>1.5-5.4</td>
<td>4.4-6.6</td>
<td>4.0-10.5(-14)</td>
</tr>
<tr>
<td>Foliage leaf sheath apex</td>
<td>fimbr. often curly, 1-2 mm long, many/tuft</td>
<td>fimbr. often curly, 1-1.5 mm long, many/tuft</td>
<td>fimbr. straight, 1-2 mm long, few/tuft</td>
</tr>
<tr>
<td>Foliage leaf length : width</td>
<td>20-40(-45)</td>
<td>(26-)30-48(-54)</td>
<td>25-40</td>
</tr>
<tr>
<td>Foliage leaf base</td>
<td>rounded-attenuate</td>
<td>attenuate</td>
<td>attenuate to rounded-attenuate tomentose</td>
</tr>
<tr>
<td>Foliage leaf abaxial pubescence</td>
<td>glabrous to sparsely pilose</td>
<td>glabrous to sparsely pilose</td>
<td>tomentose</td>
</tr>
<tr>
<td>Spikelet length</td>
<td>8.4-11.2 mm</td>
<td>9.8-11.8 mm</td>
<td>11.5-15 mm</td>
</tr>
<tr>
<td>Sterile lemma I/spikelet</td>
<td>2/3(-3/4)</td>
<td>2/3-3/4</td>
<td>5/8-2/3</td>
</tr>
<tr>
<td>Fertile lemma apex</td>
<td>subulate</td>
<td>aristate</td>
<td>subulate</td>
</tr>
</tbody>
</table>

**Chusquea subtilis** Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Villa Mills, El Sitio, confluence of Quebradas Siberia and Voltea, 2550 m asl, 9 Dec 1988 (fl), Widmer 508 (holotype, CR; isotypes, CATIE/SBN, ISC, ZT). Figure 1F-H.

Culmi 1.5-3 cm diam., 2-6 m alti. Folia culmorum 19.7-24.3 cm longa; vaginae 17-20 cm longae, 4.4-6.6 plo longior quam laminae, abaxiales pilosae ad basim, glabrae ad apicem; laminae 2.6-4.5 cm longae, erectae, abaxiales sparsim pilosae. Ramificatio infravaginalis. Laminae foliorum (9-)12-21.6 mm longae, 0.3=0.6 cm latae, L: W = (26 )30-48(-54), abaxiales glabrae, non tessellatae. Paniculae (7-)11-18 cm longae, angustae rami laxe adpressi. Spiculae 9.8-11.8 mm longae, scaberulae. Glumae 2, squamiformes. Lemmata sterilia 2; lemma sterile 17.5-9.2 mm longum, subulatum; lemma sterile II 9.3-11.8 mm longum, subulatum-aristatum. Lemma fertile 10-11.7 mm longum, aristatum. Palea 7.4-9 mm longa, sulcata tantum ad apicem.
Fig. 1. Chusquea tomentosa and C. subtilis. A-E. C. tomentosa.—A. Bud complement.—B. Panicle with subtending foliage leaves.—D. Culm leaf, abaxial view.—E. Apex of foliage leaf sheath, showing inner and outer ligules, fimbriae, and pseudopetiole. (A, D based on Clark & Clark 274; B, E based on Widmer 502; C based on Clark et al. 500.) F-H. C. subtilis.—F. Panicle with subtending foliage leaf.—G. Spikelet.—H. Apex of foliage leaf sheath, showing inner and outer ligules, fimbriae, and pseudopetiole. (F-H based on Widmer 508.) A, B, D, F: bar equal to 1 cm; C, E, G, H: bar equal to 1 mm.
Culms to 1.5-3 cm diam., 2-6 m tall, erect at the base, arching above. Internodes to 35 cm long, terete, shallowly sulcate above the central bud, usually scabrid to smooth. Culm leaves 19.7-24.3 cm long, the juncture of the sheath and blade abaxially a ± horizontal and distinct line; sheaths 17-20 cm long, 4.4-6.6 times as long as the blades, abaxially pilose toward the base, glabrous toward the apex; blades 2.6-4.5 cm long, triangular, erect, persistent, adaxially antrorsely pubescent between the nerves, abaxially sparsely pilose, the apex subulate, the base narrower than the apex of the sheath; girdle 0.5-1 cm wide, densely pilose; inner ligule 1-2 mm long, ciliolate. Nodes with one triangular central bud; sheath scar dipping away markedly below the bud/branch complement. Branching infravaginal; central bud developing tardily at the middle and upper nodes; leafy subsidiary branches to 34 cm long, occasionally rebranching basally, 70-80(-100) branches in the mature complement. Foliage leaves 3-5 per complement; sheaths glabrous, the overlapping margin ciliate, the apex with a tuft of fimbriae on either side of the summit, the fimbriae numerous per tuft, 1-1.5 mm long, usually curly; blades (9-)12-21.6 cm long, 0.3-0.6 cm wide, L: W = (26-)30-48(-54), adaxially usually glabrous, sometimes with scattered hairs near the midrib, abaxially glabrous, sometimes with scattered hairs, not tessellate, the apex short setose, the base attenuate; pseudopetiole 1-2 mm long, not distinct; outer ligule a minute, glabrous rim 0.1-0.3 mm long; inner ligule to 1 mm long, rounded to irregular, abaxially basally pubescent. Panicles (7-)11-18 cm long, narrow, fully exserted from the subtending sheath; rachis triquetrous, glabrous, the edges glabrous to scabrid; branches loosely appressed, angular, glabrous, the lower ones 2-4.5 cm long; pedicels 1-7 mm long, angular, glabrous. Spikelets 9.8-11.8 mm long, scabrid. Glumes 2, scalelike, nerves lacking; glume I ca. 1/20 the spikelet length, 0.5-0.8 mm long; glume II ca. 1/15 the spikelet length, 0.6-1 mm long. Sterile lemmas 2, abaxially scabrid-pubescent, (5-7)-nerved; sterile lemma I 2/3-3/4 the spikelet length, 7.5-9.2 mm long, subulate; sterile lemma II equalling or nearly equalling the spikelet length, 9.3-11.8 mm long, subulate-aristate. Fertile lemma 10-11.7 mm long, aristate, abaxially scabrid-pubescent, 7-nerved. Palea 7.4-9 mm long, sulcate only toward the apex, apiculate, scabrid, 4- or 6-nerved. Stamens 3; anthers 4.2-5.2 mm long. Fruit a caryopsis, 4.7-6 mm long, flattened, grooved along the hilum, the hilum dark reddish brown, the style base persistent.

The specific epithet of *C. subtilis* refers to the fine leaves and delicate aspect of the panicles. This species is characterized by the narrow foliage leaf blades and scabrid-pubescent spikelets 9.8-11.8 mm long with the fertile lemma aristate (Table 1). *Chusquea subtilis* occurs in the Cordillera de Talamanca in montane forests along streams or at humid sites at elevations of 2550 to 3000 m asl.

**Key to the species of Chusquea Sect. Swallenochloa in Costa Rica (based on vegetative specimens).**

1a. Foliage leaf blades 0.4-0.6 cm wide.................................*C. paludicola*
1b. Foliage leaf blades 0.7-2.4 cm wide.

2a. Inner ligule of foliage leaves 1-7 cm long, tapering.

3a. Culm leaf sheaths (1.5-)4.5-7 times as long as the blades, the blades adaxially glabrous; foliage leaf blades usually yellowish green.................................................*C. amistadensis*
3b. Culm leaf sheaths 5-13 times as long as the blades, the blades adaxially pubescent; foliage leaf blades green........*C. longiligulata*

2b. Inner ligule of foliage leaves 0.5-4(-15) mm long, truncate to tapering.

4a. Foliage leaf blades 3-14.5 cm long, culm leaf blades 0.35-1.5 cm long, the sheaths (7-)12-27 times as long as the blades.........................................................*C. subtessellata*
4b. Foliage leaf blades (5.5-)10-29 cm long; culm leaf blades 1-6.5 cm long, the sheaths (1.5-)2-11 times as long as the blades.

5a. Foliage leaf blades with L:W = 7-12(-17), the base rounded to rounded-truncate.........................*C. vulcanalis*
5b. Foliage leaf blades with L: W = (7-)10-20(-24), the base rounded to attenuate.
6a. Inner ligules of foliage leaves 1-2.5 mm long, truncate to rounded; foliage leaf sheaths often farinose, especially when young; culm leaf blades adaxially scabrid.  
6b. Inner ligules of foliage leaves (2-)3-15 mm long, usually tapering; foliage leaf sheaths not farinose; culm leaf blades adaxially pubescent.  

Key to the species of Chusquea Sect. Swallenochloa in Costa Rica (based on vegetative and flowering specimens)

1a. Foliage leaf blades 0.4-0.6 cm wide.  
1b. Foliage leaf blades 0.7-2.4 cm wide.  
2a. Panicles open, pyramidal with stiffly spreading branches.  
2b. Panicles ± congested, often spicate, narrow, with appressed or ascending branches.  
3a. Spikelets glabrous, often slightly falcate; inner ligules of foliage leaves 1-7 cm long, tapering.  
4a. Foliage leaf blades 14-33 cm long, 0.7-2.3 cm wide, L: W = 9-25, green; culm leaf sheaths 5-13 times as long as the blades, the blades adaxially pubescent.  
4b. Foliage leaf blades 6-20.5 cm long, 0.7-1.4(-1.8) cm wide, L: W = 7-14.5(-16), usually yellowish green; culm leaf sheaths (1.5-)4.5-7 times as long as the blades, the blades adaxially glabrous.  
3b. Spikelets with some degree of pubescence, linear; inner ligules of foliage leaves 0.5-4(-7.5) mm long, rounded to truncate.  
5a. Panicles narrow, spicate, the branches appressed; foliage leaf blades 3-14.5 cm long, 0.7-1.3 cm wide; culm leaf blades 0.35-1.5 cm long, the sheaths (7-)12-27 times as long as the blades.  
5b. Panicles somewhat narrow but not spicate, the branches loose and ascending but not tightly appressed; foliage leaf blades (5.5-)10-29 cm long, 1-2.4 cm wide; culm leaf blades 1.5-6.5 cm long, the sheaths (1.5-)2-11 times as long as the blades.  
6a. Foliage leaf blades with L: W = 7-12(-17), the base rounded to rounded-truncate, the sheaths not
farinose; spikelets completely pubescent.............................. *C. vulcanalis*

6b. Foliage leaf blades with L: W = (8-)10-20(-24), the base rounded to attenuate-rounded, the sheaths often farinose, especially when young; spikelets scabrid-pubescent except toward the bases of the bracts ..................................... *C. talamancensis*

**Chusquea talamancensis** Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Cordillera de Talamanca, on the path to Cerros Cuercí 3030 m asl, 30 May 1989 (fl), Clark, Widmer & Stein 502 (holotype, CR; isotypes, ISC, MO, NY, US). Figure 2A-F.

Culmi 0.7-3.8 cm diam., 3-6(-9) m alti. Folia culmorum 15-24 cm longa, farinosae initio; vaginae 10.6-18 cm longae, (1.5-)2-11 plio longior quam laminae, abaxiales glabrae; laminae 1.5-6.5 cm longae, erectae, adaxiales scaberulae, abaxiales glabrae. Ramificatio intravaginalis. Vaginae foliorum plurunque farinosae initio; laminae foliorum 13-29 cm longae, 1-1.8 cm latae. L: W = (8-)10-20(-24), glabrae, abaxiales tessellatae. Paniculae 11-29 cm longae, angustae; rami laxe adpressi. Spiculae 5.6-7.5 mm longae, pubescentes. Glumae 2, squamiformes. Lemmata sterrilia 2, subulata; lemma sterile I 4.2-5 mm longum; lemma sterile II 5.3-6.3 mm longum. Lemmata fertilia 6-7.1 mm longum, apiculata. Palea 5.6-6.2 mm longa, sulcata ad acicem.

**Culms** 0.7-3.8 cm basal diam., 3-6(-9) m tall, erect at the base, arching above. **Internodes** (17-19)27-37(-43) cm long, ± terete, smooth, waxy to farinose. **Culm leaves** 15-24 cm long, the juncture of the sheath and blade an irregular, slightly sloping line, abaxially indistinct, farinose when young; sheaths 10.6-18 cm long, (1.5-)2-11 times as long as the blades, abaxially glabrous; blades 1.5-6.5 cm long, erect, persistent, apiculate, adaxially scabrid, abaxially glabrous; girdle 1-6 mm wide, glabrous; corky ridge present at the juncture of the sheath and girdle; inner ligule 1-2 mm long, stiff, glabrous, irregular. **Nodes** with one triangular central bud subtended by 5-11 subsidiary buds; sheath scar dipping slightly below the branch complement. **Branching intravaginal; leafy subsidiary branches** 35-69 cm long, frequently rebranching basally; 7-30 branches in the mature complement. **Foliage leaves** 6-11 per complement; sheaths glabrous, often farinose especially when young; blades 13-29 cm long, 1-1.8(-2.4) cm wide, L:W = (8-)10-20(-24),
adaxially and abaxially glabrous, abaxially tessellate, the apex acuminate
to short setose, the base rounded to attenuate-rounded; pseudopetiole 2-4
mm long; outer ligule a stiff, glabrous rim 0.3-1 mm long; inner ligule 1-
2.5 mm long, truncate to rounded, glabrous, chartaceous. Panicles 11-29
cm long, narrow but not spicate, often the base not exerted from the
subtending sheath; rachis somewhat complanate, glabrous to scabrid, the
edges scabrid; branches loosely appressed, ascending, angular, scabrous,
the lower ones 3-9 cm long; pedicels 1.5-4 mm long, angular, scabrid.
Spikelets 5.6-7.5 mm long. Glumes 2, scalelike, abaxially scabrid to
pubescent; glume I ca. 1/10 the spikelet length, 0.6-1 mm long, nerves
absent or 1-nerved; glume II ca. 1/5 the spikelet length, 0.9-1.6 mm long,
1-nerved. Sterile lemmas 2, subulate, abaxially pubescent on the upper
1/2-2/3 otherwise glabrous; sterile lemma I ca. 2/3 the spikelet length,
4.2-5 mm long, 3- or 5-nerved; sterile lemma II ca. 9/10 the spikelet
length, 5.3-6.3 mm long, 5-nerved. Fertile lemma 6-7.1 mm long,
apiculate, abaxially pubescent on the upper 1/2-1/3, otherwise glabrous,
7- or 9-nerved. Palea 5.6-6.2 mm long, sulcate toward the apex, the
sulcus pubescent, 4-nerved. Stamens not seen. Fruit a caryopsis.

Table 2. A morphological comparison of Chusquea vulcanalis, C. talamancensis, and
C. tonduzii.

<table>
<thead>
<tr>
<th>Character</th>
<th>C. vulcanalis</th>
<th>C. talamancensis</th>
<th>C. tonduzii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Culm leaf sheath, abaxial</td>
<td>glabrous</td>
<td>glabrous</td>
<td>only basal 1/2 pubescent to completely glabrous</td>
</tr>
<tr>
<td>Culm leaf blade, adaxial</td>
<td>glabrous to scabrid</td>
<td>scabrid</td>
<td>densely pubescent</td>
</tr>
<tr>
<td>Foliage leaf blade color</td>
<td>yellowish green</td>
<td>green</td>
<td>green</td>
</tr>
<tr>
<td>Foliage leaf blade width</td>
<td>(0.7-)1.1-2.4 cm</td>
<td>1-1.8(-2.4) cm</td>
<td>(0.7-)1-1.5 cm</td>
</tr>
<tr>
<td>Foliage leaf length : width</td>
<td>7-12(-17)</td>
<td>(8-)10-20(-24)</td>
<td>(7-)10-19.5</td>
</tr>
<tr>
<td>Foliage leaf inner ligule</td>
<td>1-4(-7.5) mm</td>
<td>1-2.5 mm</td>
<td>(2-)3-15 mm</td>
</tr>
<tr>
<td>length</td>
<td>not farinose</td>
<td>often farinose when young</td>
<td>not farinose</td>
</tr>
<tr>
<td>Foliage leaf sheath</td>
<td>narrow</td>
<td>narrow</td>
<td>pyramidal</td>
</tr>
<tr>
<td>Panicle shape</td>
<td>narrow</td>
<td>narrow</td>
<td>pyramidal</td>
</tr>
<tr>
<td>Spikelet length</td>
<td>5.7-8.5 mm</td>
<td>5.6-7.5 mm</td>
<td>(5.4-)6-7.6 mm</td>
</tr>
<tr>
<td>Spikelet pubescence</td>
<td>completely pubescent</td>
<td>scabrous/pubescent except toward bases of bracts</td>
<td>glabrous except bracts abaxially apically pubescent</td>
</tr>
<tr>
<td>Sterile lemma I/spikelet</td>
<td>3/4-7/8</td>
<td>2/3</td>
<td>1/2</td>
</tr>
<tr>
<td>Sterile lemma II/spikelet</td>
<td>(9/10-)1</td>
<td>9/10</td>
<td>2/3</td>
</tr>
</tbody>
</table>
Fig. 2. Chusquea talamancensis and C. tonduzii. A-F. C. talamancensis.—A. Culm leaf, abaxial view.—B. Branch complement and foliage leaves.—C. Bud/branch complement. D.—Panicle.—E. Spikelet.—F. Caryopsis. (A-C based on Clark & Clark 273; D based on Pohl 15676; E based on Clark et al. 502; F based on Widmer s.n.)—G. C. tonduzii, culm leaf, abaxial view (based on Clark et al. 497). A-D, G: bar equal to 1 cm; E-F: bar equal to 1 mm.
ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. CARTAGO: along the Carretera Interamericana just below paramo, Clark & Clark 273 (ISC, MO, US); Villa Mills, road to Piedra Alta, Clark et al. 501 (CR, ISC, MO, NY, US); along Interamerican Highway near Cerro de la Muerte, Fisher R354 (US). CARTAGO/SAN JOSE: Cerro Jaboncillo, along access road to transmission line tower on summit, Cerro de la Muerte, Horn 129, 130 (ISC); power line 1 km W of Cerro Jaboncillo, Cerro de la Muerte, Horn 242 (ISC). LIMON: on the path to Cerro Chirripó, 2 Apr. 1989 (fl), Widmer 517 (ISC). PUNTARENAS: Cordillera de Talamanca, upper slopes of Cerro Echandi, Davidse et al. 23885, 23961 (ISC, MO). SAN JOSE: La Georgina, roadside W of Carretera Interamericana, E of restaurant, forest margin, 28 Jan. 1989 (fl), Pohl 15676 (ISC, MO); La Georgina, Pohl & Clark 13924 (ISC, MO); La Georgina opposite the restaurant, Pohl & Clark 14627 (ISC).

*Chusquea talamancensis* is characterized by the often farinose foliage leaf sheaths, green foliage leaf blades with the inner ligules 1-2.5 mm long, and pubescent spikelets with sterile lemma II 9/10 the spikelet length. As indicated by the specific epithet, this species is found in the Cordillera de Talamanca, in upper montane forests at elevations of 2600 to 3200 m asl, usually on northern or northwestern exposures.

Vegetative specimens of *C. talamancensis* were previously assigned to *C. tonduzii* Hackel (Clark, 1989), even though the inner ligules were much shorter than is typical for *C. tonduzii*. The panicle and spikelets of *C. talamancensis* are very similar to those of *C. vulcanalis* from which it is vegetatively distinct. The three species are compared in Table 2. The description of the culm leaves of *C. tonduzii* in Clark (1989) is based on specimens of *C. talamancensis*. A complete recent vegetative collection of *C. tonduzii* (Clark et al. 497) showed that its culm leaves are very similar to those of *C. paludicola* L. G. Clark (Fig. 2G), but the blades of *C. tonduzii* are adaxially pubescent as in *C. longiligulata* (Soderstrom & Calderon) L. G. Clark.

References


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CHAPTER 2

Description of vegetation and soils of the oak forests in the northwestern Cordillera de Talamanca, Costa Rica

Yvonne Widmer

Abstract

A description is presented of the vegetation and soils of the Quercus-Chusquea forests of the Cordillera de Talamanca between 2800 and 3100 m asl in Cerros Cuericí and Cerro Abarca in Costa Rica. The plots studied were selected to include one of the Chusquea species present in the area (C. talamancensis, C. tomentosa or C. foliosa) and to represent different degrees of canopy closure (closed canopy, intermediate canopy and gap). Based on a PCOA of the floristic data eight plant communities were recognized which seem to be associated with differences in topography, soil characteristics and canopy closure. The Chusquea species appear to be indicators for particular topographic situations and soil types, and are associated with certain plant species. Regarding canopy closure, the intermediate canopy plots had the greatest species richness of vascular plants and also of woody and herb species separately. Trees species richness in the various layers of the vertical profile (upper, middle tree layer, shrub layer, herb layer) are also more abundant under intermediate canopy, followed by closed canopy and gap. The data on size distribution of trees show the inhibitory effect upon tree growth of the dominance of bamboo in gaps ('bamboo gaps').

Keywords: Quercus, Chusquea, phytosociology, canopy structure, species richness, bamboo gaps.

Introduction

The montane oak forests of the Cordillera de Talamanca are dominated by Quercus trees in the overstory and Chusquea bamboos in the
understory (Figure 1 & 2). These old-growth forests are found above 2000 up to 3200 m asl, and are also called cloud forests because of the diurnal fog precipitation.

These forests were practically unknown until the Inter-American Highway (CIA) pushed into the area in 1942 (Dayton, 1945). Soon after, the uniqueness of the world's largest oak forest was recognized by botanists, and *Quercus copeyensis* C.H. Müller was described as a new species (Dayton, 1944). The unusual feature of the vegetation is the almost complete dominance in the canopy layer of *Quercus* (Klötzli, pers. com.). For example, Weber (1959) did not find such pure formations of *Quercus* as occur in Costa Rica in any Colombian montane forests. It is to the credit of the Costa Rican government and MAB that, recognizing the fragility of these tropical montane ecosystems, most of the forests are protected within the 612,570 ha Amistad Biosphere Reserve (Kappelle, 1995).

Recently, there has been growing awareness of the approaching depletion of lowland forests and the consequent increased pressure on the Forest Reserves of high-elevation forests. Scientific effort has been concentrated upon developing a plan for sustainable natural forest management of the oak forests (Jiménez et al., 1988; Beek & Sáenz, 1992). Ecological studies have provided basic information about the function of these forests (Blaser & Camacho, 1991; Orozco, 1991; Berner, 1992; Stadtmüller, 1994; Kappelle, 1995). This PhD thesis is also a contribution to our understanding of these forests.

The main oak species in the study area is *Quercus costaricensis* Liebmann, but some sites are also dominated by *Q. copeyensis*. The bamboo species present are *Chusquea talamancensis* Widmer & Clark, *C. tomentosa* Widmer & Clark and *C. foliosa* Clark (Figure 3), which form monospecific stands contiguous to each other (see Chapter 4). In the pilot area of the CATIE project in Villa Mills, Blaser (1987) described the black-oak forest (black-oak: *Q. costaricensis*) as being associated with *C. longifolia* (correctly: *C. talamancensis*), and the white-oak forest (white oak: *Q. copeyensis*) as associated with *C. meyeriana* (correctly: *C. tomentosa*).
Fig. 1. Cordillera de Talamanca. A. View from the Cerro de la Muerte to the North. In the background can be seen the Irazú volcano on the left, and the Turrialba volcano on the right hand side. B. View from the track to Cerros Cuericí to the Southeast with Chusquea tomentosa in the foreground and the ridge of Cerro Chirripó behind. C. View of a disturbed forest on Cerro Asunción from the CIA with Chusquea talamancensis in an advanced flowering stage (dead plants).
Fig. 2. **The oak forest.** **A.** *Quercus copeyensis* forest on a misty day. **B.** Seeds and seedlings of *Quercus costaricensis* in a mast year. **C.** Forest understory with Chusquea foliosa clumps.
Fig. 3. Chusquea. A. View of a secondary forest with C. tomentosa in the understory. B. Treefall gap in the primary forest with C. foliosa (fallen trunk in the centre front). C. Secondary vegetation on the roadside of the CIA predominantly formed by C. tomentosa.
In the Andes of south-central Chile there are physiognomically similar forests which are dominated by *Nothofagus*, and which also have *Chusquea* in the undergrowth (Veblen, 1982). From preliminary field observations in 1987, I recognized what Veblen (1989) had observed in the Chilean forests, namely that beneath areas of continuous tree canopy bamboos are sparse, but in treefall gaps they form dense thickets. I decided therefore to compare sites under the two extreme conditions of closed canopy and gap. In the field work I soon recognized two intermediate situations which I referred to as intermediate canopy and intermediate gap. However, because of the small number of samples the data from these plots were unified for subsequent analysis. For my detailed studies, I searched for sites in the forest with each of the three bamboo species (*C. talamancensis*, *C. tomentosa* and *C. foliosa*) and each of the three types of canopy closure (closed canopy, intermediate canopy and gap). Liebermann & Liebermann (1989) discuss the gap paradigm and suggest that attention should be directed to individual trees as objects of interest. The principal aim of this thesis was to study *Chusquea* ecology under different conditions of canopy closure.

In this Chapter the vegetation and soils are described as a foundation for the main part of the thesis. Phytosociological methods were used to assess the vegetation in synecological terms, and to determine whether there are floristic differences between sites. The soils were described as a useful complement to the vegetation classification. Stand structure was recorded in more detail to understand the effect of canopy closure on the structure and species richness of the vegetation.

**Study area**

**CHARACTERISTICS.**—The Cordillera de Talamanca runs from northwest to southeast and divides Costa Rica into an Atlantic and a Pacific watershed. The Atlantic slope is much wetter than the Pacific one due to the heavy rainfall brought by the northeastern trade winds (Kappelle, 1992). The study area lies in the northwestern part of the Cordillera de Talamanca, on the Atlantic side. It covers an area of 5 km² and comprises part of the Cerro Abarca and Cerros Cuericí, both in the
Province of Cartago (Figure 4). The altitude ranges from 2800 to 3100 m asl; the lower limit of the study area was determined by the increasing human influence at lower altitudes, while the upper boundary was determined by a transition to the forest limit on Cerro Cuericí (3200 m asl). The territory in the study area on Cerro Cuericí belongs partly to the Río Macho Forest Reserve, which is part of the Amistad Biosphere Reserve (Kappelle, 1995), and partly to private owners; the study area at Cerro Abarca is privately owned.

GEOLOGY AND GEOMORPHOLOGY.—The Cordillera de Talamanca is primarily built up of Tertiary marine sediments with intercalated volcanic and plutonic rocks. Orogenesis occurred in the Tertiary (Miocene) and was especially strong during the Pliocene. During this phase intense andesitic-basaltic vulcanism and the intrusion of plutonic rocks occurred (Weyl, 1980). Stocks of granitoid intrusive rocks have been described along the length of the crest of the Cordillera de Talamanca (Talamancan Comagmatic Series). The Río Macho intrusion is composed of granodiorite which grades to diorite at the margins and covers an area of 50 km². There was further volcanic activity during the Quaternary in the adjacent Cordillera Volcánica Central, which left ash deposits on the Cordillera de Talamanca (Castillo Muñoz, 1993). According to Castillo Muñoz (1993) the stratigraphy of the study area is composed mainly of intrusive and volcanic rocks with minor intercalations of sedimentary rock. Glaciation features have been identified in the Chirripó and Kamuk massifs (Bergoeing, 1977). There is no information on whether there was glaciation in the study area itself, though it is not very likely since the lowest glacial tongues at Cerro Chirripó are not thought to have reached down to below 3300 m asl (Barquero & Ellenberg, 1986); thus the glacially formed area probably covers the alpine level above the tree limit. The morphology of the Cordillera de Talamanca is generally characterized by a flattish Pliocene crest with steeply incised valleys, surrounded by intermediate and steep slopes (Weyl, 1980).

SOILS.—This paper follows the soil classification system according to Soil Survey Staff (1994). The U.S. system is commonly used by soil scientists in Costa Rica. Since it is continuously under revision, the nomenclature changes with time; this is especially the case for the new
Fig. 4. Map of Costa Rica with a detail of the study area.
order Andisols (mainly soils developed on volcanic ash), which was formerly treated as the suborder Andepts in the order Inceptisols (Shoji et al., 1993).

Vázquez (1983) recognised two soil types in the Cordillera de Talamanca. The first is soils developed from volcanic ash deposits on areas of mountainous relief with slopes of 30-80%. These soils are dark and deep, rich in organic matter, medium-textured, moderately fertile and excessively drained (Andepts). The second type is residual soils on steeply dissected or mountainous terrain, with slopes of 40-80% or greater. These range from deep to very shallow, with excessive external drainage, and are reddish, heavy-textured, and of very low fertility (e.g. Tropepts).

Otárola & Alvarado (1976) described profiles made on a 40 km transect on the Cerro de la Muerte (3400 m asl). They recognised Tropofolist at the higher elevations, Tropohumods and Placohumods at intermediate elevations, and Dystrandepts at about 2000 m. In a relatively flat area between the creeks of Siberia and Voltea (2600 - 2800 m asl) and near the village of Villa Mills, Blaser (1987) identified mainly Typic Dystrandept and Typic Placandept. On slopes he found Andic Humitropept, and Andaquipt by the Voltea creek. In a recent study on two transects along the Chirripó massif, Kappelle et al. (1995) described soils belonging to the subgroups Placic Humitropept, Typic Placudand and Typic, Alic and Acri Hapludand. Based on these studies, it can be assumed that the soils in the study area belong either to the order Andisol (Hapludand, Placudand) or Inceptisol (Humitropept).

CLIMATE.—It is characterized by two seasons: a rainy season, from May to November, and a dry season from December to April. Figure 5 shows the rainfall pattern during the study period (1987 - 1990) as recorded at the Villa Mills weather station. In the rainy season, monthly rainfall ranged from 153 (9/90) to 764 (9/88) mm. In the middle of this period (i.e. July or August) there is a period of reduced rainfall (Coen 1983). In the dry season monthly rainfall ranged from 7.5 (2/87) to 81.9 (4/88) mm. Total radiation is correspondingly higher in the dry season than in the rainy season (Figure 6). Daily temperature oscillations are larger than the range of mean monthly temperatures. For example, from 1987 to 1989, the daily temperature range was 9.4 - 10.3 °C in the dry season and 7.5 - 8.5 °C in the rainy season. Temperatures below 0 °C
occur in the dry season when skies are clear. Temperature conditions change with altitude by 0.52 - 0.57 °C per 100 m (Herrera, 1985; Blaser, 1987). In the dry season, from December to February, dry and cool 'northers', i.e. strong polar winds with northeast direction, affect the climate of the study area (Herrera, 1985). Characteristically, cloudless radiation weather predominates, with the formation of cold air seas at night and an outflow of cold air into the depressions of the slopes. These invasions of cold air are the cause of high interdiurnal variability of temperature (Lauer, 1973).

![Rainfall pattern during the study period (1987-1990) at the Villa Mills weather station (N° 073033, 3000 m asl). Source: Instituto Costaricense de Electricidad, Departamento de Hidrología (unpublished data).](image-url)
VEGETATION.—The pristine old-growth forests studied here are part of the Upper Montane Forest (sensu Kappelle et al., 1991). According to Klötzli (1988) these forests are evergreen broad-leaved forests. The dominant species, *Quercus costaricensis* and *Q. copeyensis*, form the canopy and are 25 to 40 m tall (in flat areas up to 50 m tall; Blaser, 1987). The oak forests are bordered at their lower limits (1800 - 2000 m asl) by Lauraceae-rich mixed forests, and at their upper limits (3200 - 3400 m asl) by transitional, subalpine, ericaceous-asteraceous dwarf forests and by bamboo-páramos (Kappelle, 1995). The understory of the *Quercus* forests is characterized by bamboos of the genus *Chusquea*. Three *Chusquea* species are present in the study area: *C. talamancensis* and *C. tomentosa* are the more abundant species, while *C. foliosa* is confined to humid patches within areas dominated by one of the other species. Forest dynamics in these old-growth forests is strongly affected by tree- and branch-fall, leading to a mosaic of areas with a closed
canopy, areas with a more open canopy with apertures, and forest gaps at various stages of regeneration. Large old gaps (>500 m², >10 years old) in the primary forest typically have a two layered vertical structure consisting of a bamboo layer and a herb layer.

In the study period from 1987 to 1990, the populations of first *C. talamancensis* and then *C. tomentosa* gradually started mass flowering, with subsequent death of the plants (Figure 1). This was a major event which affected most of the study area (see Chapter 5 and 6). *C. foliosa* did not flower in the study area but did in other parts of the Cordillera de Talamanca.

**Materials and methods**

**SELECTION AND SIZE OF PLOTS.**—The plots for description of vegetation and soil were selected to include stands containing one of the three *Chusquea* species, and to represent different degrees of canopy closure. Since the bamboo populations of *C. talamancensis*, *C. tomentosa* and *C. foliosa* built monospecific stands, the plots could be defined according to the species. The canopy closure was classified into three categories: (1) 'Gap', was a plot in a large gap of over 500 m² area with an overstory tree cover of less than 10%; 'closed canopy' (ccan) referred to sites with an old-growth oak canopy cover of more than 60%; 'intermediate canopy' sites (ican) were transitional plots, where either the overstory was represented by a few scattered mature trees (> 50 cm dbh) with a cover of 10 - 50% of the overstory canopy, or were occupied by medium sized trees (20 < dbh < 50 cm). The plots differed in altitude, aspect and slope angle (Appendix, Table 1), but were predominantly on west-, south-, and east-facing slopes with 0 - 45° inclination. Flat (fl) slopes were defined from 0 - 10°, intermediate (in) slopes from 10 - 25°, and steep (st) slopes from 25 - 40°.

In total there were 7 gap, 8 intermediate canopy and 9 closed canopy plots with *C. talamancensis*, and 4, 3 and 10 respectively with *C. tomentosa*. For *Chusquea foliosa* there were 7 gap and 6 intermediate canopy plots; this species was not found under closed canopy in the study area. Figure 7 shows detailed maps of the foot-tracks with the locations of
Quercus costaricensis primary forest

LEGEND

- Bamboo species:
  - Quercus copeyensis
  - Quercus hemistachya
  - Quercus foliosa

- Canopy closure types:
  - gap
  - intermediate canopy
  - closed canopy

- Other symbols:
  - weather station (1-5)
  - altitude (m.a.s.l.)
  - track
  - approximate borders of land utilization types

Fig. 7. A. Track to the Cerros Cuerci with the study plots. B. Track to the Cerro Abarca with the study plots.
the study plots on Cerros Cuerici and Cerro Abarca. These maps were made, with the aid of a measuring tape and clinometer, in order to locate the plots. The hand drawings were scanned, generalized (simplification of the angles) and worked on with the help of geographers using the Photoshop® and Canvas® programs at the Geographical Institute of Zurich University.

The appropriate size for the vegetation plots was determined by the 'minimum area' method as described by Kreeb (1983). Curves of number of species against plot area were made for five different sites in the forest between Villa Mills and Cuerici. Above an area of 500 m² the curves from the five sites flattened and number of species did not increase markedly with increasing area (Figure 8).

![Figure 8. Minimum area curves in five different primary forest sites: 1 + 3: Villa Mills, Chusquea talamancensis; 2 + 4: Villa Mills, C. tomentosa; 4. Cuerici, C. talamancensis.](image)

**Fig. 8.** Minimum area curves in five different primary forest sites: 1 + 3: Villa Mills, Chusquea talamancensis; 2 + 4: Villa Mills, C. tomentosa; 4. Cuerici, C. talamancensis.

SOIL DESCRIPTION.—On each of the plots, a pit was dug with a spade to a depth of 50-70 cm in order to characterize the upper soil horizons. Deeper samples, to a depth of 100-120 cm, were taken with a 7 cm diameter Edelman auger (Eijkelkamp, The Netherlands), except where there was rock. The physical description of the soils followed Richard et al. (1978) and soil colour was determined with the Revised Standard Soil Color Charts (Oyama & Takehara, 1970). Soil pH was measured in the
field with the Hellige pH indicator, and the presence of carbonate was
tested with concentrated HCl. The soils of some plots were classified
qualitatively in the field with the help of Dr. D. Kass and Dr. M. J.
Mazzarino (soil scientists from CATIE). Further classification was made
following the Keys to Soil Taxonomy (Soil Survey Staff 1994) and the

VEGETATION DESCRIPTION AND ANALYSIS.—Fifty-four relevés
were made in plots of 500 m² (20 x 25 m²), following the
phytosociological methods of the Zürich-Montpellier school. All
terrestrial, vascular plant species were determined and their growth form
was also recorded (tree, shrub, herb, fern, climber). The cover (%) for
each species was estimated as the relative projection of the aerial crown
or shoot cover over the sampled area (i.e. 500 m²). Cover was
determined separately for the upper tree layer (UTL), middle tree layer
(MTL), shrub layer (SL, excluding bamboo), herb layer (HL) and
bamboo layer (BL). Since the flora was mainly unknown to me, the
species were recorded using the vernacular names known by the field
assistants, or, if they were unknown, naming the plants after an external
characteristic (e.g. smell, stings, shape). Each plant species was collected
as an herbarium specimen and they were subsequently identified with the
help of Maarten Kappelle (Amsterdam University) and using the plant
collection of the CATIE-project in Costa Rica. Further identification was
done by specialists from the Herbario Nacional de Costa Rica, Missouri
Botanical Garden, The New York Botanical Garden, California Academy
of Science, United States National Herbarium, Royal Botanic Gardens in
Kew and Zürich University.

Data analysis was performed with the MULVA-5 program package,
a flexible multiple-technique numerical method for vegetation analysis
(Wildi, 1994). In order to simplify the analysis, the cover data were
transformed to presence-absence data. An ordination of the relevés was
made using a resemblance matrix (resemblance function: van der Maarels
coefficient), cluster analysis (algorithm: minimal variance clustering) and
a principal coordinate analysis (PCOA). Data for Chusquea species were
excluded, since these had been a criterion for plot selection. The relevés
were then grouped according to their similarity. A raw vegetation table
was produced using the relevé groupings determined by the ordination.
The final vegetation table was produced by rearranging the species with similar occurrences to form more accurate species groups. The characteristic species of a group were defined as those present in at least 80% of the relevés.

ASSESSMENT OF TREE SPECIES.—The 500 m² (20 x 25 m²) plots were also used to study other vegetation characteristics (Figure 9). The number of large (dbh>50 cm), mature (20<dbh<50 cm) and pole trees (10<dbh<20 cm) were recorded in the entire plot. The saplings were divided into two classes (5<dbh<10 cm and dbh<5 cm up to 1.50 m height) and were counted in the 100 m² (10 x 10 m²) subplot.

Fig. 9. Plot arrangement for data collection. A. (500 m²): Vegetation relevé (estimation of cover (%) in upper and middle tree, shrub and herb layer). Number of large (dbh >50 cm), mature (20<dbh>50 cm) and pole (10<dbh<20 cm) trees. B. (100 m²) Number of saplings (5<dbh<10 cm and dbh<5 cm up to 1.50 m height). Bamboo data (number of clumps, number of culms, diameter of adult and young culms, spatial distribution, basal and 1 m girth, crown width and length). C. (20 m² (5x4 m²)): Number of tree seedlings (height < 1.50 m, height measurement).
The bamboo characteristics were measured in the same subplot (these are discussed in Chapter 4). Finally, the tree seedlings (height < 1.50 m) were counted in the five 4 m² (2 x 2 m²) subplots. Descriptive statistics were performed with the Statview 4.0 (1992) program.

**Results**

SOIL PROFILE DESCRIPTION.—Two main soil types could be differentiated, one associated with a mor humus and the other with mull. As montane forest soils, the biological characteristics depend mainly on the low temperature (isomesic) and the udic soil moisture regime. In both soils the rooting depth was between 30 - 130 cm. Characteristically, the organic topsoil (0 - 10 cm) contained a dense root mat, and the rhizomes of *Chusquea* were found at 10 - 40 cm. Generalized soil profiles are given below for the two main soil types.

*Soil type I* (20 profiles, see Appendix, Table I): The main characteristics of this soil type are clearly defined horizons, a well developed mor type of humus (L-F-H), a highly organic A horizon (Aₐ), and a weakly developed but recognizable eluviated (E) horizon. The mineral soil exhibits clay displacement and accumulation in a Bₜ horizon; stones are generally weathered and FeO/MnO stains are often present. Rock was encountered at depths below 85 cm. Particle size analysis of twenty soil samples from 20-30 cm depth showed mean values of 37% sand, 33% silt and 30% clay (clay loam).

**Thickness/pH**

<table>
<thead>
<tr>
<th></th>
<th>Thickness</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>L</strong></td>
<td>1-3 cm</td>
<td>Litter loose, clearly separated from soil.</td>
</tr>
<tr>
<td><strong>F</strong></td>
<td>0-4 cm</td>
<td>Fermentation horizon usually developed under forest canopy but not in gaps, partially decomposed organic matter sometimes compacted into layers, mycelia present under forest canopy, distinctive smell.</td>
</tr>
<tr>
<td><strong>H</strong></td>
<td>1-23 cm/ 4.0-5.0</td>
<td>Reddish black (7.5R 2/1), very dark reddish brown (7.5R 2/2) or dark reddish gray (7.5R 3/1). Crumbly to pasty, abundant fine roots.</td>
</tr>
</tbody>
</table>
A 3-22 cm/ 4.0-5.0 Mainly very dark reddish brown (10R 2/2, 7.5 R 2/3) to dark reddish brown (7.5R 3/2). Mineral soil very well mixed with the organic matter, sometimes under hydromorphic conditions, then pasty, abundant fine roots.

E 3-20 cm/ 4.0-5.5 Dark reddish brown (2.5YR 3/3, 10R 3/2) to dull reddish brown (5YR 4/4) or brownish gray (5YR 4/1). Mostly thin horizon with high fading clay content, sometimes with small weathered stones, rust traces, partially compacted.

B 30-101 cm/ 4.5-5.5 Dark reddish brown (5YR 3/4) and reddish brown (5YR 4/6, 7.5 YR 4/6), sometimes bright brown (7.5YR 5/6). This horizon can be divided into subhorizons representing zones of accumulation of organic matter (Bh), clay (Bt) and FeO (BFe). Sometimes there are abundant weathered particles and stones (Bv) or even concretions (Bcn).

Soil type I was characteristic of sites at Cerros Cuerici and Cerro Abarca where the understory bamboo C. talamancensis occurred. It was also found at some sites with C. foliosa and at sites with C. tomentosa under closed canopy at the Cerro Abarca. It is of volcanic origin with a pH in NaF at 20-30 cm from 7.2 - 11.5, and an umbric epipedon (base saturation <50%). However, its properties meet only partially the criteria for andic soils. According to the US soil classification system this soil type may be qualitatively classified as Andic Humitropept (order Inceptisols), and after the FAO soil classification as an Eutric Cambisol (Mizoka & Reeuwijk 1989). Klötzli (pers. com.) identified this soil type as 'Podsolige Braunerde'.

Soil Type II (27 profiles, see Appendix, Table I): This soil is mainly yellow-red and horizons are not always well differentiated. The humus type is similar to mull (L-(F)-H), with an organic mineral horizon (A_H). The sand content of the mineral soil is relatively higher than Soil Type I, and hence drainage is better. Particle size analysis of seventeen soil samples from 20-30 cm depth showed mean values of 51% sand, 30% silt and 18% clay (sandy loam). A Bt horizon is generally present as a
consequence of clay displacement and accumulation. Sometimes there are marbled patches due to solute transport under conditions of water saturation. Variable sized stones are frequent throughout the profile, but show signs of weathering only where the soil was not interrupted by bedrock. A bed of stones or rock at depths of 50 to 85 cm often impeded further excavation.

**Thickness/pH**

<table>
<thead>
<tr>
<th>Layer</th>
<th>Thickness/cm</th>
<th>pH</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>1-4 cm</td>
<td></td>
<td>Loose leaf litter.</td>
</tr>
<tr>
<td>F</td>
<td>0-2 cm</td>
<td></td>
<td>Weakly developed, often absent, mycelia sometimes visible, no strong smell.</td>
</tr>
<tr>
<td>H</td>
<td>2-15 cm/ 4.0-5.5</td>
<td>Reddish black (2.5YR 2/1), very dark reddish brown (2.5 YR 2/2, 7.5R2/2) to dark reddish brown (7.5R 3/3). Fine crumb structure. Dense mat of fine roots.</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>2-26 cm/ 4.0-5.0</td>
<td>Very dark reddish brown (10R 2/2, 2.5 YR 2/3), dark reddish brown (2.5YR 3/2), dark brown (7.5YR 3/4) and brown (7.5YR 4/4). Mineral soil of loamy sandy texture well mixed with organic matter. Structure of loose crumbs at sites with C. tomentosa, pasty texture at sites with C. foliosa (hydromorphic conditions). Thick roots are common in this layer.</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>13-107 cm/ 4.5-5.5</td>
<td>Very dark reddish brown (5YR 2/4, 10R 2/2), dark reddish brown (2.5YR 3/3, 5YR 3/2), dark brown (7.5YR 3/3), brown (7.5YR 4/4). Horizon with sandy loamy texture, generally crumbly; there is evidence of clay displacement and the most distinct subhorizon is Bt. Stones of various sizes are concentrated in this horizon, which often overlies a stone layer.</td>
<td></td>
</tr>
</tbody>
</table>

Soil Type II was mostly found at sites dominated by the understory bamboo *C. tomentosa* at the Cerros Cuericí and Cerro Abarca. However, it was also found in places with *C. talamancensis* when this species was growing at the margins of *C. tomentosa*, and with *C. foliosa* growing in patches amidst *C. tomentosa*. It may be classified as Typic Hapludand
(order Andisols). The pH in NaF of over 9.4 (at 20-30 cm depth) suggests the presence of volcanic ash and/or amorphous Al oxides (Mazzarino et al. 1985). According to the FAO soil classification this soil type is probably a Humic Andosol (Mizoka & Reeuwijk, 1989). Klötzli (pers. com.) identified Soil Type II as 'Parabraunerde'.

Not all the soil profiles could be attributed to one of the two soil types described above. Three profiles with *C. talamancensis* (536, 5115, 5117) could not be grouped under Soil Type I because of the lack of an eluviated E horizon; however, the other properties were characteristic of Humitropept, though the horizons were not clearly differentiated. In fact, 9 of the 18 gap plots exhibited soils with no clear horizon differentiation, regardless of *Chusquea* species. Most of the plots on flat and medium slopes (< 25°) in Cerro Abarca showed compaction at 20 to 40 cm depth, perhaps due to human influence (e.g. grazing of free ranging cattle).

One site with *C. talamancensis* (431) on the crest at 2990 m was found with a Spodosol-like soil, with clearly defined horizons. The humus layer was well developed (L-F-H:1-1-4 cm). The mineral soil had a dark reddish brown Ah horizon (5YR 3/3, pH 4, 9 cm), and a grayish red E horizon (2.5YR 5/2, pH 4-5, 9 cm). There was a sequence of B subhorizons (pH 4-5) including a thin (5 cm), very dark reddish-brown (10R 2/2) Bh, a dark reddish brown (5YR 3/4) BFe, a Bt and a bright reddish brown (5YR 5/8) B/C. According to Klötzli (pers. com.) this soil is a typical 'Humus-Eisen Podsol'.

**DESCRIPTION OF THE VEGETATION.**—The complete species list of the study area is found in the Appendix (Table II). The total number of species of terrestrial vascular plants in the 54 plots of the study area (it corresponds to 2.7 ha) are 203: 46 trees, 29 shrubs, 64 herbs and epiphytes on the soil, 52 ferns, 10 climbers and 3 bamboos. The layers in the vertical profile had the following heights: upper tree layer 25 - 50 m, middle tree layer 10 - 25 m, shrub and bamboo layer 3 - 10 m and herb layer 0.2 - 1.0 m.

As represented in the ordination diagram (Figure 10) there are eight fairly distinct relevé groups. Although the eigenvalues of the first two axes explain a relatively small proportion of the species variance (they are equivalent to 9.5% and 7.1% respectively, of the 'sum of all
eigenvalues'), the arrangement of the groups can be interpreted ecologically. The relevé groups represent particular parts of the study area (Figure 7): thus 1 and 2 are from Israel (by a side track east of the main track to Cerros Cueríci), 3 is from the Cerro Abarca, and 4 - 8 are from Cueríci. Although the ordination was made excluding *Chusquea*, it is noteworthy that the groups can also be defined by the dominant *Chusquea* species.

Fig. 10. The distribution of the relevé groups of *Chusquea talamancensis*, *C. tomentosa* and *C. foliosa* on the ordination of 54 plots. The gradient on axis 1 is probably humidity and on axis 2 an undetermined soil factor. 1. Israel I, 2. Israel II, 3. Abarca, 4. Cueríci I, 5. Cueríci II, 6. Cueríci III, 7. Cueríci IV, 8. Cueríci V.

*C. tomentosa* is present in groups 1, 5 and 3 (except for two relevés with *C. talamancensis*), while *C. talamancensis* is present in groups 2, 4, and 8 and *C. foliosa* in groups 6 and 7. The ordination spaces of *C. tomentosa* and *C. talamancensis* overlap, but each of them has also a large space of its own. *C. foliosa* differentiates most clearly from the other two species, but there is nevertheless a slight overlap with *C. talamancensis*. Field observations suggest that the first ordination axis represents humidity, while the second axis probably represents an undetermined soil factor. These ordination groups are now described in more detail based on the vegetation table (Appendix, Table III); summarized data are presented in Table 1 and Figure 11.
Table 1. Summary of the data from the vegetation table for the different forest types. UTL: upper tree layer, MTL: middle tree layer, SL: shrub layer, HL: herb layer, BL: bamboo layer.

<table>
<thead>
<tr>
<th>Group number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Name</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth organic soil (cm)</td>
<td>10 - 21</td>
<td>13 - 17</td>
<td>8 - 21</td>
<td>8 - 34</td>
<td>14 - 23</td>
<td>7 - 31</td>
<td>9 - 36</td>
<td>9 + 13</td>
</tr>
<tr>
<td>Root depth (cm)</td>
<td>75 - 100</td>
<td>80 - 115</td>
<td>80 - 120</td>
<td>36 - 130</td>
<td>70 - 120</td>
<td>30 - 120</td>
<td>50 - 75</td>
<td>60 + 85</td>
</tr>
<tr>
<td>pH (A horizon)</td>
<td>4.6 ± 0.8</td>
<td>4.1 ± 0.2</td>
<td>4.2 ± 0.4</td>
<td>4.4 ± 0.4</td>
<td>4.7 ± 0.6</td>
<td>4.2 ± 0.4</td>
<td>4.2 ± 0.4</td>
<td>4.2 ± 0.4</td>
</tr>
<tr>
<td>Cover UTL (%)</td>
<td>61 - 70</td>
<td>15 - 65</td>
<td>50 - 80</td>
<td>50 - 80</td>
<td>2 - 30</td>
<td>6 - 30</td>
<td>0 - 5</td>
<td>0 - 10</td>
</tr>
<tr>
<td>Cover MTL (%)</td>
<td>16 - 28</td>
<td>15 - 42</td>
<td>12 - 43</td>
<td>4 - 26</td>
<td>0.5 - 10</td>
<td>0 - 15</td>
<td>0 - 8</td>
<td>2 - 6</td>
</tr>
<tr>
<td>Cover SL (%)</td>
<td>0.5 - 8</td>
<td>5 - 10</td>
<td>3 - 10</td>
<td>1 - 20</td>
<td>0 - 10</td>
<td>0 - 10</td>
<td>0 - 5</td>
<td>0 - 2.5</td>
</tr>
<tr>
<td>Cover HL (%)</td>
<td>1 - 5</td>
<td>2 - 10</td>
<td>10 - 100</td>
<td>5 - 30</td>
<td>2 - 10</td>
<td>5 - 40</td>
<td>0.2 - 4</td>
<td>0.5 - 1.5</td>
</tr>
<tr>
<td>Cover BL (%)</td>
<td>30 - 50</td>
<td>15 - 90</td>
<td>10 - 25</td>
<td>50 - 70</td>
<td>70 - 97</td>
<td>40 - 100</td>
<td>85 - 100</td>
<td>80 - 95</td>
</tr>
</tbody>
</table>
1. *Israel I*. Four relevés with *C. tomentosa* under closed canopy belong to this group, which covers altitudes from 2900 - 2950 m asl. The forest has a rather dry appearance, mainly due to the SE aspect, and the slopes are steep. The depth of the organic soil is 10 - 21 cm, the roots reach depths of 75 to 100 cm, and pH of the A horizon is on average 4.6. The cover of the UTL is almost complete, the MTL is intermediate, while the SL and HL are sparse; the cover of bamboo is intermediate. The single diagnostic species is the tree *Cornus disciflora*. Other canopy tree species are the dominant *Quercus copeyensis*, accompanied by *Ardisia glanduloso-marginata*, *Oreopanax capitatus*, *Oreopanax xalapense*, *Styrax argenteus*, shrubs such as *Fuchsia microphylla* and *Solanum vacciniflorum*, the herbs *Senecio heterogamus* and *Uncinia hamata* and the fern *Cyathea divergens*.

2. *Israel II*. This forest type with *C. talamancensis* is represented by four relevés from the site Israel, three in closed canopy and one in intermediate canopy; the altitudinal range is 2910 - 2990 m asl. A further relevé is from the Cuercí ridge, south of the track (N° 5115, in Figure 10 the most centered point of group 2); it is the only 'gap' plot and lies at the highest altitude (3100 m asl). The aspect of these plots is NE-ENE and the slopes are intermediate and steep. This forest type tends to be relatively dry. Organic soil depth and root depth are in the same range as Israel I, while the pH of the A horizon is lower. The UTL is intermediate to dense, the MTL is intermediate, the shrub layer and the HL are sparse, and the BL is intermediate (except N° 5115: 90%). Diagnostic species in this group are the trees *Grammadenia pellucido-punctata*, *Persea vesticula* and the herbs *Maianthemum paniculatum*, *Peperomia galioides*. The dominant tree species, *Quercus copeyensis*, is accompanied by *Cleyera theaeoides*, *Oreopanax capitatus*, *Schefflera pittieri*, *Styrax argenteus* and *Vaccinium consanguineum*. Other species present in this forest type, and also in Israel I, are the shrub *Fuchsia microphylla*, the herbs *Ageratina subcordata*, *Anthurium concinnatum* and *Senecio heterogamus*, and the climber *Macleania rupestris*.

3. *Abarca*. Eight relevés are included in this group, six with *C. tomentosa* and two with *C. talamancensis* (in Figure 10, the two bottom points of group 3); all except one (intermediate canopy) are in closed canopy. The altitude ranges from 2800 - 2850 m asl, the aspect is NE-E-SE, and the slopes are variable (steep, intermediate or flat). The depth of the organic
soil is 8 - 21 cm and the roots reach 80 - 120 cm; hence, they do not differ much from the other two groups. Acidity is high (pH 4) in all the plots. The vegetation cover is dense for the UTL and intermediate for the MTL, sparse for the SL, intermediate to dense for the HL and intermediate for the BL. Two tree species, *Ocotea pittieri* and *Rhamnus oreodendron*, are diagnostic for Abarca. Tree species are well represented in this group: *Ardisia glandulosa-marginata*, *Clevera theaeoides*, *Grammadenia myricoides*, *Ocotea austini*, *Quercus copeyensis*, *Styrax argenteus* and *Vaccinium consanguineum*. As for the shrubs we find *Miconia* sp. 2 N° 639HN and *Palicourea adusta*, the epiphyte *Anthurium concinnatum*, and the ferns *Arachniodes denticulata* and *Asplenium serra*.

4. **Cuericí I.** This forest type is represented by 13 relevés, all of which have *C. talamancensis*. The canopy cover varies from gap, intermediate canopy to closed canopy. The altitude ranges from 2900 - 3000 m asl, while the aspect covers all cardinal points except N, and the slopes range from intermediate to steep. One plot overlaps with group 3 (N° 514). The depth of the organic soil is generally greater than in the other groups, and the rooting depth also has a wider range. Soil pH is 4.2. The vegetation cover reflects the range of canopy cover types; the UTL is dense, the MTL, the SL and the HL are sparse to intermediate, and the BL is dense. The tree *Ilex pallida* and the fern *Plagiogyria semicordata* are diagnostic species for Cuericí I. Other characteristic species of this group are the trees *Drimys granadensis*, *Grammadenia myricoides*, *Ocotea austini* and *Schefflera pittieri*, the epiphyte *Anthurium concinnatum*, the ferns *Arachniodes denticulata* and *Asplenium serra* and the climber *Viburnum* sp. N° 333HN.

5. **Cuericí II.** This forest type is represented by seven relevés with *C. tomentosa*, four of them in gaps, two with intermediate canopy and one in closed canopy. The altitudinal range is very narrow (2990 - 3000 m asl), the aspect is SE-S and the slopes are mainly intermediate. Because of the higher altitude, this forest is more under the influence of mist and is thus more humid. The depth of soil organic matter is 14 - 23 cm and the root depth is 70 - 120 cm, while pH is 4.4. The cover of the UTL is sparse to intermediate, the MTL, the SL and the HL are sparse, and the BL is very dense. Diagnostic species for this forest are the herb *Asteraceae* N° 341HN (‘pelodiente’), the climber *Borreria* sp. N° 347HN (‘cuernito’) and
the tree *Ocotea callophylla*. Other species present are the trees *Ocotea austinii*, *Oreopanax xalapense*, the shrubs *Cestrum irazuense*, *Miconia* sp. 1 N° 112HN, *Miconia* sp. 2 N° 639HN, *Solanum vacciniiflorum*, the herbs *Senecio heterogamus*, *Uncinia hamata*, the ferns *Cyathea divergens*, *Dryopteris parallelograma*, and the climber *Bomarea acutifolia*.

6. *Cuerici III*. Nine relevés belong to this group, mainly in intermediate canopies and gaps with *C. foliosa*. Altitude ranges from 2940 - 3080 m asl and the aspect is SE-S-SW-W-NW, i.e., no north or east facing plots. The slopes are intermediate to flat (one plot is steep). The organic soil is well developed, the roots reach depths between 30 - 120 cm, and acidity is lower than any other group (pH 4.7). The cover of the UTL and the MTL is sparse to intermediate, the SL is sparse, the HL is sparse to intermediate and the BL is intermediate to dense. This forest type is very humid and has the greatest number of diagnostic species (none of them trees): the shrubs *Miconia carnea*, *Miconia* sp. 2 N° 639HN, *Piper pittieri*, *Solanum vacciniiflorum* and *Witheringia solanacea*, and the herbs *Begonia udisylvestris*, *Hydrocotyle pusilla*, *Oxalis vulcanicola*, *Peperomia alata*, *Peperomia hispidula*, *Salvia iodochroa*. *Drimys granadensis* is the main tree species other than the canopy species *Quercus costaricensis*. Associated species include the shrubs *Miconia* sp. 1 N° 112HN, *Palicourea adusta*, *Senecio copeyensis*, the herbs *Centropogon valerii*, *Pilea cornutocucullata*, *Senecio heterogamus*, *Uncinia hamata*, the ferns *Arachniodes denticulata* and *Blechnum falciforme*, and the climbers *Bomarea acutifolia*, *Mikania cordifolia* and *Rubus adonotrichus*.

7. *Cuerici IV*. This group is composed of five relevés, all in gaps with *C. foliosa* except for one plot with *C. talamancensis* (N° 536). The altitudinal range is from 2970 - 3060 m asl and the aspect is S-SW-W. The slopes are intermediate except for one steep plot. The organic soil is generally well developed and the root depth is not as deep as for the other groups, indicating that there are mainly bamboo roots (see also Cuerci V). The acidity of the A horizon is close to Israel II and Cuerci I (pH 4.2). The cover of the UTL, MTL, SL and HL is sparse, and only the BL is very dense. Diagnostic species for gaps with *C. foliosa* are the herbs *Asteraceae* N° 325HN (‘cerrito’), *Muehlenbeckia thannifolia*, *Pilea dauciodora* and *Stellaria cuspidata*. Other species are the tree *Symplocos austin-smithii*, the shrubs *Miconia* sp. 1 N° 112HN, *Miconia* sp. 2 N° 639HN, *Senecio copeyensis*, the herbs *Centropogon valerii*, *Pilea cornutocucullata*, the
fern *Dryopteris parallelograma*, and the climbers *Bomarea acutifolia*, *Mikania cordifolia*, *Rubus adenotrichus* and *Viburnum* sp. N° 333HN.

8. **Cuerici V.** Only three relevés are represented in this group, all with *C. talamancensis* in gaps. The altitudinal range is therefore narrow (3080 - 3100 m asl) and the aspect is SW-W and N. The slopes are intermediate to flat (crest). The soil organic layer is very thin (9 and 13 cm) and the root depth is determined by bamboo roots (60 and 85 cm). Soil pH is 4. As for Cuerici IV, the cover of the UTL, MTL, SL and HL is sparse, whereas the cover of the bamboo layer is 80 - 95%. The single diagnostic species is the herb *Peperomia dotana*. Because of the small size of the group, there are fewer associated species; these include the tree *Symlocos austin-smithii*, the shrub *Cestrum irazuense*, the herbs *Ageratina subcordata* and *Centropogon valerii*, and the climbers *Macleania rupestris* and *Viburnum* sp. N° 333HN.

**Table 2.** Mean number of vascular plant species in gap, intermediate canopy and closed canopy plots. 'n' is the number of plots.

<table>
<thead>
<tr>
<th>Types of canopy closure</th>
<th>Gap (n=18)</th>
<th>Intermediate canopy (n=17)</th>
<th>Closed canopy (n=19)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>Mean ± SE</td>
<td>Mean ± SE</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>Total number of species</td>
<td>39.9 ± 2.2</td>
<td>49.9 ± 2.6</td>
<td>32.9 ± 1.5</td>
</tr>
<tr>
<td>Total number of woody species</td>
<td>16.4 ± 1.1</td>
<td>21.9 ± 1.1</td>
<td>19.3 ± 0.8</td>
</tr>
<tr>
<td>Total number of tree species</td>
<td>10.3 ± 0.9</td>
<td>14.8 ± 1.0</td>
<td>15.6 ± 0.5</td>
</tr>
<tr>
<td>Total number of shrub species</td>
<td>6.2 ± 0.6</td>
<td>7.2 ± 0.7</td>
<td>3.6 ± 0.5</td>
</tr>
<tr>
<td>Total number of herb species</td>
<td>23.4 ± 1.7</td>
<td>27.9 ± 2.2</td>
<td>13.6 ± 0.9</td>
</tr>
</tbody>
</table>

**SPECIES RICHNESS.—**Regardless which bamboo species is dominant, the canopy cover has an influence on species richness (Table 2). The highest number of vascular plant species per plot is found under intermediate canopy (49.9), followed by gap (39.9) and finally closed canopy (32.9). If only the woody species are considered, there are still more species under intermediate canopy but, closed canopy has more species than gap. The same trends are evident for the tree species alone, though the difference between intermediate canopy and closed canopy is insignificant. The number of shrub species is again highest for the
intermediate canopy, followed closely by gap and finally closed canopy. The number of herb species is also higher for intermediate canopy, followed by gap and finally closed canopy.

The numbers of tree species divided according to the vertical structure also show interesting trends (Table 3). The upper tree layer has most species under intermediate canopy, followed by closed canopy and gap. However, the middle tree layer has the highest diversity under closed canopy, then intermediate canopy and finally gap. Similar patterns occur in the shrub and herb layers, although the differences between closed canopy and intermediate canopy are small.

Table 3. Number of tree species classified according to the layers in the vertical profile under gap, intermediate canopy and closed canopy. 'n' is the number of plots.

<table>
<thead>
<tr>
<th>Types of canopy closure</th>
<th>Gap (n=18)</th>
<th>Intermediate canopy (n=17)</th>
<th>Closed canopy (n=19)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>Mean ± SE</td>
<td>Mean ± SE</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>Upper tree layer</td>
<td>1.2 ± 0.3</td>
<td>2.2 ± 0.3</td>
<td>1.9 ± 0.3</td>
</tr>
<tr>
<td>Middle tree layer</td>
<td>3.2 ± 0.7</td>
<td>6.8 ± 0.7</td>
<td>8.6 ± 0.5</td>
</tr>
<tr>
<td>Shrub layer</td>
<td>9.1 ± 0.7</td>
<td>13.3 ± 0.9</td>
<td>13.7 ± 0.5</td>
</tr>
<tr>
<td>Herb layer</td>
<td>8.5 ± 0.7</td>
<td>11.7 ± 0.7</td>
<td>11.0 ± 0.7</td>
</tr>
</tbody>
</table>

In the 54 plots studied, oak trees accounted for 87% of the large trees and 33% of the mature trees. *Quercus* species also accounted for 63% of the seedlings, but only 20% of the saplings and 18% of the pole trees. The size distribution of trees shows differences depending on the nature of the canopy cover (Figure 12). There is a marked reduction in the number of seedlings from closed canopy, intermediate canopy to gap. The difference between closed canopy and intermediate canopy in the number of saplings and pole trees is small but, as expected, it is greater in the number of large and mature trees. In the gaps, the number of trees of all the sizes is much smaller than under the other canopy closures.
Fig. 12. Distribution of tree size classes in 'Closed canopy' (ccan), 'Intermediate canopy' (ican) and 'Gap'.

Discussion

This description of the vegetation in the study area Cerros Cuericí and Cerro Abarca is based on plots selected according to bamboo species and canopy cover; it therefore offers a detailed picture of the pattern of vegetation under specific ecological circumstances. It is not intended to provide a phytosociological description of the Cordillera de Talamanca, which would have required the selection of plots at random or on transects across a larger altitudinal range. In any case, the PhD thesis of Kappelle (1995) provides a broad scale study of the phytosociology and phytogeography of the Cordillera de Talamanca.

CLASSIFICATION OF THE VEGETATION.—As always in ecological studies in a relatively small area, the interpretation of the data is complicated by the non-independence of the environmental variables.
There are also other problems of interpreting the results of this study in terms of existing classifications (Kappelle et al., 1989; Kappelle et al., 1995). Firstly, this study presents only presence-absence data, and there is thus less information available than in some other studies. Secondly, there is uncertainty about the names used by other workers for some plant species due to the ongoing taxonomic work (e.g. Chusquea), and many species are still unknown and can only be defined by voucher numbers (e.g. Miconia, Borreria). Finally, data analysis has been performed using different methods (e.g. TWINSPLAN vs. MULVA), that can significantly affect the groupings of species obtained.

Nevertheless, it is possible to find similarities between the plant communities described by Kappelle (1992), Kappelle et al. (1989) and Kappelle et al. (1995) and the groups presented here. Cuerici I-V correspond well to the Quercus costaricensis and Miconia schnellii sociological group (02) of the Myrsine pittieri-Quercus costaricensis community (although Myrsine pittieri was only found in 3 relevés) from the Western Talamancas (Kapelle et al. 1989). There is also an affinity to the Atlantic Ilex discolor-Quercus costaricensis forest of the same community from Cerro Chirripó (Kappelle, 1992). Israel I-II and Abarca correspond fairly well with the Quercus copeyensis-Chusquea tomentosa sociological group (07) of the Quercus costaricensis-Quercus copeyensis community of the Western Talamancas (Kapelle et al., 1989). At altitudes (2800 - 2990 m asl) higher than on the Cerro Chirripó (2450 and 2650 m asl), these groups may fit into the Atlantic Ardisia palmana-Quercus copeyensis forest community (Kappelle et al. 1995).

In a more global context Kappelle et al. (1995) offer a detailed comparison of the forests in the Cordillera de Talamanca with other tropical montane forest zones. The altitudinal vegetation sequence of Cerro Chirripó is not so different from that on other tropical mountains in Colombia, Kenya, Sumatra, Borneo and Papua New Guinea. According to Klötzli (pers. com.) the oak forests of the Cordillera de Talamanca are physiognomically very similar to the oak forests in Vietnam (Thomasius 1980), the laurineous forests in East Himalaya (Miehe 1991), and the fagaceous forests in Borneo (Stein 1978).

The results of the ordination show that there is a wide diversity of distinct plant communities which have not been formally recognized in
other work. Furthermore, these plant communities appear to be associated with different topographic situations, soil characteristics and forest dynamics. It is particularly interesting that the different *Chusquea* species are associated with particular community types and occur in distinct topographic situations. Thus the plant communities in which *C. tomentosa* occurs are in areas with a S to SE, or sometimes with a NE to E aspect, while those with *C. foliosa* are mainly between NW and SW, and seldom on S and SE slopes. The communities with *C. talamancensis* appear to have the widest ecological range as they are present on all the aspects.

Regarding soil types, there is a tendency to find Andic Humitropept (Eutric Cambisol) associated with plant communities containing *C. talamancensis*, and in some cases also *C. foliosa*, and *C. tomentosa* under closed canopy. In contrast, Typic Hapludand (Humic Andosol) is mostly associated with communities containing *C. tomentosa*, as are also communities with *C. foliosa* when it grows surrounded by *C. tomentosa*. As will be shown in Chapter 3 there are differences in the soil chemical characteristics between the soils carrying the different *Chusquea* species.

Some plant species are very widely distributed. For example, the commonest tree species of the study area are *Viburnum costaricanum* (94% of the plots), *Weinmannia pinnata* (89%), *Quercus costaricensis* (85%), *Zanthoxylum chiriquinum* (80%) and *Ilex lamprophylla* (74%). The bromeliad *Vriesea williamsii* occurs frequently (35%), as does the herb *Peperomia tetraphylla* (26%). *Chusquea* species tend to be associated with particular plant species. For example, *C. tomentosa* is often found together with the tree species *Ardisia glandulosos-marginata*, *Oreopanax xalapense* and the fern *Cyathea divergens*. *C. talamancensis* associates with the tree *Schefflera pittieri*, the herb *Ageratina subcordata* and the climber *Macleania rupestris*. *C. foliosa*, which was not found under closed canopy, appears with the shrub *Senecio copeyensis*, the herb *Pilea cornutocucullata*, and the climbers *Mikania cordifolia* and *Rubus adenotrichus*.

**INFLUENCE OF CANOPY CLOSURE.**—The analysis suggests that differences in species richness can be related to the structure of the vegetation in terms of canopy closure and thus also to forest regeneration. Such associations should come as no surprise because similar patterns are
well known in temperate forests (Remmert, 1980), but less is known about the Tropics (Hubbell et al., 1999).

The higher species richness under intermediate canopy could be due to the higher microhabitat diversity caused by sunflecks compared to closed canopy or gaps. Sunflecks occur when sunlight passes through openings in the forest canopy. In the forest understory, sunflecks foster a high degree of spatial and temporal variation in light availability and have an influence on species diversity and vegetation structure (Chazdon, 1988). Although it was not measured, it is suggested that sunfleck activity was highest under intermediate canopy, followed by closed canopy and finally gaps. The result that there are fewer woody species (including trees) in gaps than under closed canopy is mainly a consequence of the characteristics of closed canopy and gap plots in this study. The oak forest is an old-growth forest and thus the closed canopy is not completely closed but has scattered openings, through which sunlight passes. Gaps are large openings of the forest canopy (> 500 m²) with an understory dominated by the Chusquea bamboos ('bamboo gaps' sensu Taylor & Zisheng, 1988). They have a two layered structure: a bamboo and a herb layer. As shown in Chapter 4, the bamboo clumps are larger and more vigorous in gaps than under closed canopy. Scarcely any light passes through the bamboo thicket of gaps to the forest floor and the sunflecks are very small and few, especially in gaps with Chusquea tomentosa. On the other hand, the herb species are more abundant in gaps than under closed canopy. Smith (1987) showed that patterns of abundance and distribution of understory herbs can mainly be explained by temporal and spatial variation in canopy gaps.

Regarding the effect of canopy closure on the tree species, there are differences in species richness depending on the tree layer considered. Under closed canopy the upper tree layer is almost entirely dominated by the large and mature oak trees, while under intermediate canopy there is more opportunity for other trees to get through, so that the species richness is greater. The greater species richness in the middle tree layer is because this layer contains both smaller oaks and the several other shade tolerant tree species which do not attain the height of mature oaks. Indeed, a slightly higher species richness is found under closed canopy than under intermediate canopy. In gaps there is the lowest species richness due to the dominance of the bamboos. The role played by
bamboos in these forests makes their dynamics quite unlike that in many tropical forests in which a higher diversity of tree species is often found in gaps (Spies & Franklin, 1989, Hubbell et al., 1999).

The overall frequency distribution of tree size classes shows a flattened shape corresponding to a forest in the ageing phase (Leibundgut, 1982), as these old-growth forests are. The larger seedling pool under closed canopy compared to intermediate canopy is probably due to the greater number of mother trees (Blaser, 1987), the ecological characteristics of the trees, and the reduced interspecific competition of trees with herbs. Finally, under large gap conditions there is a clear negative effect of bamboo on tree regeneration, as has also been shown by other authors for various forests with bamboo understory (Veblen et al., 1981; Nakashizuka, 1988; Taylor & Qin, 1988). As presented in the Discussion, the flowering and death of the bamboos is probably the most important type of disturbance in these forests, and allows the trees to regenerate in large gap conditions.

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References


CHAPTER 3

Soil characteristics and *Chusquea* bamboos in the *Quercus* forests of the Cordillera de Talamanca, Costa Rica

Yvonne Widmer

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Abstract

Soils supporting different species of *Chusquea* bamboos (*C. talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark, *C. foliosa* Clark) in the Costa Rican montane oak forests were mainly acidic (pH 3.3-6.0). pH was negatively correlated with organic matter (OM), total nitrogen (N), exchangeable acidity and clay content, but positively correlated with cation exchange capacity (CEC) and exchangeable calcium (exch. Ca). There was a positive correlation of CEC with clay. The maximum base contents (Ca, K, Mg) were found at 20-30% clay.

The concentrations of N, P, exch. K, exch. Ca and exch. Mg were significantly higher in the main rooting zone (0-10 cm) than in the rhizome zone (20-30 cm). Acidity was higher in the main rooting zone than in the rhizome zone and pH in NaF was significantly higher in the latter than in the main rooting zone, suggesting a higher phosphate retention.

The effect of canopy cover on the soil characteristics was not very conspicuous. The Ca:Mg ratio was significantly higher in open conditions than under closed canopy while the opposite was the case for the C:N ratio.

Individual bamboo species had distinct requirements in terms of soil conditions and could, therefore, serve as fairly reliable plant indicators of soil site quality. The soils carrying *Chusquea talamancensis* were significantly richer in organic matter, and had a higher C:N ratio than soils with *C. tomentosa* or *C. foliosa*. Further, they were more acidic, and had the highest content of exchangeable acidity and the highest acid saturation. *Chusquea tomentosa* grew on soils of higher pH and higher concentrations of exch. K, exch. Ca and exch. Mg, and hence had a higher base saturation. *Chusquea foliosa* usually occurred on soils which were intermediate
between those of the other two species, but in order to define its requirements more specifically, further physical analyses are required, i.e. water retention and bulk density.

**Keywords:** soil-plant relationships, soil nutrients, volcanic soils, indicator species

**Introduction**

The relationships between plants and soil conditions have been studied for a long time in central Europe. Depending on the ecological range of a species, edaphic factors may restrict its occurrence to a greater or lesser extent. Ellenberg (1950) and Landolt (1977) have assigned indicator values (*Zeigerwerte*) to the plant species of central Europe and Switzerland respectively for a range of climatic factors (light, temperature and continentality) and edaphic factors like soil moisture, soil reaction and nutrient supply. These values are of practical use in vegetation analysis and in the ecological evaluation of sites.

Soil-plant relationships have not been studied as thoroughly in the tropics though it is certain that subtle differences in soil conditions play an equally important role in determining plant species occurrence as in temperate regions. For example, Harcombe (1980) presented several examples of soil-vegetation relationships in the tropics, concluding that soils with different inherent fertility characteristics will support different vegetation. With reference to tropical bamboos, most of the literature is from India, where these plants are economically important. It has long been recognised (Yadav 1963; Qureshi et al. 1969) that the distributions of bamboo species differ depending on edaphic factors including moisture regime, fertility status and morphological features of the soils. The need for more detailed and systematic studies has been suggested, but little has been published on the subject since. Recent research is concerned mainly with the role of bamboos in nutrient conservation (Rao & Ramakrishnan 1990; Tripathi & Singh 1994), and shows that bamboos may be an important factor for the stability of some tropical ecosystems.

Uchimura (1978) has recognized the value of bamboos as indicators of soil conditions in SE-Asia. For example, the presence of *Bambusa polymorpha* indicates moist, fertile and well-drained soils while
Dendrocalamus strictus is associated with dry soils; Bambusa tulda occurs on stream bed alluvial flats, Oxytenanthera albociliata on low plateaus or hills on sandy lateritic soil, Dendrocalamus longispathus on the edges of damp ravines, Teinostachyum helferi in very damp valleys in evergreen forests, and Bambusa arundinacea on rich and moist sites such as alluvial stretches along streams. Although it is evident from this list that bamboos grow on many different types of soil, most of them appear to prefer well-drained sandy loam to loamy-clayey soils derived from river alluvium or from underlying rocks, and with pH 5.5-6.5 (Liese 1985).

A conspicuous component of the understory of the oak forests of the Cordillera de Talamanca are several species of bamboo in the genus Chusquea (Blaser 1987; Kappelle et al. 1991). Chusquea is a neotropical genus generally associated with montane forests. Recent taxonomic studies have led to the description of many new species, among them Chusquea talamancensis and C. tomentosa which are studied in this investigation (Clark 1989; Widmer & Clark 1991). There are some more recent ecological studies on Chusquea (Young 1991; Pearson et al. 1994, Stern 1995, Widmer 1998) but none have treated plant-soil relationships.

The aim of this paper is to answer the following questions: 1) What are the general characteristics of the soils in the study area in Costa Rica? 2) Is there a difference in soil nutrient status between the main rooting zone (0-10 cm) and the rhizome zone (20-30 cm)? 3) Are there differences in nutrient status of the soil associated with different degrees of canopy closure? 4) Are the various bamboo species associated with contrasting soil conditions, i.e. can particular bamboo species be used as indicators of particular soil conditions?

Study site

The study site lies in the northwestern part of the Cordillera de Talamanca, in an area of 5 km² on Cerro Abarca and Cerros Cuerici, Province of Cartago (83°39'25" - 83°44'22" W and 9°33'7" - 9°35'16" N). The selection of the study site was based on criteria such as good accessibility, no significant recent human impact, and a position below tree limit (3200 m asl). The altitudinal range considered was 2800 - 3100 m asl.
The Cordillera de Talamanca is primarily built up of Tertiary marine sediments with intercalated volcanic and plutonic rocks. During orogenesis intense andesitic-basaltic volcanism and the intrusion of plutonic rocks occurred (Weyl 1980). The Río Macho intrusion is composed of granodiorite which grades to diorite at the margins and covers an area of 50 km². Quaternary volcanic activity in the adjacent Cordillera Volcánica Central also deposited ash (from the Turrialba and Irazú volcanoes) on the Cordillera de Talamanca (Castillo Muñoz 1993). The morphology of the Cordillera de Talamanca is generally characterized by a flattish Pliocene crest with steeply incised valleys, surrounded by intermediate and steep slopes (Weyl 1980).

The soils reflect the volcanic origin of both the intrusions (Talamancan Comagmatic Series) and the ash deposits. Two main soil types have been differentiated in the study area. Soil Type I has been characterized as an Andic Humitropept (Order Inceptisol) according to the US soil classification system; according to the FAO classification this soil type may be a Dystric-umbric Regosol. Chusquea talamancensis is generally found on this soil. Chusquea tomentosa occurs mainly on Soil Type II; this is a Typic Hapludand (Order Andisol) in the US system or a Mollic Andosol in the FAO system.

The climate is characterized by two seasons: the rainy season is from May to November, and the dry season from January to the beginning of April. During the rainy season mean monthly rainfall ranges from 250 to 470 mm. In the middle of this period (i.e. July or August) there is a period of reduced rainfall (Coen 1983). In the dry season the mean monthly rainfall ranges from 20 to 35 mm. Daily temperature oscillations are larger than the range of mean monthly temperatures. For example, from 1987 to 1989 the daily temperature range was 9.4 - 10.3 °C in the dry season and 7.5 - 8.5 °C in the rainy season. Temperatures below 0 °C occur in the dry season when skies are clear. Temperature decreases with altitude by 0.52 - 0.57 °C per 100 m (Herrera 1985, Blaser 1987).

The pristine old-growth forests studied here are part of the Upper Montane Forest (sensu Kappelle et al. 1991). The dominant species, Quercus costaricensis Liebmann and Q. copeyensis C.H. Müller, form tall stands (>30 m). The understory is characterized by bamboos of the genus Chusquea which grow in monospecific stands with distribution patterns
reflecting altitudinal gradients and aspect (Widmer 1994). Three *Chusquea* species are present in the study area: *Chusquea talamancensis* and *C. tomentosa*, which are more abundant, and *C. foliosa*, which is confined to humid patches within areas dominated by one of the other species (Widmer 1994). Forest dynamics in these old-growth forests is strongly affected by tree- and branch-fall, leading to a mosaic of closed canopies, canopies with apertures, and forest gaps in various stages of regeneration. Large old gaps (>500 m², >10 years old) in the primary forest typically have a two layered vertical structure: a bamboo layer and a herb layer (Widmer 1993, Widmer 1998). The roots reach a depth between 30 and 130 cm. The main rooting zone (0-10 cm) contains a dense root mat, and the rhizomes of *Chusquea* are found at 10 - 40 cm.

**Materials and methods**

**SELECTION OF PLOTS AND SAMPLING.**—Forty-one 500 m² (20 x 25 m) plots established for vegetation analysis were selected for this study. The plots differed in altitude, aspect and slope angle. They were selected to include different species of bamboo (*Chusquea talamancensis*, *C. tomentosa* or *C. foliosa*) and to represent different degrees of canopy closure. The canopy closure was classified into three categories: (1) 'Gap', corresponds to a plot in a large gap of over 500 m² area with an overstory tree cover of less than 10%. (2) 'Closed canopy' (ccan) refers to sites with an old-growth oak canopy cover of more than 60%. (3) 'Intermediate canopy' sites (ican) are those where the overstory was represented by a few scattered mature trees (> 50 cm dbh) and a cover of 10 - 50% of the overstory canopy, or occupied by medium sized trees (20 < dbh < 50 cm). *Chusquea foliosa* was not found under closed canopy in the study area.

Soil samples were taken at random points within the plots from two depths: 0-10 cm, the main rooting zone, and 20-30 cm, the average depth at which bamboo rhizomes are found (the rhizome zone). In June 1989, 15 plots were sampled. The three random samples from each plot were combined and the material was analysed in the soil laboratory at CATIE (Costa Rica) following the methods described by Díaz-Romeu & Hunter (1978). Due to the high variability of the results a second sampling of 26
additional plots was performed in July 1990; these samples were analysed at the Geobotanical Institute ETHZ (Switzerland) following the same methods.

SOIL ANALYSIS.—Soil samples were air-dried for several days in Turrialba (625 m asl, mean annual temperature 22 °C). Before analysis the samples were ground and passed through a 2-mm mesh sieve. Soil organic matter, total N, organic C, Ca, Mg, K, Na and P were determined on a subsample that had been finely ground and passed through a 0.25-mm mesh sieve.

Soil pH was determined electrometrically in a soil:water volume ratio of 1:2.5. Phosphate retention was predicted from the pH in NaF according to the method of Alvarado (1982) and Mazzarino et al. (1985). It was measured electrometrically with a soil:solution ratio of 1:50 and a reaction time of 2 min.

Organic matter was determined by the Walkley-Black wet digestion method using a correction factor of 2.76 for unrecovered organic C and a ratio of organic matter to organic C of 1.72 (Saiz del Río & Bornemisza 1961). Total N was determined by the semi-micro Kjeldahl technique (BÜCHI 320). Total carbon and nitrogen for C:N ratio were determined using a CHN-1000 gas analyzer (LECO) at the Institut für Pflanzenwissenschaften ETHZ. The measurement of total carbon corresponds to organic carbon since it is the predominant form present in humid regions, where extensive leaching of the soil has occurred (Nelson & Sommers 1982).

Cation exchange capacity (CEC) and exchangeable bases were determined with the ammonium acetate method described by Díaz-Romeu (1982). As a first step the exchangeable bases K, Ca, Mg and Na were extracted with 1:20 NH₄OAc 1N (pH 4.8); they were subsequently determined by atomic absorption analysis (SPECTRA AA-400, Varian). After washing with ethanol, CEC was determined by titration. Exchangeable acidity (a measure for exchangeable H⁺ and Al³⁺ cations) was extracted with 1 mol l⁻¹ KCl, and determined by titration; extractable P was measured colorimetrically (SP6-550 UV-VIS Spectro) after extracting at 1:10 with Olsen reagent (as modified by Díaz-Romeu & Hunter 1978). Effective cation exchange capacity (ECEC) was calculated
as the sum of exchangeable acidity (H\(^+\) + Al\(^{3+}\)) plus the sum of bases (K\(^+\), Ca\(^{2+}\), Mg\(^{2+}\), Na\(^+\)). Base saturation was calculated as the sum of bases expressed as a percentage of ECEC. Acid saturation is the percentage of ECEC accounted for by exchangeable acidity.

Particle-size analysis was performed with the Bouyoucos method (Bazán 1975); hydrometer readings were taken at 40 s and 2 h, and the proportion of sand, silt and clay calculated.

DATA ANALYSIS.—All data analyses were performed with the statistical software package Statview 4.0 (1992). Correlation coefficients were calculated to identify the interrelationships between soil parameters. The significance of the coefficients was determined with a Fisher's r to z transformation ($P < 0.001$). Regression models were calculated using forward stepwise regression with 13 to 16 independent variables ($F$-to-remove = 4, $\alpha = 0.05$). One-factor ANOVA was calculated to determine whether variation in any soil parameters could be explained statistically by any of the following factors: *Chusquea* (C. *talamancensis*, C. *tomentosa*, C. *foliosa*), canopy closure (gap, intermediate canopy, closed canopy) or soil depth (0-10 cm, 20-30 cm). In addition, two-factor ANOVA’s (*Chusquea*, canopy closure) were calculated for each soil depth separately (0-10 cm and 20-30 cm). A Bonferroni/Dunn multiple comparison test for main effects was applied; this sets an upper overall significance level of $\alpha$ when testing multiple hypotheses (Scheiner & Gurevitch 1993).

Results

GENERAL SOIL PROPERTIES.—The analysis of chemical characteristics of the soil samples from the main rooting (0-10 cm) and the rhizome zone (20-30 cm) revealed a high but variable organic content (organic matter 5.8-90.7%, organic C 3.8-46.5%), which is characteristic of soils derived from volcanic ash (Nanzyo et al 1993). Further, effective cation exchange capacity (ECEC) was much lower (2.6-24.0 meq/100 g soil) than CEC (27.4-160 meq/100 g soil), showing the variable charge characteristics. Finally, there was a linear relationship between organic C and cation exchange capacity (CEC = 18.2 + 2.5 orgC%, $r^2 = 0.85$, $n = 36$), which is common for humus-rich Andisols.
Acidity was generally high (pH=3.28-6.04). There was a negative correlation between pH and organic matter (OM) content (Figure 1). Total nitrogen (0.34-2.34%) was also negatively correlated with pH levels. Clay content (3.6-54%) and exchangeable acidity (0.2-23.3 meq/100 g soil) were higher at lower pH. The regression model for pH (Table 1) explained 87% of the variation and included as positively correlated parameters CEC and exchangeable calcium (Exch.Ca).

**Table 1.** Regression models to describe pH in H₂O, pH in NaF, total nitrogen (Ntot), C:N ratio and phosphorus from 36 soil samples at 0-10 and 20-30 cm depth in montane oak forests with bamboo understory in the Cordillera de Talamanca (models after forward stepwise regression; Iv= independent variables tested, Sa= serial autocorrelation). Abbreviations see text.

<table>
<thead>
<tr>
<th>Regression models</th>
<th>Iv</th>
<th>r²</th>
<th>P</th>
<th>Sa</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH = 4.72 - 0.03 OM - 0.04 exch.acidity + 0.02 CEC + 0.08 exch.Ca - 0.01 clay + error</td>
<td>14</td>
<td>0.87</td>
<td>0.001</td>
<td>0.03</td>
</tr>
<tr>
<td>pH NaF = - 1.82 + 2.33 pH + 0.04 Ac.Sat. - 0.04 clay + error</td>
<td>16</td>
<td>0.90</td>
<td>0.001</td>
<td>0.41</td>
</tr>
<tr>
<td>Ntot = 0.53 + 0.03 OM - 0.01 CEC + error</td>
<td>15</td>
<td>0.84</td>
<td>0.001</td>
<td>0.03</td>
</tr>
<tr>
<td>C:N = 3.05 + 0.27 CEC - 0.19 ECEC + error</td>
<td>15</td>
<td>0.73</td>
<td>0.001</td>
<td>0.24</td>
</tr>
<tr>
<td>P = 2.67 - 0.23 pH NaF + 0.03 OM + error</td>
<td>15</td>
<td>0.48</td>
<td>0.001</td>
<td>0.15</td>
</tr>
</tbody>
</table>

As expected, the regression between organic matter and organic carbon (both parameters determined independently) was linear (%C = 0.77 + 0.51 OM, r² = 0.99, P < 0.001). Attributes such as total nitrogen, C:N ratio, phosphorus (P), CEC and indirectly the bases (Ca²⁺, Mg²⁺, K⁺) were correlated with organic matter (Figure 1), which is expected from theory (Nelson & Sommers 1982). The regression model for total nitrogen showed a positive dependence on organic matter and a negative relation to CEC (r² = 0.84, P < 0.001). C:N ratios ranged from 7.5-21.7 and correlated positively with the variable charge attributes of the soil, i.e. with CEC and ECEC (r² = 0.73).

Like pH, pH in NaF (7.2-11.7) was also negatively correlated with organic matter and total nitrogen (Figure 1). The calculated regression
model for pH in NaF included positively correlated acid saturation (Ac.Sat.) and negatively correlated clay content as explanatory parameters. The negative correlation between pH in NaF and phosphorus (0.22-19.5 μg ml⁻¹) was evident in the regression model for P, which also indicates that P was positively associated with organic matter.

The exchangeable bases K, Ca and Mg (but not Na) were correlated with each other, and there was a positive correlation of ECEC with clay (Figure 1), which is expected from theory. The bivariate scattergram of K⁺, Ca²⁺ and Mg²⁺ with clay content showed that all three elements had bell shaped curves with maximum base contents at 20-30% of clay. The relationship of KCl-extractable Al with clay was linear and exchangeable acidity also increased with clay content. The potassium contents were low but positively correlated with total nitrogen and phosphorus (Figure 1).

![Fig. 1. Significant positive (+r) and negative (-r) correlations (r > 0.50, P < 0.001) of parameters from soil sampled at 0-10 and 20-30 cm depth (total of 36 observations) in oak forests with Chusquea understory. Significance tested with Fisher's r to z transformation. See abbreviations in the text.]

RELATIONSHIPS WITH VEGETATION.—Organic matter, nitrogen and phosphorus. These components were significantly higher in the main rooting zone than in the rhizome zone (Tables 2, 3). The plots with Chusquea talamancensis in the understory had on average the highest content of organic matter followed by C. tomentosa and C. foliosa.
Table 2. Content of organic matter, total nitrogen, C:N and phosphorus for Chusquea talamancensis, C. tomentosa and C. foliosa, under gap, intermediate canopy and closed canopy conditions at 0 - 10 cm (main rooting zone, MRZ) and 20-30 cm (rhizome zone, RZ). The number of samples (n) refers to both soil depths; for C:N the number of samples is indicated in brackets (mean ± SE).

<table>
<thead>
<tr>
<th>Canopy closure</th>
<th>Chusquea species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>talamancensis</td>
</tr>
<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td></td>
<td>MRZ</td>
</tr>
<tr>
<td>Organic matter</td>
<td></td>
</tr>
<tr>
<td>(% dry weight)</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>45.5 ± 14.1</td>
</tr>
<tr>
<td>RZ</td>
<td>30.3 ± 9.8</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td></td>
</tr>
<tr>
<td>(% dry weight)</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>1.70 ± 0.17</td>
</tr>
<tr>
<td>RZ</td>
<td>1.01 ± 0.18</td>
</tr>
<tr>
<td>C:N ratio</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>17.9 (1)</td>
</tr>
<tr>
<td>RZ</td>
<td>14.2 (1)</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
</tr>
<tr>
<td>(\mu g ml(^{-1}))</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>11.4 ± 3.6</td>
</tr>
<tr>
<td>RZ</td>
<td>4.74 ± 1.71</td>
</tr>
<tr>
<td>Intermediate canopy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>talamancensis</td>
</tr>
<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td></td>
<td>MRZ</td>
</tr>
<tr>
<td>MRZ</td>
<td>65.8 ± 10.3</td>
</tr>
<tr>
<td>RZ</td>
<td>23.6 ± 3.5</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>1.69 ± 0.22</td>
</tr>
<tr>
<td>RZ</td>
<td>0.72 ± 0.09</td>
</tr>
<tr>
<td>C:N ratio</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>*</td>
</tr>
<tr>
<td>RZ</td>
<td>*</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
</tr>
<tr>
<td>(\mu g ml(^{-1}))</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>5.50 ± 2.23</td>
</tr>
<tr>
<td>RZ</td>
<td>1.24 ± 0.29</td>
</tr>
<tr>
<td>Closed canopy</td>
<td></td>
</tr>
<tr>
<td></td>
<td>talamancensis</td>
</tr>
<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td></td>
<td>MRZ</td>
</tr>
<tr>
<td>MRZ</td>
<td>23.6 ± 1.5</td>
</tr>
<tr>
<td>RZ</td>
<td>52.0 ± 8.8</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
</tr>
<tr>
<td>(\mu g ml(^{-1}))</td>
<td></td>
</tr>
<tr>
<td>MRZ</td>
<td>1.60 ± 0.20</td>
</tr>
<tr>
<td>RZ</td>
<td>2.91 ± 1.12</td>
</tr>
</tbody>
</table>
The C:N ratio did not vary significantly with depth, but was significantly different between the soils sustaining these bamboo species. It was highest for *Chusquea talamancensis* and lowest for *C. foliosa* (*P < 0.05*). C:N ratios were larger in open conditions; the strongest significant difference in the C:N ratio being between gap and closed canopy (*P < 0.01*). On the other hand, phosphorus was significantly higher under gap conditions than under intermediate canopy (*P < 0.01*).

**Table 3. Summary statistics of organic matter, total nitrogen, C:N ratio and phosphorus after one way ANOVA (α = 0.005) for the factors 'canopy closure', 'Chusquea species' and 'soil depth'. *P ≤ 0.05, ** P ≤ 0.01; *** P ≤ 0.001.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Canopy closure</th>
<th>Chusquea species</th>
<th>Soil depth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>F-Value</td>
<td>P</td>
</tr>
<tr>
<td>Organic matter</td>
<td>2</td>
<td>1.41</td>
<td>-</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td>2</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>C:N ratio</td>
<td>2</td>
<td>5.54</td>
<td>**</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>2</td>
<td>4.21</td>
<td>*</td>
</tr>
</tbody>
</table>

**Acidity.** As expected, pH was also significantly lower in the main rooting zone than in the rhizome zone (Figure 2). Table 4 and 5 show that there were significant differences in the acidity characteristics in the main rooting zone, and that these could be related to *Chusquea* species but not to canopy closure. The plots with *C. talamancensis* had the lowest pH, the highest content of exchangeable acidity, and the highest acid saturation; all these differences could be related to the higher organic content of the *C. talamancensis* soils. The differences in soil pH between sites with *Chusquea talamancensis* and those with the two other species were significant (*C. tomentosa* *P < 0.001*, *C. foliosa* *P < 0.01*). The difference in exchangeable acidity in main rooting zones was significant between *Chusquea talamancensis* and *C. tomentosa* (*P < 0.01*). Similarly, acid saturation was significantly higher in the main rooting zone and in the rhizome zone of plots with *Chusquea talamancensis* than those with *C. tomentosa* (*P < 0.05* and *P < 0.001* respectively).
Table 4. Values of pH in H2O, pH in NaF, exchangeable acidity, acid saturation and cation exchange capacity in the main rooting zone (0-10 cm), and exchangeable cations (Ca, Mg, K, Na), base saturation and Ca:Mg ratio in the rhizome zone (20-30 cm) for Chusquea talamancensis (tal), C. tomentosa (torn) and C. foliosa (fol) under gap, intermediate canopy and closed canopy conditions (mean ± SE).

<table>
<thead>
<tr>
<th>Canopy closure</th>
<th>Chusquea species</th>
<th>Gap</th>
<th>Intermediate canopy</th>
<th>Closed canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>tal</td>
<td>torn</td>
<td>fol</td>
<td>tal</td>
</tr>
<tr>
<td>pH in H2O (IN)</td>
<td>3.97 ± 0.28</td>
<td>4.59 ± 0.13</td>
<td>4.21 ± 0.12</td>
<td>3.50 ± 0.07</td>
</tr>
<tr>
<td>pH in NaF (IN)</td>
<td>7.44 ± 0.29</td>
<td>8.72 ± 0.67</td>
<td>8.12 ± 0.22</td>
<td>6.93 ± 0.28</td>
</tr>
<tr>
<td>exch. Ac. (meq/100g)</td>
<td>3.97 ± 1.48</td>
<td>2.50 ± 0.55</td>
<td>3.67 ± 1.42</td>
<td>8.52 ± 1.83</td>
</tr>
<tr>
<td>Acid Sat. (%)</td>
<td>31.0 ± 11.0</td>
<td>31.8 ± 8.7</td>
<td>35.5 ± 9.7</td>
<td>61.6 ± 7.9</td>
</tr>
<tr>
<td>CEC (meq/100g)</td>
<td>96.6 ± 9.5</td>
<td>44.6 ± 1.6</td>
<td>54.4 ± 6.9</td>
<td>108.2 ± 15.6</td>
</tr>
<tr>
<td>exch. Ca (meq/100g)</td>
<td>0.80 ± 0.31</td>
<td>2.97 ± 1.09</td>
<td>0.71 ± 0.21</td>
<td>0.40 ± 0.22</td>
</tr>
<tr>
<td>exch. Mg (meq/100g)</td>
<td>0.25 ± 0.05</td>
<td>0.34 ± 0.34</td>
<td>0.35 ± 0.07</td>
<td>0.30 ± 0.10</td>
</tr>
<tr>
<td>exch. K (meq/100g)</td>
<td>0.13 ± 0.02</td>
<td>0.39 ± 0.08</td>
<td>0.23 ± 0.02</td>
<td>0.23 ± 0.04</td>
</tr>
<tr>
<td>exch. Na (meq/100g)</td>
<td>0.21 ± 0.02</td>
<td>0.20 ± 0.02</td>
<td>0.20 ± 0.01</td>
<td>0.18 ± 0.01</td>
</tr>
<tr>
<td>Base Sat. (%)</td>
<td>96.6 ± 9.5</td>
<td>44.6 ± 1.6</td>
<td>54.4 ± 6.9</td>
<td>108.2 ± 15.6</td>
</tr>
<tr>
<td>Ca:Mg ratio</td>
<td>2.93 ± 0.67</td>
<td>4.09 ± 0.80</td>
<td>2.02 ± 0.41</td>
<td>1.10 ± 0.22</td>
</tr>
</tbody>
</table>
Table 5. Summary statistics of pH, pH in NaF, exchangeable acid, acid saturation and cation exchange capacity (CEC) on the main rooting zone (0-10 cm) and of exchangeable cations (Ca, Mg, K, Na), base saturation and Ca:Mg ratio at the rhizome zone (20-30 cm) using two way ANOVA (α = 0.05) for the factors 'canopy closure' and 'Chusquea species'. (* P<0.05; ** P <0.01; *** P ≤0.001).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Factor</th>
<th>Canopy closure</th>
<th>Chusquea species</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F-Value</td>
<td>P</td>
<td>df</td>
</tr>
<tr>
<td>pH in H₂O</td>
<td>1</td>
<td>0.68</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>pH in NaF</td>
<td>1</td>
<td>0.45</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>exch. acidity</td>
<td>1</td>
<td>1.85</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Acid saturation</td>
<td>1</td>
<td>1.05</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>CEC</td>
<td>1</td>
<td>0.27</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>exch. Ca</td>
<td>1</td>
<td>0.05</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>exch. Mg</td>
<td>1</td>
<td>0.86</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>exch. K</td>
<td>1</td>
<td>0.13</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>exch. Na</td>
<td>1</td>
<td>0.29</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Base Saturation</td>
<td>1</td>
<td>1.34</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Ca:Mg ratio</td>
<td>1</td>
<td>9.16</td>
<td>**</td>
<td>1</td>
</tr>
</tbody>
</table>

pH in NaF was significantly higher (P < 0.001) in the rhizome zone than in the main rooting zone, with values suggesting a high phosphate retention. Values of pH in NaF in the main rooting zone were significantly lower at Chusquea talamancensis sites than at sites with either C. tomentosa (P < 0.01) or C. foliosa (P < 0.01). However, in the rhizome zone there were no significant differences between species in pH in NaF.

Cations and cation exchange. There were highly significant differences in cation exchange capacity and total base content (Ca + Mg + K + Na; P < 0.001) between the main rooting and the rhizome zone (Figure 2). There were also significant differences with soil depth for the cations Ca, Mg, K considered separately (P < 0.001) but not for Na. Variation in cation content at rhizome zone was more strongly associated with species of bamboo than with degree of canopy closure. Exchangeable bases were far
Fig. 2. Means (±SE) of pH, cation exchange capacity (CEC), exchangeable acidity (Al$^{3+}$+H$^+$), sum of exchangeable bases (Ca, Mg, K, Na) of soils in plots with the Chusquea species: C. talamancensis (tal), $n = 18$; C. tomentosa (tom), $n = 13$, and C. foliosa (fol), $n = 10$. Data are given for the main rooting (0-10 cm) and rhizome zone (20-30 cm).
higher at Chusquea tomentosa sites, than at those of C. foliosa and C. talamancensis, which were very similar (Figure 2, Tables 4, 5). ECEC and also CEC were similar for Chusquea talamancensis and C. tomentosa sites, and higher than for C. foliosa, though this difference was only significant for CEC ($P < 0.001$). Finally, the base saturation data confirmed that sites with Chusquea tomentosa had a significantly higher base status in the rhizome zone than sites with C. talamancensis ($P < 0.001$) or C. foliosa ($P < 0.05$).

The Ca:Mg ratio at 20-30 cm depth showed significant differences associated with bamboo species and with canopy cover (Tables 4, 5). It was highest for Chusquea tomentosa and very similar for C. talamancensis and C. foliosa. The ratio was relatively higher in gaps than under intermediate canopy or closed canopy, which showed on average a similar ratio.

**Discussion**

Blaser (1987) measured the physical and chemical characteristics of soils in a plot of 12.4 ha at lower altitudes (2600-2800 m asl), but on the same side (Atlantic) of the Cordillera de Talamanca as the site of this investigation. From the resulting very low bulk density, the high porosity and the high pH in NaF values, he concluded that the soils were of volcanic origin. The volcanic origin of the soils is confirmed in the present study. Characteristic features of such soils include a high accumulation of organic matter (correlated with a large amount of organic C), variable (or pH-dependent) charge characteristics and a linear relationship between organic C and CEC, as described by Nanzyo *et al.* (1993). In addition, pH in NaF values were also relatively high (7.2-11.7) which suggests high allophane contents in the soil. In humid regions, volcanic ash weathers quickly into allophane, an amorphous Al-silicate mixture that forms complexes with organic matter (Sánchez 1976). Andepts and other soils containing large amounts of allophane and other amorphous minerals have high capacities for binding phosphate (Gebhardt & Coleman 1974). Thus, extractable phosphorus contents were low. However, this may also be associated with the low pH and high concentrations of Al and Fe, that can precipitate P into Al and Fe...
phosphates, the main mechanism of phosphate fixation in most soils (Bohn et al. 1985).

Montane forests are in general low in available P and N. The low temperatures are associated with low rates of decomposition and nutrient release, and favour the accumulation of organic matter in soils of volcanic origin (Vitousek & Sanford 1986). Organic matter, nitrogen and phosphorus decrease with soil depth, but the C:N ratio is less variable, perhaps because C tends to be mineralized faster than N at low pH (Sánchez 1976). The C:N ratios are correlated with CEC, reflecting the fact that N mineralization is inversely proportional to allophane contents (Sánchez 1976).

As in many montane forests, the soils of the study site are acidic to very acidic. In interpreting the exchangeable acidity, acid saturation and cation exchange capacity data one must consider the composition of the soil material. Since soil from 0-10 cm depth consists mainly of humic compounds, there is probably a greater proportion of H than Al ('acid cations') in the main rooting zone than at greater depths. At 20-30 cm there is mineral soil (generally B horizon) and the type of the clay (e.g. allophane) determines the amount of Al present. However, there may be significant translocation of humic substances to such depths, depending on the composition of the vegetation and the soil structure. The concentrations of K, Ca and Mg were also higher in the surface soil compared to the deeper soil, but Na changed little with depth. All concentrations of cations were low if compared with other tropical mountain soils as presented by Edwards & Grubb (1982). The comparison with data of the soils from the Chirripó National Park in Costa Rica (Kappelle et al. 1995) is difficult due to different sampling criteria. Only pH and the clay content of soils in the Atlantic side of the Cordillera de Talamanca are in the same range.

The degree of canopy cover proved to be relatively unimportant as a factor affecting soil conditions in this investigation. The strongest relationship was observed with the Ca:Mg ratio, which was consistently higher for all Chusquea species in open conditions than under closed canopy. Decomposition is apparently enhanced under open conditions, for the C:N ratios were higher under closed conditions than in gaps, especially for Chusquea talamancensis and C. tomentosa. Finally, for the
same two species, phosphorus seems to be more available in gaps than under closed canopy in the rhizome zone.

There is some evidence for differences in soil conditions associated with the various *Chusquea* species. The soils supporting *Chusquea talamancensis* showed on average the highest organic matter content, C:N ratio, and acidity, followed by *C. foliosa*. There were no noticeable differences between the species in the contents of soil nitrogen and extractable phosphorus. Soils carrying *Chusquea tomentosa* had the highest pH, the highest concentration of exchangeable cations and hence the highest base saturation, especially at the rhizome zone. Although these findings have to be supported by future research, they confirm what Yadav (1963) first suggested and Qureshi et al. (1969) supported with more data: that individual species of bamboos have distinct requirements in terms of soil conditions and can, therefore, serve as fairly reliable plant indicators of soil site quality. This can be of practical importance for the foresters working in the montane oak forests of the Cordillera de Talamanca, in order to develop the most suitable sustainable management.

**Acknowledgements**

Field work was funded by the Swiss Development Agency (DEH-EDA) and logistic support was offered by the Silviculture of Natural Forests Project at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Costa Rica. Many soil scientists who advised me at different stages are hereby thanked: M. J. Mazzarino, R. Díaz-Romeu, D. Kass (CATIE); S.K. Gupta (FAC Liebefeld); H. van Baren (ISRIC Wageningen). Many thanks to the field assistant Martín Mena Granados; for the laboratory analysis: Carlos Alberto Castillo and Mario Jiménez (CATIE), Miguel Baldomá and Kathrin Rentsch (Geobotanisches Institut ETHZ), and Anna Dürsteler (Institut für Pflanzenwissenschaften ETHZ). Thanks to Diethart Matthies (Inst. Umweltwissenschaften, Universität Zürich) for the statistical advice. P.J. Edwards, J. Kollmann, F. Klötzli, L.P. van Reeuwijk, and the anonymous reviewers are thanked for corrections and valuable comments of earlier versions of the manuscript.
References


CHAPTER 4

Pattern and performance of understory bamboos *(Chusquea spp.)* under different canopy closures in old-growth oak forests in Costa Rica

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Abstract

The effect of canopy closure on spatial and morphological pattern of three understory *Chusquea* species were studied in pristine upper montane oak forests. Plots with either *Chusquea talamancensis* Widmer & L.G. Clark or *C. tomentosa* Widmer & L.G. Clark were set out in gaps, under intermediate tree canopy and under closed canopy. The third species, *Chusquea foliosa* L.G. Clark, was only found in gap and intermediate canopy sites in the study area. Clumps of all bamboo species tend to be few and large under open conditions and numerous and small under more shady conditions. The larger size of clumps in gaps is reflected in the number of culms per clump, the diameter of the culms and, as a consequence, clump basal area, clump crown area and biomass (index of plant volume) compared to intermediate and closed canopy. The smaller clump density in gaps compared to closed canopy implies that there is more intraspecific competition and density dependent mortality (self-thinning effect) when a bamboo species is dominant under favourable light conditions. Parameters of performance like culm length, number of nodes per culm, number and length of primary branches and number of branch nodes seem not to be affected by the light regime, unlike total number of branches, total branch length and the branching pattern. Species differ in their response to the light environment: *Chusquea tomentosa* and *C. foliosa* have a higher degree of morphological plasticity than *C. talamancensis*, which in turn, appears to be more shade tolerant. No difference between species has been found regarding their contribution to vegetation, parameters reflecting abundance per unit area
(site clump area, site crown area and site index of clump volume) were similar for all three species.

**Keywords**: Chusquea; bamboo; canopy cover; gaps; light environment; morphological plasticity; tropical montane forest; understory plants.

**Introduction**

The evergreen oak forests of the Cordillera de Talamanca form the largest area of undisturbed primary forest left in Costa Rica, mostly within the 612,560 ha International Biosphere Reserve 'La Amistad' (Kappelle, 1995). These oak forests are also called cloud forests due to the orographic cloud formation, presenting abundant epiphytes and moss cover on tree stems and branches. The understory is dominated by different species of the bamboo genus *Chusquea* (Widmer, 1994; Kappelle, 1995).

*Chusquea* species are medium sized woody bambusoid grasses. They are recognisable in their vegetative phase by their solid culms and the dimorphic buds at the nodes (Clark, 1989) which generally develop into one central branch and multiple subsidiary branches. To date, there are 13 species of *Chusquea* known in the Cordillera de Talamanc (Widmer, 1994). This study focused on three species distributed in Cerros Cuericí and Cerro Abarca below the timberline (which is at 3200 m): *Chusquea talamancensis* Widmer & Clark (Section Swallenochloa), *C. tomentosa* Widmer & Clark and *C. foliosa* Clark (both in Section Longifoliae). The three species appear to occupy different ecological niches forming monospecific stands of different sizes, which are contiguous to each other. They are clump-forming bamboos with pachymorph rhizomes (short rhizome necks). When growing among trees, clumps have an erect habit and the culms show either pendulous tips (*Chusquea talamancensis*), or climbing tips which ascend along the tree trunks foraging for light (*Chusquea tomentosa*). In large open sites the growth habit of the bamboos is more arched and the culms of the different clumps are intermingled forming an impenetrable thicket, so that passage is only possible by creeping below or climbing over the culm mat.

As Veblen (1982) described for *Chusquea* species in *Nothofagus* forests in Chile, the understory *Chusquea* bamboos in the Costa Rican
Quercus forests, often seem to repress the establishment of trees after deforestation. In some areas, the destruction of forests by clear cutting has allowed Chusquea to overgrow disturbed areas forming almost pure bamboo stands. These characteristics of bamboos (invasiveness after human disturbance, inhibition of tree regeneration) have often been described for Asiatic species (Huberman, 1959; Soderstrom & Calderón, 1979; Ahmad, 1986; Kawahara, 1987). In view that the old-growth oak forests of the Cordillera de Talamanca are study objects for future forest management (Chaverri et al., 1986; Berner & Stadtmüller, 1988; Blaser & Camacho, 1991; Beek & Sáenz, 1992), it was necessary to investigate the ecology of these dominant understory plants.

The aim of this study is to assess the effect of canopy conditions upon spatial and morphological pattern of the bamboo populations and the vegetative performance of individuals (sensu Kershaw & Looney, 1985). There is a general lack of data on relative performance of the various life history stages of a plant species under different canopy conditions (Cipollini et al., 1993). Because of the nature of Chusquea's life history, as semelparous plants with a long flowering cycle of probably more than 30 years (Seifriz, 1950; Widmer, 1998a), a full picture would require long term observation of a cohort from seedling establishment to seed production. During the course of this research (1987 - 1989) the populations of Chusquea talamancensis and, subsequently, of C. tomentosa gradually started to flower in the study area and died after profuse seed production (Widmer, 1998a). In total, six Chusquea species showed mast seeding in the Cordillera de Talamanca within a period of 10 years (Widmer, 1994). As a consequence, it is assumed that all plants of a species studied within the area are even-aged (see also Young, 1991). Besides, the onset of mass flowering may imply that the present data were taken at the most mature age of the plants, i.e. the vegetative age (sensu Lacey, 1986) was attained to switch on flowering. This study represents only a snapshot in time. It was an observational experiment in the primary oak forest, in which sites with different degrees of canopy closure were selected for comparison. The most important differences in site conditions were in light; it is shown elsewhere that soil properties did not vary significantly depending on canopy closure (Widmer, 1998b). The main questions addressed were: How do Chusquea plants develop under different degrees of canopy closure? Are there ecological differences
between the species in their response to light or shade? How do differences in performance due to light conditions affect the structure of populations and their contribution to vegetation?

Materials and methods

STUDY AREA.—The Cordillera de Talamanca runs from northwest to southeast and is the largest and highest mountain range in Costa Rica. It is built up of Tertiary marine sediments with intercalated volcanic and Upper Miocene plutonic rocks (Weyl, 1980). The topography is generally characterized by a flattish crest with steeply incised valleys and surrounded by intermediate and steep slopes (Blaser, 1987; Berner, 1992).

The study area covers 5 km² on Cerro Abarca and on Cerros Cuericí within the Cordillera de Talamanca, in the Province of Cartago (Figure 1). The altitudinal range considered was from 2800 (above this elevation vegetation was not significantly affected by human impact) to 3100 m asl (i.e. at least 100 altitudinal meters below timberline). The slopes of the plots are predominantly west-, south- and east-facing with 0 - 45° inclination. Soils in the study area have volcanic origin and belong to the order of Inceptisols and group Humitropept or the order Andisols and the group Hapludand (US Soil Classification System).

Mean annual rainfall at Villa Mills weather station at 3000 m is 2610 mm (Blaser, 1987). From 1987 to 1989 mean monthly rainfall in the wet season (May to November) ranged between 220 and 764 mm (data from the Instituto Costaricense de Electricidad). In the dry season (December to March) mean monthly rainfall was between 7.5 and 110 mm. In the same period (1987 - 1989), mean annual air temperature was 8.2 °C, with mean daily temperature variation of 9.4 - 10.3 °C in the dry season and 7.5 - 8.5 °C in the wet season. Mean maximum temperatures reached up to 14.4 °C in April and minimum temperatures down to 3.1 °C in January.

The pristine old-growth forests of the study site belong phytosociologically to the Upper Montane Forest (sensu Kappelle, 1991) and show dominance of Quercus species in the overstory, with the endemic Q. costaricensis Liebmann and Q. copeyensis C.H. Müller forming a high forest canopy (> 30 m). According to (Kappelle, 1992) these forests consist
Fig. 1. Location of the study site in Costa Rica and the study areas (dotted line) on Cerros Cuérici and Cerro Abarca at the Cordillera de Talamanca.
of five layers. In the upper canopy layer *Quercus* is associated with *Podocarpus* and *Magnolia*. The more diverse intermediate tree layer presents *Weinmannia, Ilex, Zanthoxylum, Viburnum, Vaccinium, Styrax, Symlocos, Clusia, Lauraceae, Melastomataceae* and *Myrsinaceae*. The shrub layer consists of *Chusquea* bamboos intermingled with tree ferns (*Cyatheaceae*), and shrubs of *Acanthaceae, Ericaceae, Rubiaceae* and *Solanaceae*. Finally, the herb layer presents terrestrial aroids, ferns and gesneriads and the bryophyte layer covers mainly bare soil or decaying wood.

**SELECTION OF PLOTS.**—Fifty-four 500 m² (20 x 25 m) plots established for vegetation analysis were used for this study. These plots differed in aspect and slope angle, but within a plot these parameters were homogeneous. The main criterion for their selection was the presence of *Chusquea* bamboos, either *Chusquea talamancensis, C. tomentosa* or *C. foliosa*, and the degree of canopy closure. 'Gap', refers to a plot in a large gap of over 500 m² area and with overstory tree cover of less than 10%. 'Closed canopy' (ccan) refers to sites with an old-growth oak canopy cover of more than 60%. Characteristically these forest stands have canopy windows, through which skylight can penetrate in the understory. 'Intermediate' canopy sites (ican) were defined as forest where the overstory was represented by a few scattered large trees (> 50 cm DBH) with a small overall canopy cover, or occupied by medium sized trees (20 < DBH < 50 cm). Thus, an intermediate site could have a canopy of old-growth trees sieved with large canopy windows (small gaps), or be an assemblage of different successional stages after formation of a big gap. In total there were 7 gap, 8 intermediate canopy and 9 closed canopy plots with *C. talamancensis*, and 4, 3 and 10 respectively with *C. tomentosa*. For *Chusquea foliosa* there were 7 gap and 6 intermediate canopy plots; this species was not found under closed canopy in the study area. Data for this study were obtained from 100 m² (10 x 10 m) subplots which were set out in the centre of the 500 m² plots.

**CLUMPS.**—The spatial patterns of the *Chusquea* species in the 100 m² subplots were assessed using following parameters: height of the bamboo understory, number of culms per clump, number of clumps (clump density), circumference at base of the clumps, circumference at 1 m height, and crown breadth along the N-S and W-E axes. Spatial arrangement of clumps
in the 100 m² plots was determined by measuring the x (W-E) and y (S-N) coordinates from the center of each clump to the sides of the plots.

_Clump area_ was calculated from the circumference of a clump at 1 m height; crown area was estimated using the formula for an ellipse (length × width × π). _Site clump area_ (corresponding to the stand area or total area covered by a species in 100 m²) and _site crown area_ (corresponding to the bamboo canopy cover area) were calculated by summing the areas of the clumps in 100 m². In the case of site crown area, there is a systematic error due to crown overlap resulting in higher values than in reality. The _index of clump volume_ (a surrogate for above-ground biomass) was calculated from the formula for a cone: clump base area × height / 3 (clump base area was determined with the circumference at base). _Site index of clump volume_ results from multiplying the mean index of clump volume for each plot with the corresponding clump density in 100 m².

The data were subjected to a two-factor ANOVA (Chusquea species and canopy closure), and post hoc testing of the main effects was performed with Fisher's PLSD multiple comparison test.

CULMS AND BRANCHES.—In order to quantify the morphological performance of _Chusquea talamancensis_ and _C. tomentosa_, culms were considered modules with individual character. Although culms are linked together through the rhizome and culm size depends strongly on the accumulated starch and nutrients in the rhizome (Ueda, 1960), their individuality can be assumed from the fact that they are potential ramets, _i.e._ vegetative units capable to survive independently when fragmented from the mother plant (Urbanska, 1992).

Two clumps of _Chusquea talamancensis_ and two of _C. tomentosa_ were selected randomly under closed canopy and one of each species under gaps. The _number of culms per clump_, _clump circumference at base_ (to calculate the _clump base area_) were determined. Culm vigour was assessed using following criteria: _dead_ (no living tissue), _senescent_ (pale yellow brittle culms, < 30% leaves on branches, sometimes with dead branches), _diseased_ (culm damaged due to grazing, insect attack or fungi rot), _mature_ (lignified green culm in full vigour) or _young_ (green culms, not lignified, culm sheats still attached to the nodes).
On each culm the following morphological parameters were measured: total culm length, clear length (i.e. the distance from the culm base to the first branch), number of culm nodes, culm diameter at base, culm diameter at 1 m, culm diameter at clear length (all diameters were measured at the internode to the nearest 0.1 mm). The following branch parameters were also examined on each culm: number of branches, branch position (number of node on the main stem counted from the base of the culm), branching order (Figure 2), length of each branch and number of nodes. Total branch length was calculated by summing the length of all branches in a culm, and mean branch length by dividing the total branch length by the number of branches. The degree of branching of the primary branches was described by a branching index which was calculated for each primary branch as follows: $\sum (N_x * x) / N$ where $N_x$ is the number of branches of order $x$ and $N$ is the total number of branches.

Two-factor ANOVA and Fisher's PLSD (Chusquea species, canopy closure) were performed using combined data for each site. Young culms
were omitted from the analysis because they had not reached the final culm length and were still unbranched.

Results

CLUMPS.—There is a significant decreasing trend of number of culms per clump and clump area at 1 m (also at base, not presented here) with increasing shade, which is also reflected in the ratio gap:\textit{ican} and gap:\textit{ccan} (Table 1, 2). Regarding differences between species, Chusquea

\textbf{Table 1. Morphological and spatial pattern of Chusquea talamancensis, C. tomentosa and C. foliosa in gap, intermediate canopy (ican) and closed canopy (ccan).}

<table>
<thead>
<tr>
<th>Types of canopy closure</th>
<th>Gap \hspace{1cm} Intermediate canopy (ican) \hspace{1cm} Closed canopy (ccan)</th>
<th>Ratio gap:ican \hspace{1cm} Ratio gap:ccan</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>Mean ± SE (n) \hspace{1cm} Mean ± SE (n) \hspace{1cm} Mean ± SE (n)</td>
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<tr>
<td>N culms/clump</td>
<td></td>
<td></td>
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<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>19.3 ± 3.1 (7) \hspace{1cm} 18.5 ± 3.34 (8) \hspace{1cm} 8.9 ± 1.4 (9)</td>
<td>1.04 \hspace{1cm} 2.16</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>30.5 ± 3.4 (4) \hspace{1cm} 22.7 ± 12.3 (3) \hspace{1cm} 6.5 ± 1.2 (10)</td>
<td>1.34 \hspace{1cm} 4.69</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>31.9 ± 5.0 (7) \hspace{1cm} 17.7 ± 2.1 (6) \hspace{1cm} n.d.</td>
<td>1.80 \hspace{1cm} -</td>
</tr>
<tr>
<td>Clump area at 1 m [m²]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>1.36 ± 0.27 \hspace{1cm} 0.69 ± 0.11 \hspace{1cm} 0.47 ± 0.13</td>
<td>1.97 \hspace{1cm} 2.89</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>3.25 ± 0.58 \hspace{1cm} 2.92 ± 2.29 \hspace{1cm} 0.39 ± 0.11</td>
<td>1.11 \hspace{1cm} 8.33</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>4.16 ± 0.82 \hspace{1cm} 1.40 ± 0.36 \hspace{1cm} n.d.</td>
<td>2.97 \hspace{1cm} -</td>
</tr>
<tr>
<td>Clump crown area [m²]</td>
<td></td>
<td></td>
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<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>52.72 ± 9.24 \hspace{1cm} 39.03 ± 5.65 \hspace{1cm} 21.82 ± 4.23</td>
<td>1.35 \hspace{1cm} 2.42</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>201.95 ± 30.62 \hspace{1cm} 118.93 ± 53.72 \hspace{1cm} 26.85 ± 6.56</td>
<td>1.70 \hspace{1cm} 7.52</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>163.75 ± 31.62 \hspace{1cm} 153.49 ± 36.86 \hspace{1cm} n.d.</td>
<td>1.07 \hspace{1cm} -</td>
</tr>
<tr>
<td>Clump density/100 m²</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>12.6 ± 1.2 \hspace{1cm} 22.0 ± 2.6 \hspace{1cm} 20.3 ± 1.2</td>
<td>0.57 \hspace{1cm} 0.62</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>5.0 ± 0.4 \hspace{1cm} 12.0 ± 4.7 \hspace{1cm} 19.0 ± 2.6</td>
<td>0.42 \hspace{1cm} 0.26</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>5.6 ± 0.6 \hspace{1cm} 9.2 ± 2.3 \hspace{1cm} n.d.</td>
<td>0.61 \hspace{1cm} -</td>
</tr>
<tr>
<td>Site clump area [m²/100 m²]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>17.36 ± 3.96 \hspace{1cm} 13.47 ± 1.29 \hspace{1cm} 9.39 ± 2.42</td>
<td>1.29 \hspace{1cm} 1.85</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>15.87 ± 2.28 \hspace{1cm} 14.10 ± 4.40 \hspace{1cm} 5.53 ± 1.08</td>
<td>1.13 \hspace{1cm} 2.87</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>21.08 ± 3.45 \hspace{1cm} 9.30 ± 1.49 \hspace{1cm} n.d.</td>
<td>2.27 \hspace{1cm} -</td>
</tr>
<tr>
<td>Site index clump volume [m³/100 m²]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>\textit{Chusquea talamancensis}</td>
<td>23.32 ± 6.29 \hspace{1cm} 15.31 ± 1.95 \hspace{1cm} 7.74 ± 2.02</td>
<td>1.52 \hspace{1cm} 3.01</td>
</tr>
<tr>
<td>\textit{Chusquea tomentosa}</td>
<td>24.24 ± 3.52 \hspace{1cm} 21.34 ± 8.20 \hspace{1cm} 7.74 ± 2.18</td>
<td>1.14 \hspace{1cm} 3.13</td>
</tr>
<tr>
<td>\textit{Chusquea foliosa}</td>
<td>43.00 ± 7.19 \hspace{1cm} 14.02 ± 1.94 \hspace{1cm} n.d.</td>
<td>3.07 \hspace{1cm} -</td>
</tr>
</tbody>
</table>

(n)= number of samples=number of 100 m² plots, valid for all parameters.
*Chusquea talamancensis* has in gaps a smaller clump area than *C. tomentosa* and *C. foliosa*. Under intermediate canopy *Chusquea talamancensis* clumps seem still to be smaller than the other two species, but the differences are only significant between *Chusquea talamancensis* and *C. foliosa* (*P* <0.001). Clump crown area is consistently smaller for *Chusquea talamancensis* compared to the other two species in the different canopy closures (*P* <0.001).

The differences between canopy closure types of area related parameters as clump density, site clump area and site index of clump volume are significant (Table 2). As the clump density increases with increasing canopy cover for all species, the site clump area and the site index of clump volume present a reverse situation (Table 1). The relative decline in clump density, as measured by the ratio *gap:ccan* is stronger for *Chusquea tomentosa* than for *C. talamancensis*. On the other hand, the ratio *gap:ican*, is greatest for *Chusquea foliosa*, followed by *C. talamancensis* and *C. tomentosa*. Meanwhile, site clump area and site index of clump volume do not show any significant difference between species. The site index of clump volume shows a very similar ratio *gap:ccan* for *Chusquea talamancensis* and *C. tomentosa* (and in the case

**Table 2. Summary statistics of morphological and spatial pattern in 100 m² for the factors canopy closure (gap, intermediate canopy and closed canopy) and Chusquea species (*C. talamancensis*, *C. tomentosa* and *C. foliosa*). * = *P* ≤ 0.05; ** = *P* ≤ 0.01; *** = *P* ≤ 0.001.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Factor Canopy closure</th>
<th>Chusquea species</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF F-Value</td>
<td>DF F-Value P</td>
<td>DF F-Value P</td>
</tr>
<tr>
<td>N culms/clump</td>
<td>1  5.97 *</td>
<td>1  2.15 -</td>
<td>3  2.34 -</td>
</tr>
<tr>
<td>Clump area at 1 m</td>
<td>1  7.39 **</td>
<td>1  9.27 **</td>
<td>3  3.95 *</td>
</tr>
<tr>
<td>Clump crown area</td>
<td>1  3.60 -</td>
<td>1  18.8 **</td>
<td>3  4.54 **</td>
</tr>
<tr>
<td>Clump density/ 100 m²</td>
<td>1  10.79 **</td>
<td>1  10.51 **</td>
<td>3  2.02 -</td>
</tr>
<tr>
<td>Site clump area/ 100 m²</td>
<td>1  6.31 *</td>
<td>1  0.51 -</td>
<td>3  1.39 -</td>
</tr>
<tr>
<td>Site index clump vol/ 100 m²</td>
<td>1  12.2 **</td>
<td>1  0.4 -</td>
<td>3  3.21 *</td>
</tr>
</tbody>
</table>
Figure 3. Spatial distribution of clumps of Chusquea talamancensis (tal), C. tomentosa (tom) and C. foliosa (fol) in some representative 100 m² plots under gap, intermediate canopy (ican) and closed canopy (ccan). Clumps are numbered. The first inner circle is the clump area at base, the second is the area at 1 m height and the outer circle is the crown area.
of *C. foliosa*, the ratio *gap:canopy*), which means that the total biomass of the three bamboo species varies in a similar way under different conditions of canopy closure.

Diagrams of representative 100 m² plots for different canopy closure types (Figure 3) show the spatial distribution and the size of clumps at base, at 1m height and the size of the clump crown of *Chusquea talamancensis*, *C. tomentosa* and *C. foliosa*. There is a strong negative relationship between plant size and density in a light gradient from gap to closed canopy (Figure 4a, b). Interesting differences were evident between the species, in gaps *Chusquea talamancensis* has a much higher density of smaller individuals than *C. tomentosa* (and *C. foliosa*) though in the closed canopy the mean values of the two species are very similar. *Chusquea foliosa* shows a stronger decline in clump volume from gap to intermediate canopy compared with *C. tomentosa*. The regression equation of density against index of clump volume (log axes) for the data from gap and intermediate canopy (all three species) is: \[ \text{Mean log index of clump volume} = -1.32 \times \text{Mean log density} + 1.60 \] \( r^2 = 0.7 \); \( p < 0.001 \); \( n=34 \). The relationship between number of culms per clump and clump density shows a similar pattern. The data for *Chusquea tomentosa* and *C. foliosa* can be described by the regression: \[ \text{Mean log number of culms/clump} = -0.75 \times \text{Mean log density} + 1.96 \] \( r^2 = 0.68 \); \( p < 0.001 \); \( n=20 \). The data from the closed canopy fell well below the predicted relationship, suggesting that light is a strongly limiting resource at these sites.

**CULMS AND BRANCHES.**—It was shown above that there is an effect of light on the spatial pattern of bamboo plants; there is also an effect on the performance of the individual plant. The analysis of culm structure (Table 3) offers an insight of the vigour of the clumps sampled in February - April 1989: (i) young culms were more likely to be found in open sites, and (ii) the relatively low proportion of mature culms and the high proportion of diseased and senescent culms of *Chusquea talamancensis* compared with *C. tomentosa* indicates the approaching semelparous flowering of this species (Ueda, 1960; Widmer, 1998a).

Interesting differences show up when the culms of *Chusquea talamancensis* and *C. tomentosa* are analysed as single samples (Table 4). The culms of *Chusquea tomentosa* are significantly longer (total length and clear length) than those of *C. talamancensis*, while the number of nodes is
Fig. 4. Relationship between density and the means of index of clump volume (a) and number of culms per clump (b) for Chusquea talamancensis, C. tomentosa and C. foliosa under gap (O), intermediate canopy (ican, ●) and closed canopy (ccan, ○).
Table 3. Characteristics of individual clumps of Chusquea talamancensis and C. tomentosa. For both species one clump was measured in gap and two under closed canopy.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Chusquea species</th>
<th>C. talamancensis</th>
<th>C. tomentosa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>gap</td>
<td>closed canopy</td>
<td>gap</td>
</tr>
<tr>
<td>Clump #</td>
<td>5</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>N tot culms</td>
<td>37</td>
<td>32</td>
<td>30</td>
</tr>
<tr>
<td>N living culms</td>
<td>21</td>
<td>22</td>
<td>17</td>
</tr>
<tr>
<td>Clump base area [m²]&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.44</td>
<td>0.56</td>
<td>0.44</td>
</tr>
<tr>
<td>% Mature culms</td>
<td>13.5</td>
<td>21.9</td>
<td>13.3</td>
</tr>
<tr>
<td>% Young culms</td>
<td>8.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>% Diseased/senescent culms</td>
<td>35.1</td>
<td>46.9</td>
<td>43.3</td>
</tr>
<tr>
<td>% Dead culms</td>
<td>43.2</td>
<td>31.3</td>
<td>43.3</td>
</tr>
</tbody>
</table>

<sup>a</sup> Calculated from measured circumference at base  <sup>b</sup> Culm vigour classes, see text

not significantly different (Table 5). Chusquea tomentosa has generally thicker culms than C. talamancensis but both species have significant larger base diameters in gap than under closed canopy. The ratio culm base diameter:diameter clear length shows that culms of Chusquea tomentosa have an approximately cylindrical form and they do not change depending on the light environment (the ratio is identical for gap and closed canopy = 1.48). The culm growth form of Chusquea talamancensis from the base to the first branch is nearly cylindrical in closed canopy (ratio = 1.35) but more conical in gaps (ratio = 2.02). The ratio culm length:base diameter varies according to canopy closure in a similar proportion, regardless of the bamboo species.

The biggest effects of shade are seen in the branching pattern. The proportion of branched culms (i.e. the degree to which main stems produce branches) is 66% in gaps and 100% in closed canopy for Chusquea tomentosa, and 81% and 85% respectively, for C. talamancensis. The branching pattern of culms (Figure 5) reflects how the plant invests in
Table 4. Morphological characteristics of *Chusquea* talamancensis and *C.* tomentosa culms under gap and under closed canopy.

<table>
<thead>
<tr>
<th>Chusquea species</th>
<th>Canopy closure</th>
<th><em>C.</em> talamancensis</th>
<th><em>C.</em> tomentosa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>gap</td>
<td>closed canopy b</td>
</tr>
<tr>
<td>Parameter</td>
<td>Mean ± SE (n)</td>
<td>Mean ± SE (n)</td>
<td>Mean ± SE (n)</td>
</tr>
<tr>
<td>Culm length [m]</td>
<td>2.29 ± 0.29 (21)</td>
<td>3.10 ± 0.21 (39)</td>
<td>5.06 ± 0.27 (41)</td>
</tr>
<tr>
<td>Total number (N) of nodes</td>
<td>12.5 ± 1.3 (21)</td>
<td>15.3 ± 0.8 (39)</td>
<td>16.9 ± 0.87 (41)</td>
</tr>
<tr>
<td>Clear length [m]</td>
<td>1.77 ± 0.19 (17)</td>
<td>1.69 ± 0.14 (33)</td>
<td>2.75 ± 0.13 (27)</td>
</tr>
<tr>
<td>Culm base diameter [cm]</td>
<td>1.66 ± 0.12 (21)</td>
<td>1.34 ± 0.08 (39)</td>
<td>3.34 ± 0.06 (41)</td>
</tr>
<tr>
<td>Diameter clear length [cm]</td>
<td>0.82 ± 0.08 (15)</td>
<td>0.99 ± 0.06 (34)</td>
<td>2.26 ± 0.08 (28)</td>
</tr>
<tr>
<td>Culm length /base diameter</td>
<td>15.1 ± 1.7 (21)</td>
<td>23.7 ± 1.4 (39)</td>
<td>15.1 ± 0.8 (41)</td>
</tr>
<tr>
<td>Number (N) of branches</td>
<td>4.8 ± 1.2 (17)</td>
<td>3.8 ± 0.5 (34)</td>
<td>2.2 ± 0.3 (27)</td>
</tr>
<tr>
<td>Mean N of primary branches</td>
<td>3.41 ± 0.74 (17)</td>
<td>2.34 ± 0.32 (34)</td>
<td>1.70 ± 0.19 (27)</td>
</tr>
<tr>
<td>N branches /N primary branches</td>
<td>1.51 ± 0.23 (17)</td>
<td>1.73 ± 0.20 (34)</td>
<td>1.39 ± 0.21 (27)</td>
</tr>
<tr>
<td>Total branch length [m]</td>
<td>4.78 ± 1.25 (17)</td>
<td>5.16 ± 0.85 (34)</td>
<td>4.78 ± 0.48 (27)</td>
</tr>
<tr>
<td>Branch length /culm length</td>
<td>1.81 ± 0.34 (17)</td>
<td>1.98 ± 0.33 (34)</td>
<td>1.19 ± 0.18 (27)</td>
</tr>
</tbody>
</table>

---

\( a \) (n) = number of culms  
\( b, c \) data from 2 clumps
further axes to occupy more above-ground space. *Chusquea tomentosa's branching structure seems to be herringbone (or monopodial) in gaps, and dichotomous (or sympodial) under closed canopy (herringbone and dichotomous branching models according to Fitter, 1991). In contrast, *Chusquea talamancensis* seems to develop a herringbone structure for both canopy conditions, with multiple branching at the same node. These observations are supported by the branching magnitudes or number of external links (those terminating in a meristem), which are 2 - 6 for

**Table 5. Summary statistics for the morphological performance of Chusquea talamancensis and *C. tomentosa* culms in gaps and under closed canopy. * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Canopy closure</th>
<th>Chusquea species</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Factor</td>
<td>DF</td>
<td>F-Value</td>
</tr>
<tr>
<td>Culm length</td>
<td></td>
<td>1</td>
<td>0.32</td>
</tr>
<tr>
<td>Total N nodes</td>
<td></td>
<td>1</td>
<td>0.42</td>
</tr>
<tr>
<td>Clear length</td>
<td></td>
<td>1</td>
<td>1.03</td>
</tr>
<tr>
<td>Culm base diameter</td>
<td></td>
<td>1</td>
<td>40.21</td>
</tr>
<tr>
<td>Diameter clear length</td>
<td></td>
<td>1</td>
<td>9.32</td>
</tr>
<tr>
<td>Culm length /base diameter</td>
<td></td>
<td>1</td>
<td>18.85</td>
</tr>
<tr>
<td>N branches</td>
<td></td>
<td>1</td>
<td>13.70</td>
</tr>
<tr>
<td>Mean N primary branches</td>
<td></td>
<td>1</td>
<td>0.80</td>
</tr>
<tr>
<td>N branches /N primary bran.</td>
<td></td>
<td>1</td>
<td>19.81</td>
</tr>
<tr>
<td>Total branch length</td>
<td></td>
<td>1</td>
<td>16.14</td>
</tr>
<tr>
<td>Branch length /culm length</td>
<td></td>
<td>1</td>
<td>10.54</td>
</tr>
<tr>
<td>Mean branch length</td>
<td></td>
<td>1</td>
<td>3.10</td>
</tr>
</tbody>
</table>
**Fig. 5.** Branching pattern of culms of *Chusquea tomentosa* and *C. talamancensis* in gap and under closed canopy.

*Chusquea tomentosa* in gaps and 6 - 36 under closed canopy; 2 - 18 under closed canopy for *Chusquea talamancensis*. In general, culms of *Chusquea talamancensis* develop more primary branches on a culm than *C. tomentosa*, with up to eleven primary branches in gap and eight in closed canopy, while the latter develops in both closure types maximally four primary branches on a culm (Figure 6), but there is no significant difference between gap and closed canopy for both species. The branching index, however, shows that rebranching of primary branches in
**Fig. 6.** Vertical distribution of branches in culms of Chusquea tomentosa and C. talamancensis under closed canopy and in gaps based on the branching index of primary branches. The letters indicate the vertical sequence of primary branches starting with the lowest branch (A).

closed canopy is more accentuated in *Chusquea tomentosa* than *Chusquea talamancensis*. This is confirmed by the ratio number of branches:number of primary branches, which shows significant differences between species and between types of canopy closure. In shady conditions, the proportion of primary branches of *Chusquea tomentosa* is relatively low but rebranching of existing branches reached the 8th order. In contrast, culms of *Chusquea tomentosa* in gaps were branched only to the 2nd order.

Branching on *Chusquea talamancensis* culms on the other hand, proceeded in gap and in closed canopy until the 3rd order. There are significant differences in branch length between species and also a significant interaction, *i.e.* species differ in their response to canopy closure (Table 4, 5). Branch length is almost identical for both species in gap, while under closed canopy *Chusquea tomentosa* has about four times the branch length of *C. talamancensis*. The ratio branch length:culm length shows that the species differ in their allocation to the main axis and secondary axes.
Chusquea talamancensis has almost twice the investment in branch length compared to culm length, regardless of canopy closure. Chusquea tomentosa on the other hand, has relatively the same investment for the culm and for branches in gaps and about six times more in closed canopy. Primary branch length was not significantly different for either species or canopy closure, but the mean branch length is greater for Chusquea tomentosa than C. talamancensis.

Discussion

Studies of the influence of canopy cover on pattern and performance of dominant understory Chusquea species often show divergent and sometimes contradictory results, which are mainly due to differing habitat conditions and thus reflect different life history strategies of the bamboo species studied. Veblen et al. (1977; 1979) studied the influence of tree dominants on the distribution and dominance of Chusquea tenuiflora Phil. in Chile, finding that bamboos were more abundant and taller beneath evergreen trees, apparently because of the less persistent snow cover, compared to mixed sites with deciduous Nothofagus species. Young (1991) found that Chusquea sp. was not a light-gap species in the timberline forest studied in Peru. In the present case, previous field observations in the old-growth forests of the Cordillera de Talamanca showed that there might be differences in habit and size of the same bamboo species, according to whether it grows in presence or absence of a tree canopy.

Various special aspects of this system help to interpret the differences in pattern and performance as direct responses to canopy conditions. These aspects include:

1. The Chusquea species are physically separated clump-forming bamboos and no rhizomatous connections between clumps were observed in any of the species studied.

2. All plants of one species, regardless the size, have approximately the same age, as a consequence of semelparous mass flowering followed by regeneration from seed (Widmer, 1994; 1998a).
(3) The plants were mature and at least two species (*Chusquea talamancensis* and *C. tomentosa*) were shortly before mass flowering, which may indicate that vegetative age was reached to onset reproduction.

(4) In the studied plots only single species of *Chusquea* were the dominant understory bamboos, and consequently, competitive interactions between different *Chusquea* species were not very likely.

(5) Soil chemical analyses of the sites indicate no significant differences associated with canopy closure (Widmer, 1998b).

The discussion will not only treat the effect of canopy closure and the differences between *Chusquea* species, but also self-thinning as an effect of intraspecific competition, and morphological plasticity as an expression of performance.

**EFFECT OF CANOPY CLOSURE.**—The forest canopy has a clear effect on the morphological performance of mature *Chusquea* clumps of all species and thus also upon the spatial distribution of the populations. Clumps of all species tended to be few and large in gaps and numerous and small under closed canopy, the intermediate situations lied in between. In the old-growth forest, as long as the canopy is closed, plant growth is relatively slow because of the low light intensity. After disturbance, e.g. by multiple tree fall, the understory plants respond dramatically both at individual and at population level. Other bamboos, like *Chusquea culeou* (Schlegel, 1991) or *Sasa* species (Kawahara, 1987), were also influenced by the degree of canopy closure, but the morphological responses were variable depending on the species and site conditions. Generally, bamboo species grow more vigorously and biomass is greater in the open than under the forest canopy (Ueda, 1960).

The following comparison of clumps, culms and branches (Table 6) is made between gap and closed canopy of the species *Chusquea talamancensis* and *C. tomentosa*. The results for *Chusquea foliosa* in gaps are similar to *C. tomentosa*, but this species is excluded from comparison because it was not found under closed canopy.

The greater biomass in gaps is shown by the greater number of culms per clump and the diameter of the culms, and is also reflected in the clump area, the clump crown area and the index of clump volume. The results
Table 6. Summary of the relationships of area (100 m²) related parameters and parameters in clumps, culms, branches to canopy closure: gap, closed canopy (ccan) and Chusquea species: Chusquea talamancensis (tal) and C. tomentosa (tom). N.S. = not significant.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Canopy closure</th>
<th>Chusquea species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Area related</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clump density</td>
<td>ccan &gt; gap</td>
<td>tal &gt; tom</td>
</tr>
<tr>
<td>Number of culms</td>
<td>N.S.</td>
<td>tal &gt; tom</td>
</tr>
<tr>
<td>Site clump area</td>
<td>gap &gt; ccan</td>
<td>N.S.</td>
</tr>
<tr>
<td>Site crown area</td>
<td>gap &gt; ccan</td>
<td>N.S.</td>
</tr>
<tr>
<td>Site index of clump volume</td>
<td>gap &gt; ccan</td>
<td>N.S.</td>
</tr>
<tr>
<td><strong>Clumps</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of culms</td>
<td>gap &gt; ccan</td>
<td>N.S.</td>
</tr>
<tr>
<td>Clump area (1 m)</td>
<td>gap &gt; ccan</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Clump crown area</td>
<td>gap &gt; ccan</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Index clump volume</td>
<td>gap &gt; ccan</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td><strong>Culms</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culm length and clear length</td>
<td>N.S.</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Culm diameter</td>
<td>gap &gt; ccan</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Culm length /base diameter</td>
<td>ccan &gt; gap</td>
<td>N.S.</td>
</tr>
<tr>
<td>Number (N) of branches</td>
<td>gap &gt; ccan</td>
<td>interaction</td>
</tr>
<tr>
<td>Mean N of primary branches</td>
<td>N.S.</td>
<td>tal &gt; tom</td>
</tr>
<tr>
<td>N branches /N prim. branches</td>
<td>ccan &gt; gap</td>
<td>interaction</td>
</tr>
<tr>
<td><strong>Branches</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Branch length</td>
<td>ccan &gt; gap</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Mean branch length</td>
<td>N.S.</td>
<td>tom &gt; tal</td>
</tr>
<tr>
<td>Branch length /culm length</td>
<td>ccan &gt; gap</td>
<td>interaction</td>
</tr>
</tbody>
</table>

obtained differ from other works (Watanabe, 1990; Schlegel, 1991), who found an inverse relationship between culm density and culm size. The difference may be because soil nutrients were not limiting in the natural
environment of this study compared to sites with anthropogenic disturbance. Culm length, but also number of nodes per culm, number and length of primary branches and number of branch nodes seem not to be affected by the light regime. The longer branch length and the higher proportion of secondary to primary axes in closed canopy are presumably a result of the phototropic reaction of the bamboos to the canopy windows.

The population parameters of *Chusquea talamancensis* and *C. tomentosa* show that favourable light conditions result in a lower clump density in gaps compared with closed canopy, which implies that there are strong effects of intraspecific competition when the tree canopy is largely open. The effect of intraspecific competition might be reduced if bamboo seedling establishment occurred after gap formation, since bamboo seedling density might be lower in open areas than beneath the forest (Taylor & Qin, 1993). Besides, site clump area, site crown area and the site index of clump volume are greater in gaps for *Chusquea talamancensis* and *C. tomentosa* showing the competitive success of both bamboo species under favourable light conditions.

DIFFERENCES BETWEEN *CHUSQUEA* SPECIES.— There are consistent differences between *Chusquea talamancensis* and *C. tomentosa*, both in morphological performance and in population structure (Table 6). Clumps of *Chusquea talamancensis* and *C. tomentosa* do not differ in the number of culms, but in spatial dimensions such as clump area, clump crown area and index of clump volume. *Chusquea tomentosa* is typically larger than *C. talamancensis*, with longer culm lengths, longer clear lengths and wider culm diameters. But if the allometric relationship culm length/base diameter is compared, it is noticeable that both species have almost identical values in open conditions and very similar ones under closed canopy, which suggests that the growth form of the culms is mainly a response to physical environmental conditions.

All the culms of *Chusquea tomentosa* are branched under closed canopy, while in gaps only 2/3 of the culms bear branches. *Chusquea talamancensis* is more constant, having nearly the same proportion (4/5) of branched culms under closed canopy and in gaps. Even if *Chusquea talamancensis* produces more primary branches than *C. tomentosa*, and the primary branch length is similar for both species, total branch length and mean branch length are greater in the latter. The interaction in the number
of branches shows that the bamboos have different patterns of branching behaviour, depending on the degree of canopy closure. While *Chusquea talamancensis* develops twice as many branches as *C. tomentosa* in gaps, it is *Chusquea tomentosa* which has almost three times more branches in closed canopy than *C. talamancensis*. Species differ also in the culm branching structure. For instance, *Chusquea talamancensis* is similar to the herringbone structure described by Fitter (1991) for root systems, and *C. tomentosa* produces a herringbone structure in gaps, but is dichotomous under closed canopy, indicating a more plastic behaviour.

*Chusquea talamancensis* shows a higher clump density per area, both under closed canopy and in gap than *C. tomentosa*. This species has also a significantly higher number of culms/100 m², on average 260 culms compared to 128 and 153 for *Chusquea tomentosa* and *C. foliosa*, respectively. Although *Chusquea talamancensis* and *C. tomentosa* differ in the size structure of their populations under different canopy closures, there is no difference between the species in the proportion of space occupied with respect to a unit forest area. The total (basal) area occupied by clumps (site clump area), the area covered by the bamboo canopy (site crown area) and the total bamboo biomass (site index of clump volume) per unit area are similar for all species. Thus, there are no differences between the bamboo species with regard to their contribution to the understory vegetation.

DENSITY DEPENDENT RELATIONSHIPS.—Population structure is clearly different under differing degrees of canopy closure. After gap formation, some clumps develop rapidly and dominate the above-ground space, while others remain small or die. This process is called asymmetric competition, where larger plants have competitive advantage over small ones. The present study supports the findings of Weiner (1990), that competition for light is asymmetric. Although models of asymmetric competition predict higher size inequality (Weiner & Thomas, 1986), the design of this study was unsuitable to estimate this parameter.

The relationship between plant size (index of clump volume and number of culms per clump) and density of *Chusquea tomentosa* and *C. foliosa* are very similar in the more open light environment of gap and intermediate canopy. *Chusquea foliosa* showed a stronger decrease in size compared to *C. tomentosa* and *C. talamancensis*, suggesting that this
species is more affected by canopy shade than the other two species. This may explain the fact that it was not found under closed canopy. The spatial pattern of the bamboos in conditions where light is not limiting, gives some evidence for self-thinning or density dependent mortality (De Kroon, 1993). The density and size relationship approximates the \(-3/2\) power rule predicted from theory for populations under intraspecific competition (White, 1985; Begon et al., 1990). This is an interesting and unexpected result since in this case the sites vary not simply in density but also in light availability.

MORPHOLOGICAL PLASTICITY.—Morphological plasticity is a manifestation of phenotypic plasticity that can have adaptive significance (Bradshaw, 1965). Phenotypic plasticity in the bamboos studied occurs at the level of the ramet, \textit{i.e.} at the level of a single culm. The size of new bamboo shoots is determined by the nutrient supply from the rhizomes (Ueda, 1960), which itself depends on the nutrient status of the soil and on the photosynthetic capacity of the leaf canopy. If water and nutrients in the soil are in adequate supply (which is the general case for the pristine high mountain oak forests), then light is probably the limiting factor controlling rate of growth and the production of dry matter (Kershaw & Looney, 1985).

The species studied exhibit a high degree of phenotypic plasticity in response to light conditions. There are large differences in biomass between gap and closed canopy. In bamboos, there is a positive relationship between culm size and rhizome size: larger culms arise from larger rhizomes (Ueda, 1960, Pearson et al., 1994). Therefore, the increased culm diameters and number of culms per clump in gaps are an integration over time of the favourable environmental conditions. Phenotypic plasticity depending upon light availability is found in the culm growth form of \textit{Chusquea talamancensis} in a similar way as in \textit{Dendrocalamus hamiltonii} (Rao et al., 1990) where culms are more conical under favourable light conditions and cylindrical under shade. \textit{Chusquea tomentosa} is nearly cylindrical under both environments. Nevertheless, this bamboo appears to be the most plastic species, showing greater culm diameters, clump area and crown area, and thus overall biomass in gaps. Under closed canopy this bamboo switches allocation from the main axis (the orthotrophic culm) to secondary axes, developing more branches as foraging structures to exploit the favourable light patches. This
morphological response is expected to increase the acquisition of resources from the habitat and thus enhances plant fitness (De Kroon & Hutchings, 1995). Therefore, it is under closed canopy where plastic changes in the branching pattern allowed Chusquea tomentosa to search the environment for patchily distributed resources (see also Hutchings, 1988).

Chusquea talamancensis seems to be the least plastic but also the most shade tolerant of the species studied. The morphological parameters are generally more constant, regardless of canopy closure. Chusquea talamancensis develops more primary branches than C. tomentosa, but the degree of rebranching is the same for gap and closed canopy. In the soil studies presented elsewhere (Widmer, 1998b) it was shown that this species grows in poorer soils than Chusquea tomentosa and C. foliosa.

In summary, this study has shown that to varying degrees the three Chusquea species show a wide ecological amplitude and a high degree of morphological plasticity in response to light. Two of them are capable of growing and producing viable seed in gaps and in shady conditions. One of them shows remarkable variation in clump size and in branching structure according to light conditions. It is interesting to speculate that such ecological adaptability may be a necessary trait in a long-lived forest species with a synchronised semelparous life cycle. Given this type of life cycle, a plant must be capable of maturing and producing seed in whatever light environment it becomes established. There is no opportunity for exploiting seed dormancy as a way of escaping temporarily unfavourable light conditions, as is exhibited in many woodland herbs which only germinate in gaps (Fenner, 1985; Horvitz & Schemske, 1994). Apparently, it is not the clonal spread (as described by Lovett & Lovett, 1982) which characterizes the invasiveness of Chusquea species, but the remarkable morphological plasticity, which enables the plant to optimize the efficiency of light use in its growth. This only applies to pristine forest where nutrient supply is guaranteed through cycling. The performance of these bamboo species in more disturbed sites (eg. after clearcut with consequent soil nutrient loss) needs to be addressed in further studies, since changed environmental factors may lead to different plastic responses.
Acknowledgements

The field work of this research, which is part of the PhD thesis of the author, was funded by the Swiss Development Agency (DEH-EDA) and logistic support was given by the Silviculture of Natural Forests Proyect at the Centro Agronómico Tropical de Investigación y Enseñanza in Costa Rica. Special thanks go to Marvin and Martín Mena Granados for assistance in the field. A. Hegi and P. Wegmann for their help with the figures. The Biotropica reviewers are thanked for their critical and constructive observations. Thanks to my husband P.J. Edwards, who supported me morally and scientifically in the different stages of writing this paper.

References


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CHAPTER 5

Flowering phenology of Chusquea bamboos with special reference to Chusquea talamancensis in Costa Rica

Yvonne Widmer


Abstract

Mass flowering of Chusquea talamancensis Widmer & L.G. Clark, C. tomentosa Widmer & L.G. Clark, and C. subtilis Widmer & L.G. Clark was observed in the Cordillera de Talamanca, Costa Rica from 1987 to 1990. These wind-pollinated bamboos are semelparous after growing vegetatively for at least three decades. There is no seed production when isolated plants flower; seedlings appear only after mass flowering, indicating that reproductive success depends on cross-pollination. The different phenological states are coupled with the seasonal rainfall pattern. Flower formation, fruit formation and germination of seeds occur in the rainy season, whereas pollination, fruit maturation and abscission occur in the dry season. In the montane forests Chusquea talamancensis seeds germinate two years after flowering started when the forest floor is covered with seedlings. In the large population of Chusquea talamancensis, different flowering phases were recognized. Preliminary sporadic flowering was followed by mass flowering in two cohorts on successive years, though some isolated plants remain in vegetative condition and may flower out of phase.

Keywords: bamboo, Chusquea, mass flowering, mast seeding
Introduction

Most woody bambusoid grasses are semelparous, *i.e.* the life cycle of the plant ends with flowering and interfloral periods may extend over 15 - 60 years. Temperate bamboos flower even at intervals of 100 years (Numata, 1974). There are several different evolutionary hypotheses to explain bamboo life cycles, semelparity, and synchronism within the flowering population (Kawamura, 1927; Uchimura, 1980; Campbell, 1985). To date, the most generally accepted hypothesis is the consumer satiation or predator-escape hypothesis where the long interfloral period is interpreted as a response to predation by animals, as a 'mechanism for escape from seed predators through satiation' by means of a high seed production (Janzen, 1976; 1985).

Campbell (1985) summarizes the life-cycles of bamboos as follows: (a) continual or seasonal yearly flowering, without mortality; (b) sporadic flowering at irregular intervals, generally with some recovery of the clone or in other cases with complete mortality; (c) periodic mass flowering at approximately regular intervals, generally with mortality, in some cases with partial survival of the weakened rhizomes. Still, the understanding of the life-cycles of bamboos is not conclusive, not only because of the time factor, but because the records for one species are mostly fragmentary and geographically dispersed, and herbarium specimens often lack information about the extent and the phenological stage of the flowering process. When records of bamboo flowering are compiled, there is rarely any distinction made between bamboo growing in its natural environment and bamboo growing in areas with significant human impact or in cultivation. Data on bamboos at anthropogenically disturbed sites, following logging, burning, and grazing, as well as cultivated bamboos (usually obtained from vegetative propagation) provide only a partial understanding of the flowering process because of their uncertain history and often unknown provenance. Management practices can change the intrinsic characteristics of bamboos (*e.g.* the periodicity of flowering). For example, Liao (1990) found that *Phyllostachys pubescens* which has been intensively propagated vegetatively rarely flowers because the long-term vegetative growth is continued, and further, that a flowered stand often recovers vegetatively if it is artificially watered and fertilized. Observations on a native bamboo species that is established in a natural community may facilitate the interpretation of the flowering and seeding process. McClure (1966) refers
to this point indirectly: 'abundant yields occur only in a few species out of hundreds observed in flower; and these are principally bamboos not under cultivation'.

The aim of this study is to offer information on the flowering and seeding process of some *Chusquea* species which grow naturally as understory in the oak forests of the Cordillera de Talamanca. The research on *Chusquea* bamboos in Costa Rica was initiated in 1985 by the CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) project 'Silviculture of Natural Forests'. This project is working on a sustainable management plan of the montane forests and was therefore interested in the study of the ecology of the *Chusquea* bamboos. Unexpectedly, during the investigation between 1987 and 1990, flowering of several *Chusquea* species was spreading gradually across the study area. In total, six *Chusquea* species showed mass flowering in the Cordillera de Talamanca (Widmer, 1994). The present paper deals with three species described by Widmer & Clark (1991): *Chusquea talamancensis*, *C. tomentosa* and *C. subtilis*. It was a rare and unexpected opportunity to observe bamboo mass-flowering over an area of almost 30 km$^2$ of largely undisturbed forest.

**Study site**

The observations on flowering phenology of the three *Chusquea* species were carried out on the Atlantic side of the Cordillera de Talamanca in the area of Cerro Asunción, La Georgina, Cerro Abarca, Villa Mills, and Cerros Cuercicí, Province of Cartago (Figure 1). The area is part of the Costa Rican System of National Parks and Forest Reserves and is predominantly covered by old-growth forest with *Quercus* species dominating. The understory *Chusquea* species in this mountainous region are woody, clump-forming bamboos with pachymorph (sympodial) rhizomes. *Chusquea talamancensis* and *C. tomentosa* are the most widely distributed species at altitudes from 2600 to 3100 m asl. *Chusquea subtilis* is more patchily distributed and confined to more humid sites near streams at altitudes from 2500 to 2800 m asl (Widmer, 1994).

Mean annual rainfall at Villa Mills weather station is 2610 mm (Figure 2). The dry months are January to March when mean monthly rainfall ranges from 20 - 35 mm. Most rain falls between May and
Fig. 1. The area of phenological observations in the Cordillera de Talamanca, Costa Rica. (Topographic map reproduced with the permission of the Instituto Geográfico Nacional, San José, Costa Rica; November 3, 1992). Dots: ecological CATIE plots; squares: silvicultural CATIE plots.
November, mean monthly rainfall between 250 - 470 mm. From 1987 to 1989 mean annual air temperature was 8.2 °C, with mean daily temperature variation of 9.4 - 10.3 °C in the dry season and 7.5 - 8.5 °C in the rainy season. Mean maximum temperatures reached up to 14.4 °C in April and minimum temperatures down to 3.1 °C in January (data from the Instituto Costaricense de Electricidad).

**Fig. 2.** Climate diagram of Villa Mills (Costa Rica) showing the seasonal rainfall regime. Adapted from Blaser (1987).

**Materials and methods**

The inflorescences of randomly selected plants were monitored to observe the phenological sequence. The spikelets (Figure 3) were collected and opened to determine the phenological state. Voucher specimens (Table 1) were made and classified as incipient flower, immature flower, mature flower, incipient fruit, immature fruit, mature fruit, and empty (vain) flowers.

Quantitative data on the flowering of Chusquea talamancensis, C. tomentosa, and C. subtilis were gained from a survey made from CATIE plots between October - November, 1989. The plots were situated between
**Fig. 3.** Chusquea talamancensis. A. Spikelet (1120); B. Caryopsis; C1,2. Anterior (1) and posterior (2) view of a caryopsis without lemmas and palea (1112). Chusquea tomentosa. D. Spikelet; E. Open flower (1053). Ant: anthers, E: embryo, Fl: fertile lemma, Fu: Furrow, Gl: glume I, GlII: glume II, Pal: palea, Rac: rachilla, Rad: radicle, SII: sterile lemma I, SIII: sterile lemma II, Stc: stylar column, Sti: stigma.
Table 1. List of voucher specimens of *Chusquea* species.

<table>
<thead>
<tr>
<th>Voucher</th>
<th>Date</th>
<th>Site</th>
<th>Altitude (m asl)</th>
<th>Phenological state</th>
<th>Herbarium</th>
</tr>
</thead>
<tbody>
<tr>
<td>1099</td>
<td>24.10.87</td>
<td>Cerro Asunción (1 km N CIA)</td>
<td>3000</td>
<td>immature flower</td>
<td>CR/HZH(2)</td>
</tr>
<tr>
<td>520</td>
<td>10.08.88</td>
<td>Cerros Cuercí (Plot 533)</td>
<td>3010</td>
<td>vain flower</td>
<td>CR/CATIE-SBN/HZH(3)</td>
</tr>
<tr>
<td>521</td>
<td>11.08.88</td>
<td>Cerros Cuercí (Plot 415)</td>
<td>2980</td>
<td>vain flower</td>
<td>CR/HZH(5)</td>
</tr>
<tr>
<td>559</td>
<td>09.12.88</td>
<td>Villa Mills (&quot;El Sitio&quot;)</td>
<td>2600</td>
<td>immature flower</td>
<td>HZH</td>
</tr>
<tr>
<td>523</td>
<td>25.10.89</td>
<td>Villa Mills (Plot Area CATIE)</td>
<td>2700</td>
<td>incipient flower</td>
<td>CR/HZH(2)</td>
</tr>
<tr>
<td>518</td>
<td>26.10.89</td>
<td>Cerro Abarca (Plot Faja CATIE)</td>
<td>2980</td>
<td>incipient flower</td>
<td>CR/HZH(2)</td>
</tr>
<tr>
<td>522</td>
<td>26.10.89</td>
<td>on the track to Cerro Abarca</td>
<td>2800</td>
<td>immature fruit</td>
<td>CATIE-SBN/CR/HZH</td>
</tr>
<tr>
<td>1134</td>
<td>09.11.89</td>
<td>Cerros Cuercí (Plot AN3 CATIE)</td>
<td>2830</td>
<td>incipient flower</td>
<td>HZH</td>
</tr>
<tr>
<td>1136</td>
<td>09.11.89</td>
<td>Cerros Cuercí (Plot Puma CATIE)</td>
<td>2830</td>
<td>immature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1138</td>
<td>09.11.89</td>
<td>Cerros Cuercí (Plot Puma CATIE)</td>
<td>2830</td>
<td>immature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1140</td>
<td>15.11.89</td>
<td>Villa Mills (Plot PlacIII CATIE)</td>
<td>2720</td>
<td>immature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1120</td>
<td>07.03.90</td>
<td>Cerros Cuercí (Plot 431)</td>
<td>3000</td>
<td>mature flower</td>
<td>HZH</td>
</tr>
<tr>
<td>1112</td>
<td>07.03.90</td>
<td>Cerros Cuercí (Plot 512)</td>
<td>2990</td>
<td>mature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1113</td>
<td>07.03.90</td>
<td>Cerros Cuercí (Plot 536)</td>
<td>3060</td>
<td>mature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1110</td>
<td>08.03.90</td>
<td>Cerros Cuercí (Plot 411)</td>
<td>2970</td>
<td>mature flower</td>
<td>HZH</td>
</tr>
<tr>
<td>1111</td>
<td>08.03.90</td>
<td>Cerros Cuercí (Plot 4114)</td>
<td>2980</td>
<td>mature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1131</td>
<td>09.02.90</td>
<td>Cerros Cuercí (Plot 425)</td>
<td>2900</td>
<td>mature fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>524</td>
<td>23.03.90</td>
<td>La Georgina (1 km SW CIA)</td>
<td>3100</td>
<td>vegetative</td>
<td>CR/CATIE-SBN/HZH(3)</td>
</tr>
<tr>
<td>550</td>
<td>03.06.90</td>
<td>on the track to Cerros Cuercí</td>
<td>3000</td>
<td>vegetative</td>
<td>CATIE-SBN/HZH(4)</td>
</tr>
<tr>
<td>1107</td>
<td>11.12.90</td>
<td>on the track to Cerros Cuercí</td>
<td>3000</td>
<td>seedlings</td>
<td>HZH</td>
</tr>
<tr>
<td>1108</td>
<td>11.12.91</td>
<td>on the track to Cerros Cuercí</td>
<td>3000</td>
<td>seedlings</td>
<td>HZH</td>
</tr>
<tr>
<td>1020</td>
<td>04.05.89</td>
<td>by the road to Cerros Cuercí</td>
<td>2850</td>
<td>vain flowers</td>
<td>CR(2)/HZH(6)</td>
</tr>
<tr>
<td>500</td>
<td>19.08.89</td>
<td>Villa Mills (quebrada Voltea)</td>
<td>2680</td>
<td>incipient flower</td>
<td>ISC/CR/HZH(3)</td>
</tr>
<tr>
<td>501</td>
<td>10.11.89</td>
<td>Villa Mills (Plot Area CATIE)</td>
<td>2700</td>
<td>mature flower</td>
<td>ISC/CR/HZH(2)</td>
</tr>
<tr>
<td>502</td>
<td>15.11.89</td>
<td>Cerros Cuercí (Plot AN2 CATIE)</td>
<td>2710</td>
<td>immature fruit</td>
<td>ISC/CR/HZH</td>
</tr>
<tr>
<td>1050</td>
<td>09.12.89</td>
<td>Cerros Cuercí (Plot Puma CATIE)</td>
<td>2800</td>
<td>mature flower</td>
<td>CR/HZH(3)</td>
</tr>
<tr>
<td>1053</td>
<td>11.12.89</td>
<td>on the track to Cerros Cuercí</td>
<td>3000</td>
<td>mature fruit (anthesis)</td>
<td>CR/HZH</td>
</tr>
<tr>
<td>1027</td>
<td>06.03.90</td>
<td>Cerro Abarca (Plot 621)</td>
<td>2800</td>
<td>incipient fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1033</td>
<td>07.03.90</td>
<td>Cerros Cuercí (Plot 513)</td>
<td>3020</td>
<td>incipient fruit</td>
<td>HZH</td>
</tr>
<tr>
<td>1023</td>
<td>07.03.90</td>
<td>Cerros Cuercí (Plot 513)</td>
<td>3010</td>
<td>vegetative</td>
<td>HZH</td>
</tr>
<tr>
<td>527</td>
<td>09.12.88</td>
<td>Villa Mills (Plot Area CATIE)</td>
<td>2700</td>
<td>immature flower</td>
<td>CATIE-SBN/HZH/CR</td>
</tr>
<tr>
<td>508</td>
<td>09.12.88</td>
<td>Villa Mills (&quot;El Sitio&quot;)</td>
<td>2580</td>
<td>mature flower</td>
<td>ISC/CR/CATIE-SBN/HZH(4)</td>
</tr>
<tr>
<td>993</td>
<td>15.11.89</td>
<td>Cerros Cuercí (Plot 515)</td>
<td>3010</td>
<td>mature flower</td>
<td>HZH</td>
</tr>
<tr>
<td>514</td>
<td>15.11.89</td>
<td>Villa Mills (&quot;El Sitio&quot;)</td>
<td>2580</td>
<td>mature fruit</td>
<td>ISC/CR/CATIE-SBN/HZH</td>
</tr>
<tr>
<td>994</td>
<td>15.11.89</td>
<td>Villa Mills (&quot;El Sitio&quot;)</td>
<td>2580</td>
<td>seedlings</td>
<td>HZH</td>
</tr>
</tbody>
</table>

* There are two kinds of plots: 1) those of the Silviculture of Natural Forests Project with the abbreviation CATIE (Centro Agronómico Tropical de Investigación y Enseñanza, and 2) those from the author's ecological study (eg. 533).

CIA: Carretera Interamericana (Panamerican Highway)

Cerro Abarca and Cerro Cuericí at altitudes from 2650 to 2830 m asl. They included 21 randomly-placed plots and, in addition, a grid of nine 1-ha plots (Figure 1, dots and squares, respectively). Bamboo clumps were counted along a 4 x 100 m band on the center line of the plot. The phenological state of each clump was determined on the basis of the spikelet (Table 2) and voucher specimens were collected. In March 1990 an extensive survey was carried out in the fifty-three 100 m² plots of the author's ecological study using the same methods described above.

Table 2. Differential characteristics of flowers and fruits in Chusquea talamancensis, C. tomentosa, and C. subtilis used for phenological classification in the field.

<table>
<thead>
<tr>
<th>Chusquea species &amp; phenological state</th>
<th>Glume</th>
<th>Sterile lemma</th>
<th>Fertile lemma</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. talamancensis</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>flower</td>
<td>violet (green)</td>
<td>violet (green)</td>
<td>green</td>
</tr>
<tr>
<td>fruit</td>
<td>dry</td>
<td>dry</td>
<td>green</td>
</tr>
<tr>
<td><strong>C. tomentosa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>flower</td>
<td>dry (violet)</td>
<td>violet</td>
<td>green</td>
</tr>
<tr>
<td>fruit</td>
<td>dry</td>
<td>dry</td>
<td>green</td>
</tr>
<tr>
<td><strong>C. subtilis</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>flower</td>
<td>green</td>
<td>green</td>
<td>green</td>
</tr>
<tr>
<td>fruit</td>
<td>dry</td>
<td>dry</td>
<td>green</td>
</tr>
</tbody>
</table>

To estimate seed production, 100 panicles were collected in March 1990 from two clumps of Chusquea talamancensis in La Georgina and in Cerros Cuericí, respectively. The panicles were dried for 3 days, then shaken and scrubbed. Seeds were separated through water immersion for 24 hours; the viable seeds sank (while the non-viable seeds floated), and their wet and dry weight were determined.

Viability of the seeds of Chusquea talamancensis was further tested in vivo and in vitro at the CATIE facilities. Seeds collected in January 1990, were kept in a cool chamber intended for seed collections. Some seeds were sown in February 1990 on a germination bed with sand under warm (22°C) humid greenhouse conditions. In April 1990, other seeds were put in an agar medium with nutrients and kept at 15 °C.
Results

The flowering sequence of *Chusquea talamancensis*, *C. tomentosa* and *C. subtilis* is represented in Table 3. Isolated clumps of *Chusquea talamancensis* (Figure 4, 5) began to flower at the end of 1987 in the area Cerro Asunción and Cerro Cuericí. These plants died gradually without producing any seed. In October 1988, larger patches of this bamboo species flowered in the area of Cerro Asunción, La Georgina, Villa Mills and Cerro Cuericí. Flower development took 3 months, anthesis occurred in the following dry season (March 1989), and fruit formation took about a year. Mature seeds were found in the dry season of 1990. At the beginning of the month of June 1990, the panicles were almost fruitless; fruit set had already occurred, but no seedlings were located. Seedlings up to 5 cm tall were observed in July 1990, when the rains started. After flowering, the parent plants dried out and died.

The seeds sown under warm (22°C) greenhouse conditions germinated in April, 1990 (Figure 5C), three months earlier than under natural conditions in the forest (mean temperature of 11.9 °C, Blaser 1987), and the seeds sown in vitro germinated at the same time as in the forest.

About 43.5% of the population of *Chusquea talamancensis* initiated flowering a year later, in October 1989. These clumps followed a similar flowering schedule as the plants that flowered a year earlier. In December, 1991, the forest floor was covered with seedlings and one-year-old plantlets. Meanwhile, the whole parent population was in the process of senescence, except for a few isolated clumps which remained in vegetative condition; it is not known whether they flowered after 1991.

Six hundred and seven clumps of flowering *Chusquea talamancensis* were surveyed at the end of 1989 over an area of 1.2 ha. Half of them had inflorescences, half had infructescences (Table 4a). The survey carried out in March 1990 in the author’s ecological plots resulted in a similar finding; out of a total of 447 clumps of *Chusquea talamancensis*, 0.7% began to flower in 1987, 55.7% in 1988, and 43.6% in 1989 (Table 4b).

The phenological state of the caryopses was determined from 14 voucher specimens of *Chusquea talamancensis* sampled in March 1990. From a total of 140 caryopses, 25% were mature, while the majority (46%)
Table 3. Phenological table with the flowering sequence of Chusquea talamancensis, C. tomentosa and C. subtilis in the area of Cerro Asunción to Cerros Cueticí from 1987 to 1992.

<table>
<thead>
<tr>
<th>Chusquea</th>
<th>Season Event</th>
<th>%</th>
<th>Year</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
<th>Months</th>
</tr>
</thead>
</table>

**LEGEND**

- Flower formation = leafy branches with terminal inflorescence
- Anthesis / leaffall and yellowing of culms
- Fruit formation / senescence of mother plant
- Fruit maturation and fruitfall / death of mother plant
- Germination => seedlings (new generation)
- Degradation and death of plants / without seeds
- No information
- Estimation
Fig. 4. Chusquea talamancensis. Panicles A. with incipient flowers, B. with open flowers, C. with fruits on a senescent plant.
Fig. 5. Chusquea talamancensis. A. Forest understory with plants in the phase of fruit fall and senescence. B. Seedlings on the forest floor (Photo: M. Kappelle). C. Seedlings in a germination bed in the greenhouse at CATIE.
were immature, and 29% were empty. The total seed production was estimated to be 3 - 4 kg/clump of bamboo.

There was a remarkable synchronism in the phenological sequence, even at distant locations such as Cerro Chirripó. M. Kappelle sampled specimens in anthesis in January 1989, in April 1989 the collected sample showed immature fruits. The event took place not only in the Eastern Cordillera de Talamanca (Atlantic side), but also on the Western (Pacific) side. H. van Velten sampled specimens at the valley of the Río Savegre that had incipient fruits in 1989.

*Chusquea tomentosa* (Figure 6) showed a pattern of flowering in the area of Cerro Abarca-Cerro Cuercí similar to that of *C. talamancensis*: in the first year isolated clumps flowered without producing seeds; a year later mass flowering was observed throughout the whole area. Sporadic flowering started in 1989, a year later than *Chusquea talamancensis*, but the flowering sequence took place earlier in the year (Table 3). The incipient flowers appeared in August, anthesis occurred in December 1989, and incipient fruits were already present in March 1990. The flowering survey at the end of 1989 showed that 5% out of a total of 904 clumps of *Chusquea tomentosa* were flowering.

In the author's ecological plots, 8% of *Chusquea tomentosa* clumps were in flower in March 1990, while in December, 1991, almost all plants were flowering. Seedlings were observed in the study area in 1992 (G. Sáenz, pers. comm.). In the greenhouse in Switzerland, two plants of *Chusquea tomentosa* also flowered in 1991 and in 1992 respectively, but produced no seed and died thereafter.

*Chusquea subtilis* is less widely distributed in the study area than *C. talamancensis* and *C. tomentosa* and its phenology was not studied in detail. In December, 1988, however, clumps at Villa Mills bore immature flowers in the primary forest and mature flowers in an open site (Table 3). In November 1989, the plants in the forest still had immature fruits whereas those in the open site already bore mature fruits, and seedlings were found beneath the senescent, almost leafless parent plants. The survey made in the forest in November 1989 showed that *Chusquea subtilis* had 80% of the clumps bearing fruits.
Table 4. a) Phenological states of clumps of Chusquea talamancensis, C. tomentosa and C. subtilis in October/November 1989 (data from CATIE plots); b) Proportion of flowering plants in a temporal sequence from 1987 to 1989 (data from plots of the author's ecological study).

### a) Phenological states of clumps of Chusquea species

<table>
<thead>
<tr>
<th>Phenological state</th>
<th>Chusquea species</th>
<th>C. talamancensis</th>
<th>%</th>
<th>N clumps</th>
<th>C. tomentosa</th>
<th>%</th>
<th>N clumps</th>
<th>C. subtilis</th>
<th>%</th>
<th>N clumps</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetative</td>
<td>C. talamancensis</td>
<td>13</td>
<td>2</td>
<td>858</td>
<td>95</td>
<td>1</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flower (1)</td>
<td></td>
<td>297</td>
<td>49</td>
<td>46</td>
<td>5</td>
<td>1</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruit (2)</td>
<td></td>
<td>297</td>
<td>49</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total clumps</td>
<td></td>
<td>607</td>
<td>100</td>
<td>904</td>
<td>100</td>
<td>10</td>
<td>100</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Total clumps 1 or 2</td>
<td></td>
<td>594</td>
<td>98</td>
<td>46</td>
<td>5</td>
<td>9</td>
<td>90</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### b) Proportion of flowering plants

<table>
<thead>
<tr>
<th>Flowering year</th>
<th>Chusquea species</th>
<th>C. talamancensis</th>
<th>%</th>
<th>N clumps</th>
<th>C. tomentosa</th>
<th>%</th>
<th>N clumps</th>
</tr>
</thead>
<tbody>
<tr>
<td>1987</td>
<td></td>
<td>3</td>
<td>0.7</td>
<td>0</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>1988</td>
<td></td>
<td>249</td>
<td>55.7</td>
<td>0</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td>195</td>
<td>43.6</td>
<td>19</td>
<td>8.0</td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>Total clumps</td>
<td></td>
<td>447</td>
<td>100</td>
<td>246</td>
<td>100</td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>Total clumps 1 or 2</td>
<td></td>
<td>447</td>
<td>100</td>
<td>19</td>
<td>8</td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>
**Fig. 6.** Chusquea tomentosa. A. *Culm complement, panicles with incipient flowers* (500). B. *Culm complement, panicles with mature flowers* (502). C. *Flowering plant in Switzerland.*
Discussion

FLOWERING CYCLE.—The flowering cycle of semelparous *Chusquea* species is equivalent to its entire life cycle (Figure 7). The zygote develops into a mature caryopsis within a year while still attached to the mother plant. After abscission and a brief dormancy period, the seed germinates with the first rains. The 'seedling' refers to the stage of development following germination until acquiring the full complement of vegetative structures (McClure, 1966). A seedling lives for less than a month on the endosperm reserves and increases its assimilating surface with rapid leaf development. After the establishment of a rhizome axis, a bamboo plant enters the juvenile phase as it acquires a bushy habit and also lignified culms, larger leaves and further rhizome development (McClure, 1966). In these bamboo species, there is seasonality in the sprouting of new culms. In the rainy season and under favourable growth conditions (enough light and nutrients, no grazing), culm diameter and rhizome branch diameter increase annually. In an optimal environment, early development of the plants is nearly exponential (Gadgil & Prasad, 1984). Development slows down as the clump approaches maturity. After mass flowering it may take about 10 years for the clump to produce culms of the same diameter as they were before flowering in some Japanese species (Ueda, 1960). McClure (1966) calculated 3 - 20 years as the time needed for the plant to attain mature stature, depending on genetic constitution and the nature of its environment. According to Campbell (1985) a period of 15 - 20 years may be necessary for the clump biomass to recover completely.

The vegetative phase of *Chusquea talamancensis* and probably other *Chusquea* species in the Cordillera de Talamanca is estimated to be 30 - 35 years, based on data on culm size before flowering (Widmer, 1998) and from observations by local people. A flowering period of 31 to 33 years was reported four times for *Chusquea abietifolia* Griseb. in the Blue Mountains of Jamaica. Seifriz (1950) described mass flowering in 1884 - 1885, 1918 - 1919, and 1948 - 1949, and K. Amman (pers. comm, 1993) observed flowering in 1981. This interval is similar to the majority of bamboos which show a periodicity of between 30 and 35 years (Liese, 1985).
**Fig. 7. Life cycle of Chusquea as represented by C. talamancensis based upon phenological observations. Adapted from Harper (1977).** *assumptions*
The generative phase begins with flower initiation and finishes with fruit fall, senescence, and death. Panicles are formed terminally on the subsidiary branches of a culm and are morphologically axillary to the main axis of the plant (Clark, 1989). At flower initiation the mother plant is still fairly vital, probably because the flower generally has a lower priority than the fruit in attracting assimilates (Ho, 1992). After fertilization the mother plant undergoes leaf loss (about 50% of the leaves are shed) and the culms and branches become yellowish while the plant allocates vital energy resources to seed production. Assimilates are continually translocated to the fruits, which become irreversible storage sinks in terms of assimilate partitioning (Goldwin, 1992; Ho, 1992). The process of culm decay is hastened by increased insect (borers) and fungal attack on the parent plant, as observed on Asiatic bamboo species (Numata, 1970). At fruit formation, vegetative growth has ceased completely and the parent plants gradually dry out. The culms crack easily and the plant has about 5 - 10% of its foliage left. Prior to fruit abscission the only visible green part of the mother plant is the pedicel, linking the caryopsis to the rachis of the panicle.

SEASONALITY OF REPRODUCTION BY SEED.—Seasonality is not only observed in the vegetative development of a Chusquea bamboo in the montane oak forests, but also in the process of flowering. The flowering pattern of a single plant of Chusquea talamancensis follows the seasonal rainfall pattern. A single plant or a clump is defined as either a sexually derived individual, i.e. a genet, or a disconnected ramet resulting from self cloning (sensu Urbanska, 1992).

The diminished culm production or the reduced diameter of new culms in the preceding rainy season are signals for future flowering of a bamboo plant. This has also been observed in Asiatic bamboo species (Deogun, 1937; Ueda, 1960). Flower initiation begins in the late rainy season (October) and the spikelets develop until the beginning of the next dry season (December). The culms of a clump do not always flower in synchrony, some plants have culms in two different phenological states. Flower formation lasts for about three months until the flower has developed the generative parts. Flowers are hermaphroditic and monomorph; dichogamy was not observed. As another example, flowers of Ochlandra travancorica (Bedd.) are hemaphroditic and typically dichogamous and protogynous (Venkatesh, 1984). Anthesis occurs
simultaneously in all flowering clumps during the dry season (January-February). Fertilization takes place within a very short time and incipient fruits are soon found in the spikelets. Fruit formation lasts for about a year until the fruits reach maturity, which is a long time compared to other bamboo species. The low temperature and the daily short time of direct radiation in the montane cloud forests may be the principal factors that limit physiological processes such as assimilation, respiration, or, in the case of flowering, translocation of nutrients from the mother plant to the fruits. Fruit maturation is attained in the dry season. A desiccated fully mature grain of *Chusquea talamancensis* is built with a resistant seed coat as wheat and barley grains. The caryopsis has the appearance of a rice grain with a furrow which runs along the ventral side and the embryo is at the base of the caryopsis on the opposite dorsal side (Figure 3C). Germination takes place with the beginning of the rainy season; the onset of rain may be the dormancy-breaking mechanism. Dormancy may be enforced because the seeds collected in January in the forest and sown under warm and humid greenhouse conditions germinated three months earlier than in the forest. Besides, the seeds sown under cooler climate chamber conditions germinated almost simultaneously with those in the forest. In the oak forests of the Cordillera de Talamanca *Chusquea talamancensis* needs two years from the initiation of flowering until the seeds germinate and the forest floor is covered with seedlings. Similar observations were made by Tong-Wei (1985) in China with the montane species *Fargesia nitida* (Mitford) Keng.

**PREDATION AND SEED DISPERSAL.**—Predation by insect larvae occurs in the spikelets of *Chusquea talamancensis* and *C. tomentosa* while the flowers are formed. The larvae grow to the size of the palea, feed on the reproductive organs and develop to a pupa. The adult insects found in the spikelets of herbarium specimens are likely to belong to a phytophagous group of the parasitoid genus *Aprostocetus* (Chalcidoidea: Tetrastichinae) (J. LaSalle, Natural History Museum, London, 1994).

At the time of fruit maturation and fruit fall, the bamboos were actively visited by birds. Apart from parrots, the nomadic species *Acantidops bairdii* (Emberizidae), endemic to Costa Rica, increased its population while feeding on *Chusquea* seeds (J. Sánchez, Museo Nacional de Costa Rica, 1990). The rodent population must also have increased, as it has been observed for other bamboo species (Janzen, 1976).
Birds and rodents may also be passive dispersal agents when caryopses that have been eaten are not digested but pass to feces. In addition, spikelets are externally scabrous and adhesive and bear an awn on the fertile and sterile lemmas (Figure 3), which enables the fruit to attach to the fur or plumage of animals and may thus be dispersed over a potentially large area ('armed seeds', Radosevich & Holt, 1984).

FLOWERING AT POPULATION LEVEL.—Depending on the population size and its genetic diversity, the time of flowering at population level extends over more than 3 years. Mass flowering of other bamboo species has been described as beginning at one site and then extending over the whole area within a period of 2 - 4 years (Seifriz, 1920; Deogun, 1937; Dwiwedi, 1988).

There is a temporal sequence of flowering at the population level in *Chusquea talamancensis* where groups of plants flower in successive years. These cohorts have different sizes and are patchily distributed over the whole area. According to Troup (1921 in Huberman, 1959), flowering follows a sequence of at least three phases at the population level: preliminary sporadic flowering, mass flowering, and final sporadic flowering. Filgueiras and Pereira (1988) observed in flowering populations of *Actinocladum verticillatum* (Nees) McClure ex Soderstrom that in the first year a few clumps flowered erratically, and in the second year most of the population flowered while some clumps remained sterile. The present work suggests that the flowering in *Chusquea talamancensis* includes four phases. In the first year, some isolated plants flower but bear no seed, then two mass-flowering cohorts flower in subsequent years (each about 49% of the population) with profuse seed production, and at last a few isolated plants remain in vegetative condition or may flower out of phase.

Mass flowering of *Chusquea tomentosa* seems to follow the same pattern. At least three phases can be distinguished: 1) isolated plants flowering in the first year without progeny, 2) a cohort comprising 5 - 8% of the population, and 3) a mass flowering cohort. It must be said that the area studied by the author corresponds to the uppermost limit of distribution for this bamboo. *Chusquea tomentosa* populations at lower elevations (La Esperanza del Guarco, Trinidad de Dota) were already in full flower when the event was just starting at higher elevations (Cuerici),
indicating that the flowering time may also be dependent on the local environmental conditions (Widmer, 1994).

*Chusquea subtilis* shows three cohorts, the largest one consists of plants with mass flowering, whereas two smaller ones form flowers before and after the mass flowering cohort. In this bamboo species it was observed that the rate and duration of fruit growth and maturation are affected by the prevailing environmental conditions as described by Duffus (1992), being shorter in open areas.

Seedlings of all the *Chusquea* species studied here were only observed after mass flowering, suggesting that reproductive success depends on cross-pollination. Neither the isolated or sporadic flowering clumps in the forest, nor the transplanted ones in the greenhouse (which flowered in successive years), produced seeds. The reproductive mechanism is probably species-specific, since self-compatibility was shown for other bamboo species such as *Sasa nipponica* and *S. senanensis* (Nishiwaki & Konno, 1990) and *Ochlandra travancorica* (Venkatesh, 1984). Nevertheless it is obvious, that the genetic variability of a population can only be maintained through outbreeding, and the best opportunity for the *Chusquea* species of the Cordillera de Talamanca is when mass flowering occurs.

**Acknowledgements**

I would like to dedicate this paper to my mentor, the late C.U. Kramer. The author gratefully acknowledges the comments and corrections made by P.J. Edwards, K.M. Urbanska and D. Storz. Many thanks to an anonymous reviewer for his valuable suggestions, and thorough analysis of the manuscript. Martín Mena Granados from Villa Mills is thanked for his help in the field. Logistic support was given by the Silviculture of Natural Forests Project at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Costa Rica; funding of the field work was provided by the Swiss Development Agency (PhD grant DEH-EDA).
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CHAPTER 6

Distribution and flowering of six *Chusquea* bamboos in
the Cordillera de Talamanca, Costa Rica

_Yvonne Widmer_

*Brenesia* (1994) 41-42: 45-57

Abstract

The most abundant species of *Chusquea* bamboos in the Cordillera de
Talamanca (*C. longifolia* Swallen, *C. patens* L.G. Clark, *C. foliosa* L.G.
Clark, *C. subtilis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G.
Clark and *C. talamancensis* Widmer & L.G. Clark) show an altitudinal
zonation and distributional differences between the Atlantic and Pacific
slopes. *Chusquea longifolia* is associated with Lower Montane Forest, *C.
patens* and *C. foliosa* with Lower and Upper Montane Forests, and *C.
subtilis, C. tomentosa* and *C. talamancensis* with Upper Montane Forest
*sensu* Kappelle (1991). The six species had mass flowering with interspecific
overlap of the flowering periods in the same area within a 10 year period and
regenerated from seeds. Except for *Chusquea talamancensis* (*sect.
Swallenochloa*) all species belong to the sect. *Longifolieae. Chusquea
talamancensis* was also the only species which showed some overlap of the
flowering time over geographically distant populations. Therefore, it is
suggested to study in future questions of natural hybridization and speciation
of these bamboos.

Keywords: *Chusquea, bamboo, distribution, mass flowering, mast
seeding, flowering periods*
Introduction

Bamboos of the genus *Chusquea* form a significant part of the natural oak forest vegetation (*Quercus* spp.) in Costa Rican mountains and volcanoes (Clark, 1989; Haber, 1990; Kappelle *et al.*, 1991). These woody clump-forming bamboos are often dominant understory plants and competitively strong after natural and human disturbance (Widmer, 1990; 1993).

The more accessible areas of the oak forests of the Cordillera de Talamanca experienced very strong deforestation and fire after the construction of the Panamerican Highway (Carretera Interamericana, CIA) in 1943 (Dayton, 1945). The area was colonized by peasants from the lowlands and the forests were converted into pastureland and agricultural land (Orozco, 1991). Fire and intensive grazing reduced effectively the area covered by secondary vegetation with bamboo, especially affected were species like *Chusquea pittieri*, *C. longifolia* and *C. pohlii*. Nevertheless, through the Costa Rican National Park and the Forest Reserve System established in the 1970’s, much forest has been preserved from further destruction (Boza, 1993), especially at the higher elevations (>2800 m asl) and in less accessible areas.


Like many bamboos, most *Chusquea* species exhibit monocarpic and synchronized flowering. Mass flowering of bamboos in the natural environment usually implies mast seeding (Janzen, 1976), i.e a synchronized seed production in a population of plants. The *Chusquea*
bamboos described here showed strict masting *sensu* Kelly (1994) and the individuals of the parent population died after producing seeds (semelparity).

The aim of this paper is to discuss the distribution of the montane forest species of *Chusquea* in the Cordillera de Talamanca in Costa Rica and report on the latest flowering events. This information may be an important basis for future research work on ecology, community dynamics, phytosociology and management in the oak-bamboo forests of the Cordillera de Talamanca, one of the largest unfragmented montane forest ecosystems in Central America (Kappelle & Zamora, 1995).

**Study area**

The main observation area was located between 9°30' - 9°35' N and 83°40' - 83°45' E at altitudes between 2000 and 3200 m asl (Figure 1). It comprised the mountains Cerro Asunción, Cerro Abarca, Cerros Cuericí and the localities La Georgina, Villa Mills and Macho Mora, Prov. Cartago. Additionally, occasional observations were made alongside the Carretera Interamericana (CIA) including the localities El Empalme, La Esperanza del Guarco, Tres de Junio-Macho Gaff, Ojo de Agua in the Province of Cartago, Trinidad de Dota, San Gerardo de Dota, Providencia de Dota and División in the Province of San José and on the mountains Cerro Vueltas, Cerro de la Muerte (Province of San José) and Cerro Chirripó (Province of Limón). This whole area (approx. 2000 km²) belongs to the Forest Reserves Los Santos and Río Macho and to the Chirripó National Park which are all part of the 612.560 ha International Biosphere Reserve La Amistad.

Herrera (1985) describes the climate in these mountainous regions as very humid temperate to cold. Mean annual rainfall is 2000 - 5100 mm, mean annual temperature 9 - 15°C and potential annual evapotranspiration ranges from 997 - 1275 mm. In the dry months of January, February and March mean monthly rainfall ranges from 20 to 35 mm at Villa Mills weather station (Source: Instituto Costarricense de Electricidad, Depto. Hidrología).
Fig. 1. Location of the northern and central Talamancan range with the sites where the Chusquea species were studied.
Materials and Methods

Several one and two day expeditions were carried out on the Cordillera de Talamanca in 1985, from 1987 to 1990 and in December 1991, initially to record the distribution of the *Chusquea* species and subsequently to describe the pattern of flowering. Since mass flowering cannot be predicted, the first detection of flowering was incidental or casual. The detailed flowering phenology and sequence at the population level of *Chusquea talamancensis*, *C. tomentosa* and *C. subtilis* are discussed elsewhere (Widmer, 1998a) and will not be treated here.

Herbarium specimens of flowering plants in different phenological stages as well as seedlings, young plants and dead parts of parent plants (rhizomes, culms) were collected to confirm the field observations (Table 1). The age states used for the *Chusquea* bamboos correspond to those described for *Chusquea talamancensis* (Widmer, 1998a), i.e. incipient flower, immature flower, mature flower, incipient fruit, mature fruit. Collector's name and herbarium numbers are shown in the text in brackets and italics. The author's collections have only numbers and are not in chronological order because the collection numbers were given in a later stage while working with the dried specimens.

Results

DISTRIBUTION OF THE *CHUSQUEA* SPECIES.—The bamboos observed were found in different natural and man-made ecosystems. The natural ecosystems were the Upper and Lower Montane Forests *sensu* Kappelle (1991) where the overstory is mainly formed by *Quercus* species (Table 2). At these sites the *Chusquea* species studied are part of the understory vegetation, forming either extensive stands of one species beneath the canopy or are distributed in patches at suitable sites, e.g. by a stream or a brook, in gaps or in more protected habitats at the higher distributional limit (i.e. moulds). *Chusquea* species seldom intermingle but build up uniform, monospecific stands of variable size contiguous with one another.

Man-made ecosystems included secondary vegetation originating from logged oak forests which partly recovered to a secondary forest, but
Table 1. List of voucher specimens of Chusquea species.

<table>
<thead>
<tr>
<th>Voucher</th>
<th>Collection date</th>
<th>Site*</th>
<th>Altitude (m asl)</th>
<th>Phenological state</th>
<th>Herbarium (duplicates)</th>
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</thead>
<tbody>
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<td><strong>Chusquea longifolia</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Widmer 514</td>
<td>06.03.85</td>
<td>División-Monte Carmelo (Plots CATIE)</td>
<td>2100</td>
<td>fruit</td>
<td>CR</td>
</tr>
<tr>
<td>Widmer 989</td>
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<td>División-Monte Carmelo (Plots CATIE)</td>
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<td>dead parent rhizome</td>
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</tr>
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<td>14.11.85</td>
<td>División-Monte Carmelo (Plots CATIE)</td>
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<td>plantlet</td>
<td>HZH</td>
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<tr>
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<td>2100</td>
<td>plantlet</td>
<td>HZH</td>
</tr>
<tr>
<td>Widmer 549</td>
<td>17.05.88</td>
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<td>2100</td>
<td>young plant</td>
<td>ISC/CR/HZH(2)</td>
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<tr>
<td><strong>Chusquea patens</strong></td>
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<td></td>
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<td>25.07.88</td>
<td>La Esperanza del Guarco (Plots ECOMA)</td>
<td>2490</td>
<td>immature fruit</td>
<td>CR/CATIE/HZH</td>
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<td>CR/HZH(4)</td>
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<td>Widmer 528</td>
<td>25.07.88</td>
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<td>2370</td>
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<td>CR/HZH(5)</td>
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<tr>
<td>Widmer 1078</td>
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<td>2370</td>
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<tr>
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<tr>
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<td>09.12.88</td>
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<td>mature flower</td>
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<td>Widmer 512</td>
<td>09.11.89</td>
<td>Cerro Cuerici (Plot AN3 CATIE)</td>
<td>2800</td>
<td>immature fruit</td>
<td>ISC/CR/CATIE/HZH(9)</td>
</tr>
</tbody>
</table>
**Chusquea tomentosa**

| Widmer 505 | 19.01.90 | La Esperanza del Guarco (Plots ECOMA) | 2550 | incipient fruit | ISC/CR/CATIE/HZH(2) |
| Widmer 507 | 06.02.90 | Trinidad de Dota | 2550 | incipient fruit | ISC/CR/HZH(2) |
| Widmer 536 | 15.06.89 | San Gerardo de Dota (by the road to...) | 2800 | immature fruit | CR |
| Widmer 1049 | 27.10.89 | Cerro Abarca (Plot Matinal CATIE) | 2680 | immature flower | CR/HZH(2) |
| Widmer 1041 | 06.03.90 | Cerro Abarca (Plot 614) | 2810 | mature flower | HZH |
| Widmer 1019 | 09.12.88 | Cerros Cuerici (by the track to ...) | 2800 | incipient fruit | CR/HZH(2) |
| Widmer 1053 | 11.12.89 | Cerros Cuerici (by the track to ...) | 3000 | mature flower (anthesis) | CR/HZH |
| Widmer 1051 | 25.10.89 | Villa Mills (Pilot Area CATIE) | 2700 | immature flower | CR/HZH(2) |
| Widmer 506 | 05.02.90 | Cerros Cuerici (by the track to ...) | 2990 | mature flower | ISC/CR/CATIE/HZH(3) |
| Widmer 1031 | 07.03.90 | Cerros Cuerici (Plot 414) | 2990 | mature flower | HZH |

**Chusquea talamancensis**

| van Velzen 61 | May-Aug 1989 | San Gerardo de Dota | 2800 | mature flower | HZH |
| van Velzen 311 | May-Aug 1989 | San Gerardo de Dota | 2800 | incipient fruit | HZH |
| Widmer 1145 | 24.10.87 | Cerro Asunción (1 km N CIA) | 3000 | immature flower | CR/HZH |
| Widmer 518 | 26.10.89 | Cerro Abarca (Plot Faja CATIE) | 2800 | incipient flower | CR/HZH(2) |
| Widmer 539 | 09.12.88 | Villa Mills (El Sitio) | 2600 | immature flower | HZH |
| Widmer 1142 | 07.09.89 | Cerro Chirripó (by the track to...) | 3170 | vegetative | HZH(2) |
| Widmer 523 | 25.10.89 | Villa Mills (Pilot Area CATIE) | 2700 | incipient flower | CR/HZH(2) |
| Widmer 1119 | 07.03.90 | Cerros Cuerici (Plot 5115) | 3100 | incipient fruit | HZH |
| Widmer 1120 | 07.03.90 | Cerros Cuerici (Plot 431) | 3000 | mature flower | HZH |
| Widmer 1122 | 08.03.90 | Cerros Cuerici (Plot 412) | 2990 | mature flower | HZH |
| Widmer 1133 | 09.03.90 | Cerros Cuerici (Plot 514) | 3000 | incipient fruit | HZH |
| Widmer 1125 | 09.03.90 | Cerros Cuerici (Plot 533) | 3010 | mature fruit | HZH |
| Widmer 1107 | 11.12.90 | Cerros Cuerici (by the track to...) | 3000 | seedlings | HZH |
| Widmer 1108 | 11.12.91 | Cerros Cuerici (by the track to ...) | 3000 | seedlings | HZH |
| Koppelle 4590 | 16.01.89 | Cerro Chirripó (Paso de los Indios) | 3150 | immature flower | CR/HZH |

There are different kinds of plots: 1) plots of the Silviculture of Natural Forests Project (SBN) with the abbreviation CATIE (Centro Agronómico Tropical de Investigación y Enseñanza), 2) plots of ECOMA: Proyecto Ecología y Manejo de las Montañas Altas de Costa Rica (Escuela de Ciencias Ambientales, Universidad Nacional, Heredia), and 3) plots with numbers (e.g. 614) of the authors ecological study.

also from burnt areas which had been converted to pastureland. At these sites, depending on the intensity of disturbance, *Chusquea* species were either confined to the borders (along roads, fences) or in protected sites e.g. by a stream. Where burning and pasturing have been very intensive the *Chusquea* bamboos have disappeared completely.

*Chusquea longifolia* was found in a primary forest patch at División-Monte Carmelo, from 2000 to 2100 m asl. This Lower Montane Forest is characterized by the codominant canopy tree species *Quercus copeyensis* and *Q. seemanii* (Orozco, 1991). *Chusquea longifolia* is completely replaced by the understory palm *Geonoma hoffmanniana* at lower elevations. In the same forest one of the largest *Chusquea* species, *C. pittieri*, is found on steep slopes to the southeast at 2300 - 2400 m asl. *Chusquea longifolia* was also reported in the Cordillera de Talamanca at the Cerro Burú and in the area between Río Bella Vista and Sitio Colón, Prov. Puntarenas (Clark, 1989).

*Chusquea patens* covers the area from El Empalme, La Esperanza del Guarco to Tres de Junio-Macho Gaff on the Atlantic side of the Cordillera de Talamanca, at an altitudinal range from 2400 to 2750 m asl. The area comprises Lower and Upper Montane Forest. At La Esperanza del Guarco it is found in primary forest dominated by *Quercus copeyensis* (Lower Montane Forest) the most diverse *Chusquea* flora is found: *C. patens* growing with *C. foliosa*, *C. tomentosa* and *C. tonduzii*. At Tres de Junio-Macho Gaff *Chusquea patens* grows from 2600 - 2750 m asl adjoining *C. tonduzii* at the higher elevation. In between, *Chusquea patens* is found in secondary vegetation on the borders of the CIA. *Chusquea patens* often occurs in primary forest on the Cerro Chirripó at altitudes from 2200 to 2400 m asl and (according to Clark, 1989) on the Cerro Echandi (2600 - 2850 m asl) and Cerro Zurquí. In 1989 a young population, whose parent population may have flowered 4 or 5 years ago, was found on the eroded riverbanks of the Río Buenavista at 2400 m asl.

*Chusquea foliosa* is found over a wide altitudinal range (2200 - 3100 m asl) but generally in small populations together with other *Chusquea* species. At lower elevations at El Empalme it grows in the understory of *Quercus copeyensis-Q. seemanii* forests (Kappelle et al., 1989) associated with *Chusquea pohlii*. Further, at La Esperanza del Guarco, *Chusquea foliosa* is found associated to *C. patens*, *C. tomentosa* and *C. tonduzii*.
<table>
<thead>
<tr>
<th>Chusquea species</th>
<th>Site</th>
<th>Altitudinal range</th>
<th>Actual vegetation*</th>
<th>Dominant Quercus species</th>
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<td>Lower Montane Forest</td>
<td><em>Q. seemani, Q. copeyensis</em></td>
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<td>Upper Montane Forest</td>
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* Altitudinal zonation based on KAPPELLE (1991)
(Lower Montane Forest). Because of severe deforestation in the past at lower elevations, *Chusquea foliosa* is often found in secondary vegetation by the roadside. At higher elevations at Tres de Junio-Macho Gaff (3000 m asl), at Cerro Cuerici (2940 - 3100 m asl) *Chusquea foliosa* occurs patchily in moulds or basins, humid, shady sites with SE-E-NE aspect. In these forested areas dominated by the canopy species *Quercus costaricensis*, the most common bamboo species is *Chusquea talamancensis*. The largest population of *Chusquea foliosa* was observed at Cerro Vueltas from 3000 - 3100 m asl in a primary forest (Upper Montane Forest) with *Quercus costaricensis* overstory.

*Chusquea subtilis* has been observed in the area of Cerro Abarca, Villa Mills and Cerros Cuerici at altitudes from 2550 - 2800 m asl, but only in Upper Montane Forest. It characteristically occurs near brooks or streams forming patches in areas where either *Chusquea tomentosa* or *Chusquea talamancensis* are the dominant understory bamboos. At El Sitio in Villa Mills (2580 - 2600 m asl), the three species appear together in a relatively small area. Because of its similarity in habit and vegetative morphology to *Chusquea foliosa*, it has only been recently described as a new species after it had flowered (Widmer & Clark, 1991).

*Chusquea tomentosa* is the most widely distributed bamboo at the Cordillera de Talamanca in areas where *C. talamancensis* is less prevalent. *Chusquea tomentosa* is mainly associated with Upper Montane Forests with *Quercus copeyensis* as dominant canopy species. It is the dominant bamboo species on the Pacific side (Trinidad de Dota, San Gerardo de Dota, Providencia de Dota) and on south and southeast aspects of the Atlantic side (Cerro Abarca, Cerro Cuerici) of the Talamancan range at altitudes from 2300 - 2900 m asl. Ascending onto the crest of the Cordillera de Talamanca along the Carretera Interamericana, the area occupied by *Chusquea tomentosa* begins at La Esperanza del Guarco where it is found with *C. patens*, *C. foliosa* and *C. tonduzii*. At Trinidad de Dota and Madreselva and at lower elevations it is now only found in disturbed forest patches or as part of secondary vegetation on roadsides. This species can reach altitudes of 3000 m asl at Cerro Cuerici and Cerro Chirripó, there it is usually growing in large canopy gaps.

*Chusquea talamancensis* is mainly distributed at elevations from 2600 - 3100 (3200) m asl on the Atlantic side of the Cordillera de Talamanca,
but it can also be found on the Pacific side at San Gerardo de Dota (van Velten 61). It is generally an understory species of Upper Montane Forests associated with Quercus costaricensis (Blaser 1987). Chusquea talamancensis covers the area from Cerro Asunción to the Cerros Cuerci and reaches south at the Cerro Chirripó (25 km SE aerial line distance from Villa Mills) going up to 3170 m asl (1142). At the lower distributional limit at Villa Mills (2600 m asl) Chusquea talamancensis grows together with C. tomentosa. The latter bamboo occupies the more fertile sites, while Chusquea talamancensis remains where soil conditions are poorer (Widmer, 1998b). Along the Carretera Interamericana Chusquea talamancensis starts at Ojo de Agua, replacing Chusquea tonduzii at higher altitudes. Above tree limit (3200 m asl) at the páramo Chusquea talamancensis is replaced by C. subtessellata. Sometimes at the tree line another, unnamed Chusquea sp. makes a transition between C. talamancensis and C. subtessellata occupying the more protected niches.

MASS FLOWERING OF CHUSQUEA SPECIES.—In 1985 the population of Chusquea longifolia (Figure 2 A, B) in División-Monte Carmelo was observed to be regenerating after mass flowering. The herb layer of the forest was covered with young plantlets (996, 998) of 20 to 40 cm height and 0.1 - 0.2 cm diameter, but a few plants were up to 100 cm height and 0.5 cm diameter. The parent population was dead and remains, such as rhizomes and culms hanging on the branches of trees (989) were still evident. By 1988 the new population formed a dense thicket in the forest understory reaching the shrub layer with culm lengths of 3 to 5 m and diameters of 1.0 to 2.0 cm; in sites where the overstory canopy was closed the size of the bamboos was smaller (e.g. 1.0 m height and 0.3 - 0.4 cm diameter) (549). Based on what has been reported by local people, and assuming that the time needed for flowering is similar to that for Chusquea talamancensis (Widmer, 1998a), flowering of C. longifolia at this site may have had its peak in 1983. In early 1985 a few plants were still bearing fruits (534) and probably represented the last phases of the mass flowering.

The results of mass flowering of Chusquea patens (Figure 3 A) was first observed when plants were at an advanced fruiting stage at La Esperanza del Guarco in 1987. An extensive area was covered with dying plants in gaps as well as under the forest; culms were dried out and brittle (Figure 1). The following year more plants flowered (529). Similarly, in
Fig. 2. Chusquea longifolia: A. 1 year old plantlet (Widmer 998); B. 2 year-old plant (Widmer 549). C. foliosa: C. flowering plant at anthesis; D. culm complement with flowering branches (Widmer 528).
Fig. 3. Culm complement with flowering branches: A. Chusquea patens (Widmer 531); B. C. subtilis (Widmer 512), C. C. tomentosa (Widmer 1053); D. C. talamancensis (Widmer 1133).
the primary forest of Tres de Junio-Macho Gaff there were plants in the flowering stage in 1988 and 1989 (1062, 531). Seedlings were observed in May 1989 at the latter site (1069). These observations may indicate that *Chusquea patens* flowered a year earlier at lower elevations rather than at higher ones and that at population level there are at least two cohorts of plants which flower in successive years, *i.e.* there are seedlings of two different years.

On the other hand, plantlets in a young population of *Chusquea patens* (1073) and dead culms of parent plants (1075) in 1989 on the river banks of the Río Buenavista, indicate that flowering may have occurred there around 1985. Similarly, flowering of *Chusquea patens* at Cerro Chirripó probably occurred in 1985, to judge from the size and the developmental stage of the young plants in the forest understory (1063). Hence, in this species distant populations exhibited different flowering times.

Flowering times of *Chusquea foliosa* (Figure 2 C, D) also differed according to the location of the population. At El Empalme (2370 m) mass flowering started in 1987, whereas fruiting plants were found in 1988 (528) and seedlings in 1989 (1078). In 1987, the population in the pristine forest at Cerro Vueltas (3000 m), which had probably flowered in 1985 or earlier, was regenerating and the forest understory was covered with young plants (1151) with diameters of 0.5 - 1.0 cm and heights of 0.5 - 2.5 m. Similarly as for *C. longifolia*, decomposing remains of the parent plants were found (1158) with culm diameters of more than 3.0 cm. On the other hand, the population at Cerro Cuericí was not seen in flower until the end of 1991.

*Chusquea subtilis* (Figure 3 B) flowered in the area of Villa Mills (508, 510, 511) and Cerro Cuericí (512) between 1988 and 1989, and seedlings (994) were found below the fruiting mother plant (514) at El Sitio (Villa Mills) in 1989.

Flowering plants of *Chusquea tomentosa* (Figure 3 C) were collected at La Esperanza del Guarco (505), Trinidad de Dota (507), San Gerardo de Dota (536), Cerro Abarca (1041, 1049), Villa Mills (1051) and Cerro Cuericí (506, 1031, 1053). Mass flowering started a year earlier (1988) at lower elevations on the Pacific side rather than at higher elevations on the
Atlantic side (>2800 m asl). Nevertheless at higher elevations some sporadic flowering plants were already indicating the coming event of mass flowering (1019). There was no report on flowering on the Cerro Chirripó. Seedlings of *Chusquea tomentosa* were observed in 1992 in the Cerro Cuericí (pers.comm., Grace Sáenz, Silviculture of Natural Forests Project). Grau and Rivera-Ospina (submitted) reported that in January 1992, there was an average density of 969,000 living seedlings/ha at El Jaular.

*Chusquea talamancensis* (Figure 3 D) flowered in the whole area of distribution described above. In 1987 the first isolated plants were seen in flower in the Cerro Asunción (1145). The following years mass flowering spread over the area from Ojo de Agua, Cerro Asunción, Cerro Abarca (518), Villa Mills (523, 539) and Cerro Cuericí (1119, 1120, 1122, 1125, 1133). The peaks of mass flowering of *Chusquea talamancensis* were observed in 1988 and 1989. Even at Cerro Chirripó *Chusquea talamancensis* was observed in flower (Kappelle 4590) in 1989, but not all the plants were flowering (1142), i.e. geographically distant populations show some overlap in the flowering time. Germination occurred at Cerro Cuericí in 1990 (1107) and 1991 (1108), as a consequence, the plants building the new population formed two cohorts which regenerated successively.

**Discussion**

At the Cordillera de Talamanca there is an altitudinal zonation of the *Chusquea* species (Figure 4). *Chusquea longifolia* is found at lower elevations (2000 - 2100 m) and *C. talamancensis* at high elevations (2600 - 3100 m). *Chusquea patens* tends to be most abundant at lower elevations, whereas *C. tomentosa* occurs at middle to higher elevations. *Chusquea foliosa* has the widest altitudinal range (2200 - 3100 m) and *C. subtilis* the narrowest (2550 - 2800 m). Some species are only found on the drier Pacific side (*Chusquea longifolia*) and others only on the wet Atlantic side (*Chusquea patens, C. subtilis*) of the Cordillera de Talamanca. *Chusquea tomentosa, C. foliosa and C. talamancensis* are on both sides of the mountain range. Correspondingly, studies on the vegetation of the Cordillera de Talamanca showed that there is a vegetational zonation in
Fig 4. Altitudinal distribution and relative area covered by the main Chusquea species in the northern and central Cordillera de Talamanca. Note the difference between the Pacific and Atlantic slopes.

relation to altitude and floristic (and structural) differences between the Atlantic and Pacific slope, related to the prevailing climatic conditions (Hooghiemstra, et al., 1992; Kappelle, 1992). *Chusquea longifolia* is associated with Lower Montane Forest, *C. patens* and *C. foliosa* with Lower and Upper Montane Forests, and *C. subtilis*, *C. tomentosa* and *C. talamancensis* with Upper Montane Forest sensu Kappelle (1991).
Chusquea bamboos are nowadays found in the understory of the remnant pristine forests, in secondary forests, and in other secondary vegetation such as grasslands and shrublands (Blaser & Camacho, 1991; Kappelle et al. 1989; Spreuwenberg, 1989).

The reconstruction of past flowering events of the Chusquea species treated here based on literature in order to follow up the flowering cycle of the species, is extremely difficult. On one hand, the new species described by Widmer & Clark (1991) show similarities to other species (Chusquea talamancensis to C. tonduzii and C. vulcanalis; C. tomentosa and C. subtilis to C. foliosa). On the other hand, there is little and fragmentary information even on herbarium specimens (Herbario Nacional, Costa Rica) on the population size and on the extent of flowering at population level. Besides, the collections originate from different locations and there is no certainty on the synchronicity of flowering in geographically distant populations. Most of the species studied here show differences in flowering time between geographically distant populations. Chusquea talamancensis is the only species whose flowering time seems to overlap within populations over greater distances.

Only Chusquea longifolia and C. patens have records of flowering back to 1892 (Patarra, Prov. San José) the first and 1919 (Cascajal, Prov. San José) the latter (Clark, 1989). Pohl (1982) observed that the intervals between known flowering and fruit collections of Chusquea longifolia range from eight to 29 years.

It is remarkable that six Chusquea species out of the 13 known from the Cordillera de Talamanca showed mast seeding within a period of 10 years. Chusquea patens, C. foliosa, C. tomentosa, C. subtilis and C. talamancensis showed interspecific overlap of the mass flowering periods (Figure 5). This was the case at La Esperanza del Guarco, with a population of Chusquea patens and C. tomentosa and at Cerro Cuericí with large populations of C. talamancensis and C. tomentosa and a small population of C. subtilis.

Questions on speciation and natural hybridization arise in view of the overlap of flowering periods of different Chusquea species in a same area, and the fact that pollination is anemophilous. Based on phenological
observations in the natural forest, it seems that *Chusquea talamancensis* and *C. tomentosa* are outbreeders, *i.e.* recombination of genetic material within a species occurs through cross-pollination (Widmer, 1998a). But if different species are not geographically isolated and they flower nearly simultaneously, there must be a mechanism of reproductive isolation which preserves the species as such. Anyhow, there may be some individuals which lack this internal barrier and may produce hybrids. Hybrids have been reported by Clark *et al.* (1989) for *Chusquea* species of the sect. *Swallenochloa* with continuous flowering, on the basis of morphological intermediacy. Still, the probability of hybridization for bamboos with cyclical flowering is low, but the fact that there is overlapping of flowering periods, especially if the species are in geographical vicinity, may increase the chances of interspecific cross-pollination within *Chusquea* species.

![Diagram of flowering peaks of different populations of Chusquea species](image)

**Fig. 5.** Flowering peaks of different populations of *Chusquea* species (peak: mass flowering of ≥50% of the population).
According to the systematics, all flowering *Chusquea* species except *C. talamancensis* (sect. *Swallenochloa*) belong to the sect. *Longifoliae*, which are very alike in their vegetative and floral morphology. Species of different sections may have separated in an evolutionary earlier stage of the same section.

The remaining natural populations of several *Chusquea* species in the Cordillera de Talamanca therefore offer a good opportunity to investigate the evolutionary phenomena of these bamboos.

**Acknowledgements**

I would like to thank the Centro Agronómico de Investigación y Enseñanza (CATIE) in Costa Rica and the Geobotanisches Institut ETHZ in Switzerland for the support given to my work on bamboo ecology. The Swiss Development Agency (DEH-EDA) funded the field work in Costa Rica on the basis of a PhD grant. I am very grateful to Marvin and Martín Mena Granados from Villa Mills for their assistance in the field. Thanks are also given to P. J. Edwards, L. G. Clark, J. Furrer for valuable comments and corrections.

**References**


DISCUSSION

Life history of some *Chusquea* species in old-growth oak forest in the Cordillera de Talamanca, Costa Rica

Yvonne Widmer


Abstract

Most of the species of the genus *Chusquea* in Costa Rica are understory components of high-mountain *Quercus* forests. The highest diversity of *Chusquea* is found in the Cordillera de Talamanca, where 13 species have been recorded.

Detailed studies of three species (*Chusquea talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark and *C. foliosa* Clark) show that they exhibit a high degree of phenotypic plasticity in response to light, reflected primarily in the number of culms produced and the diameter of the culms. Under closed tree canopy the cover of all species is 30-40% and in large tree-fall gaps it is 85-90%.

During the main study period (1987-1990) six species exhibited mass flowering or were in a phase of regeneration after mast seeding. Observations of *Chusquea talamancensis*, *C. tomentosa* and *C. subtilis* Widmer & L.G. Clark showed that flowering at population level occurs in phases and extends over at least 3 years. All parent plants die and are followed by vigorous regeneration by seed.

The influence of *Chusquea* upon forest dynamics is discussed, concluding that *Chusquea* species have the potential to influence the pattern of tree regeneration. In the question of the evolution of the life cycle of bamboos, it is hypothesized that the forest environment may be a driving force for the selection of periodic flowering in bamboos.
Introduction

The aim of this paper is to present a paradigm of how the life history of Chusquea plants which grow in a montane forest environment can be understood. It is the result of three years of continuous field observations and research from 1987 - 1990 and two short visits in 1985 and 1991. This study was initiated in 1985 by the Silviculture of Natural Forests Project at CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) in Costa Rica, when foresters working in the high-mountain oak forests of the Cordillera de Talamanca, realised that to develop a natural forest management plan there is need to know how to manage the understory bamboos. In areas which were extensively logged, various species of Chusquea bamboo, commonly called 'cañuela', often developed pure stands. Therefore, they were considered weeds which inhibited tree regeneration, which in the foresters view had to be controlled or even exterminated.

Against this background, the study of the ecological role of Chusquea in the oak forests was started as a PhD thesis, with the main question of what is the ecological behaviour of these bamboos in the natural, undisturbed forest. The pristine old-growth forests observed presented the dominant endemic species Quercus costaricensis Liebmann and Q. copeyensis C.H. Müller, which form a high forest canopy (> 30 m). Kappelle et al. (1992) describe these forests as consisting of five layers. In the upper canopy layer Quercus is associated with Podocarpus and Magnolia. The intermediate tree layer (or subcanopy layer) is more diverse, with trees of the genus Weimannia, Ilex, Zanthoxylum, Viburnum, Vaccinium, Styrax, Symplocos, Clusia, Lauraceae, Melastomataceae and Myrsinaceae. The shrub layer is mainly composed of Chusquea bamboos, treeferns (Cyatheaceae), and shrubs belonging to Acanthaceae, Ericaceae, Rubiaceae and Solanaceae. The herb layer consists of terrestrial aroids, ferns and gesneriads, and the bryophyte layer covers bare soil or decaying wood.
Forest dynamics in these old-growth forests is strongly affected by treefall (single or multiple) and branchfall, leading to a spatial structure characterized by a mosaic of closed canopy, canopies with windows (apertures through which skylight penetrate), and gaps in various stages of regeneration. Large old gaps (>500 m², >10 years old) in the primary forest are characteristically dominated by the understory *Chusquea* bamboos and have a two layer vertical structure: a bamboo layer (shrub layer) and a herb layer. Therefore, plots were set out under closed canopy, intermediate canopy and tree-fall gaps, and in these measurements were made of the morphology and spatial distribution of three *Chusquea* species. Synecological aspects like species composition and abundance of the forest vegetation and soil properties were also included in the study. During the course of the field work, unexpectedly, six species of *Chusquea* were observed in flower in the Cordillera de Talamanca, including the three species whose vegetative growth had been studied. This event permitted the description of new species and additionally allowed observations on flowering phenology and regeneration of the bamboo populations (Widmer & Clark, 1991; Widmer, 1994; 1998a).

Different aspects of the biology of *Chusquea* species in the natural environment will be described which lead to understand how natural forest dynamics is influenced by these plants. Finally, evolutionary aspects will be discussed on *Chusquea*’s life history associated to the forest environment.

**Distribution**

The highest diversity of *Chusquea* in Costa Rica is found in the Cordillera de Talamanca (Figure 1) where thirteen species have been recorded: *C. foliosa* L.G. Clark, *C. longifolia* Swallen, *C. longiligulata* (Soderstrom & Calderón) L.G. Clark, *C. paludicola* L.G. Clark, *C. patens* L.G. Clark, *C. pittieri* Hackel, *C. pohlii* L.G. Clark, *C. talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark, *C. tonduzii* Hackel, *C. subtessellata* Hitchcock, *C. subtillis* Widmer & L.G. Clark and *C. vulcanalis* (Soderstrom & Calderón) L.G. Clark at altitudes from 2000 to 3500 m.a.s.l. (Pohl, 1976; Clark, 1989; Widmer & Clark, 1991). Most of
the *Chusquea* species in Costa Rica are characteristic understory components of oak forests, with exception of *Chusquea subtessellata* Hitchcock, which grows above timberline (>3200 m).

Species of *Chusquea* differ in their altitudinal zonation and distribution between the Atlantic and the Pacific slopes on the Cordillerade Talamanca (Widmer 1994). Other studies on the vegetation have shown that there is a vegetational zonation in relation to altitude and floristic (and structural) differences between both aspects of the mountain range (Hooghiemstra *et al.*, 1992; Kappelle, 1992). *Chusquea longifolia* Swallen and *C. pittieri* Hackel are distributed in the Lower Montane Forests (*sensu* Kappelle, 1991). *Chusquea patens* and *C. foliosa* are found on Lower and Upper Montane Forest while *C. subtilis*, *C. tomentosa* and *C. talamancensis* have only been observed in the Upper Montane Forest. With respect to aspect, it seems that *Chusquea longifolia* occurs mainly on the drier Pacific slope, and *C. patens* and *C. subtilis* mainly on the wetter Atlantic slope. All the other species occur on both aspects, but *Chusquea tomentosa* is more abundant on the Pacific side and *C. talamancensis* on the Atlantic side. However, these generalizations have to be viewed cautiously, since much past deforestation, burning and pasturing especially at low elevations, may have caused the disappearance of many bamboo populations.

![Fig. 1. Map of Costa Rica with the location of the Cordillera de Talamanca.](image-url)
All species appear to occupy different ecological niches, and form monospecific stands of different sizes contiguous to each other, which may be associated to distinct floristic associations or occur on different types of soil as observed by Blaser (1987). *Chusquea talamancensis* is found in more acidic soils than *C. tomentosa* or *C. foliosa*, with a higher content of organic matter and C:N ratio in the topsoil (0-10 cm). *Chusquea tomentosa* seems to grow on soils with a better nutrient status than the other two species studied, reflected in the amount of exchangeable bases (Ca, K, Mg) at the rhizome depth (20-30 cm) (Widmer, 1998c).

**Response to light conditions in the forest**

In the pristine montane oak forests of Cerros Cuericí and Cerro Abarca (Province of Cartago), in an area of 5 km² at elevations from 2800-3100 m, the tree canopy has a marked effect on the growth and spatial pattern of *Chusquea* populations (Widmer, 1998b). *Chusquea talamancensis* and *C. tomentosa* are found under different degrees of shade ranging from gaps to closed canopy, while *C. foliosa* has not been found under closed canopy. The cover of *Chusquea* is usually 85-90% in gaps and reduces to 30-40% under closed canopy (Table 1). Clumps of all species tend to be few and large under open conditions and numerous and small under shady conditions (Figure 2). The smaller clump density (clumps per unit area) in gaps compared to closed canopy implies that there is a stronger intraspecific competition and density dependent mortality (or self-thinning effect *sensu* De Kroon, 1993) after gap formation, when a bamboo species becomes dominant under favourable light conditions. Species also differ in their response to the light environment: *Chusquea tomentosa* and *C. foliosa* have a higher degree of morphological plasticity than *C. talamancensis*, though this species seems to be more shade tolerant. The number of culms per clump and the diameter of adult and young culms provide evidence of the plastic responses of *Chusquea* species to light.

Performance parameters like total number of branches, total branch length and branching pattern are affected by the light regime, whereas culm length, number of nodes per culm, number and length of primary
**Fig. 2.** Spatial distribution of clumps of *Chusquea tomentosa* and *C. talamancensis* in representative 100 m² plots under closed canopy and gaps. Clumps are numbered. The first inner circle is the clump area at base, the second is the area at 1 m height and the outer circle is the crown area. Detailed methods in Widmer (1998b).
Table 1. Data on spatial and morphological pattern obtained from 100 m² plots. There were 7 gap and 9 closed canopy plots with Chusquea talamancensis, 4 and 10 respectively with C. tomentosa and 7 gap plots with C. foliosa. Detailed methods in Widmer (1998b). Diameter was measured on randomly selected culms (one per clump). Mean ± Standard error, n.d. = not determined.

<table>
<thead>
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<th>Chusquea species</th>
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<th>Gap</th>
<th>Closed canopy</th>
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<td></td>
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<td>Mean ± SE</td>
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<td>n.d.</td>
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<tr>
<td>Number of culms per clump</td>
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<td>n.d.</td>
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<tr>
<td>Diameter of adult culms [cm]</td>
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<td>1.44 ± 0.14</td>
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<tr>
<td>Diameter of young culms [cm]</td>
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<td>1.27 ± 0.22</td>
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<td>Chusquea foliosa</td>
<td>3.48 ± 0.18</td>
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</tbody>
</table>

branches and number of branch nodes seem to be uninfluenced by the light (Widmer, 1998b). No differences were found in soil properties between sites of different canopy closure, which could explain such variation in growth (the only difference recorded was in the ratio Ca:Mg, which seems to be higher in gaps compared to closed canopy; Widmer, 1998c).
Reproductive biology

VEGETATIVE REPRODUCTION.—Most of the *Chusquea* species of the Cordillera de Talamanca are clump-forming because of their pachymorph rhizomes (*i.e.* rhizome with a sympodial branching and short rhizome necks). Due to the compact habit, vegetative reproduction through clonal growth seems to be limited to a phalanx-type of strategy (Lovett Doust & Lovett Doust, 1982, Urbanska, 1992).

Nevertheless, it has been observed in *Chusquea talamancensis*, *C. tomentosa* and *C. foliosa* that some branch bases also bear rhizomatous swellings as was described by Wong (1991), which allow the culms to root when they come in contact with soil (*i.e.* layering). Stein & Weberling (1992) observed the development of these rhizome-like structures in *Chusquea subtessellata* when the culms were physically prevented from leaving the soil.

Another, more guerrilla-like strategy (*sensu* Lovett Doust & Lovett Doust, 1982) has been observed in juvenile plants developed from seeds of *Chusquea longifolia*. New and still un lignified culms fall over and develop roots at those nodes which are in contact with the soil. These layered culms may later decompose and leave two or more physiologically independent plants. Hence, it is postulated that clonal spread is greatest in clump-forming *Chusquea* species at the juvenile stage of plants originated from seed, where physiologically independent ramets can develop from fragmentation of a genet.

REPRODUCTION BY SEED.—It is remarkable that during the same period six *Chusquea* species out of the 13 known from the Cordillera de Talamanca were observed either mass flowering or in regeneration after mast seeding (Figure 3 & 4). Except *Chusquea talamancensis* (Section Swallenochloa), all species belong to the Section Longifoliae. The periods of mass flowering of *Chusquea patens*, *C. foliosa*, *C. tomentosa*, *C. subtilis* and *C. talamancensis* overlapped (Widmer, 1994). In the case of *Chusquea talamancensis* overlap of flowering time even occurred in geographically distant populations.
Fig. 3. Flowering and regeneration of Chusquea species in the forest understory. A. Clump of C. tomentosa (Villa Mills). B. Dried parent plants of C. talamancensis (Cerros Cuerici) 2 years after initiation of flowering. C. Dead remains of parent plants among plantlets of C. foliosa (Cerro Vueltas). D. Juvenile plants of C. foliosa (Cerro Vueltas).
Fig. 4. Location of the Chusquea species (C. talamancensis, C. tomentosa, C. foliosa, C. patens, C. longifolia, C. subtilis) which were observed mast seeding in the Cordillera de Talamancan and on the volcanoes Turrialba and Irazú, Costa Rica. Observations from 1985 to 1990.
Flowering at population level may extend over more than 3 years (Seifriz, 1920; Deogun, 1937) following a temporal sequence of flowering. This was first observed in the area for *Chusquea talamancensis* (Widmer, 1998a). The first sign of flowering is the occurrence of a few sporadic flowering plants which do not produce seeds. The clumps of the remaining population show reduced culm production and culm vigour as another signal of future flowering. In the second year about half of the population is flowering and in the third year the second half, and at last a few isolated plants remain in the vegetative state or may flower out of phase.

The flowering phenology observed in populations of *Chusquea talamancensis*, *C. tomentosa* and *C. subtilis* showed that the phenological stages are closely linked to the seasonal climatic pattern (Widmer, 1998a). Flower formation, fruit formation and germination of seeds occur in the rainy season, whereas pollination, fruit maturation and abscission from the panicle occur in the dry season. The period from initiation of flowering until germination of seeds in *Chusquea talamancensis* is two years. The protracted nature of this process may be due to the cold climatic conditions of the montane forests.

Animals seem to have an effect on seed production through predation of the flowers by insects and of the Caryopses by birds and rodents. Further, the Caryopses are externally scabrous and adhesive and bear an awn on the fertile and sterile lemmas (Figure 5) which enables the seed to attach to the fur or plumage of animals. These 'armed seeds' (according to Radosevich & Holt, 1984) can thus be dispersed over a potentially large area.

**Life cycle of *Chusquea talamancensis***

The flowering cycle of a semelparous bamboo species corresponds to the life cycle, since the existence of a genetic individual finishes with flowering. Based on observations by local people, the flowering cycle of the *Chusquea* species in the oak forests of the Cordillera de Talamanca may last 30 - 40 years. The best records of flowering cycles of a *Chusquea* species are of *C. abietifolia* from the Blue Mountains in
Jamaica, where a period of 31 - 33 years has been confirmed four times (Widmer, 1998a).

Fig. 5. Spikelets of A. Chusquea foliosa (Widmer 528) B. C. tomentosa (Widmer 1031); C. C. subtilis (Widmer 508); D. C. patens (Widmer 1062); E. C. talamancensis (Widmer 1120). Fl: fertile lemma, GlI: glume I, GlII: glume II, Pal: palea, SLI: sterile lemma I, SLII: sterile lemma II.
The life cycle of *Chusquea talamancensis* presented here is based on the observations on vegetative development and the flowering behaviour of the species.

The zygote develops into a mature caryopsis within a year while still attached to the parent plant. After abscission and a brief dormancy period the seed germinates with the first rains. At first it lives on the endosperm reserves and increases its assimilating surface with rapid leaf development. The plant is bushy in the juvenile phase, culms start to lignify, and the rhizome develops. Under favourable environmental conditions (enough light, water and nutrients) it takes at least 15-20 years for the woody bamboo plant to recover its previous biomass (Campbell, 1985). The vegetative phase of most of the forest *Chusquea* species of the Cordillera de Talamanca may last about 25-30 years.

The generative phase begins with the appearance of terminal panicles on the subsidiary branches of the culms. The parent plant is still vital during the flowering stage and at anthesis. After anthesis, *i.e.* after fertilization, the parent plant undergoes a strong defoliation and a steady degradation of the culms until they become pale and brittle. This is the consequence of translocation of assimilates from different parts of the parent plant to fruit production. The weakened plant is more susceptible to insect and fungal attack which enhances the decay. Prior to fruit abscission the parent plant is completely dry and the only visible living tissue is the pedicel which links the fruit to the rachis of the panicle. Seeds of the size of a rice grain drop, generally near the parent clump, and germinate best where the forest floor is covered with moss.

**Quercus-Chusquea forest dynamics**

The primary oak forests of the Cordillera de Talamanca are pristine, old-growth forests, characterised by the dominance of *Quercus* spp. in the overstory and *Chusquea* spp. in the understory (Orozco, 1991; Kappelle *et al.*, 1992). Until now, dating of old *Quercus* trees was not possible, because the growth rings are not clearly visible (Blaser, 1987). However, to judge from the high ages that oaks can reach in the Northern Hemisphere and the humid cold climatic conditions of these Upper
Montane forests, it can be assumed that the age of the oldest trees is several hundred years.

A hypothetical comparison of the life cycle of *Quercus* trees and the life cycle of *Chusquea* bamboos allows to understand how these species interact over a larger time scale (Figure 6). The premises are: (i) the life cycle of *Quercus* spp. is of the order of 200 years; (ii) it exhibits mast seed production at intervals of three years as was found for *Q. copeyensis* (Camacho, 1990); (iii) the flowering cycle of *Chusquea* spp. is around 30 years. Given this pattern it is clearly evident, that both species do not compete with each other if the process is understood over a larger time scale, but their life cycles oscillate independently. This equilibrium is kept as long as there is no human disturbance which endangers the survival of either species.

**Fig. 6. Hypothetical comparison of life cycles of the dominant overstory tree Quercus sp. with the dominant understory bamboo Chusquea sp.. Chusquea sp. is presumed to have semelparous mass flowering every 30 years. The life cycle of Quercus sp. is assumed to be 200 years and mast seeding to occur every three years.**
Another aspect of forest dynamics are the processes which follow natural disturbance like tree-fall due to the age of the trees. Gap formation seems to be a natural process in these old-growth forests and is especially frequent in the period of the 'northers' (strong polar winds from the north) in the dry season (Coen, 1983) or during the heavy rainfalls in the rainy season. A model of gap-phase dynamics of a high mountain *Quercus-Chusquea* forest is presented in Figure 7 involving the following steps:

1. It starts with a closed canopy of old-growth trees where understory *Chusquea* clumps are small because of limited light conditions.
2. The site is disturbed with a multiple tree-fall event and the understory vegetation is damaged.
3. After a time *Chusquea* plants become the dominant species and develop a closed canopy. In general, saplings are found beneath windows of the bamboo canopy. Under low light conditions saplings are suppressed and wait for several years in this state until the environment changes.
4. A physiognomic change of the forest occurs when all the *Chusquea* plants flower synchronously and start to wither.
5. When the *Chusquea* population has flowered and died, the forest floor is more illuminated and the suppressed trees shoot up. Bamboo seedlings also appear.
6. A new generation of *Chusquea* is developed while the trees have reached the overstory. The structure of the forest may be therefore characterised by cohorts of even-aged trees.

Thus, oak forest regeneration is pulsed as a consequence of the synchronous life cycle of the *Chusquea* bamboos. Detailed studies in Asiatic old-growth forests with bamboo understory discuss the influence of the life cycle of bamboos on the age structure of tree populations, and the tendency of synchronization of tree regeneration following bamboo die-back (Nakashizuka, 1984; 1988 and Taylor & Qin, 1992; 1995).
Fig. 7. Model of gap dynamics in a Quercus-Chusquea forest. Stages: (1) closed tree canopy with suppressed Chusquea clumps. (2) Gap formation after multiple tree fall. (3) Chusquea builds an understory canopy; suppressed tree regeneration. (4) Semelparous flowering of Chusquea. (5) Death of flowered Chusquea plants and establishment of new plants from seeds; vigorous growth of formerly suppressed trees. (6) Juvenile Chusquea understory; 'even-aged' Quercus trees fill the gap in the overstory.
Evolutionary hypotheses

Most bamboos are associated to the forest environment. Actually, primitive bambusoid grasses are found generally in association with woody plants (Soderstrom & Calderón, 1974). The widely distributed woody bamboos are naturally understory plants of wet or dry tropical forests and temperate forests (Raizada & Chatterji, 1956; Huberman, 1959). It is postulated here that the life cycle of bamboos needs to be interpreted in relation to its natural forest environment.

Bamboos are derived from herbaceous ancestors (Soderstrom & Calderón, 1974; Takhtajan, 1981). According to Tzvelev (1989) they probably originated from a phylogenetically-ancient, highly specialized group in the family of grasses, known under the name of Bambusites, at the beginning of the Tertiary period. He hypothesizes that grasses originated above the upper limits of the forest during a time of orogeny and at the general climatic change at the Cretaceous they descended from the mountains and occupied niches which were formerly occupied by mesozoic plants. The primitive bambusoid grasses originated through the occupation of places underneath trees. In a rapid evolutionary process towards increase of the overall size of the plant, a 'grandization' took place by increase in the number of internodes of the stem and elongation of the internodes by means of an intercalary meristem, as well as by branching of the upper part of the shoot and developing larger leaves.

In the case of the Quercus-Chusquea forest, it is still unknown when the association of bamboos and trees had occurred. Quercus migrated from the north to the south about 1 mill. years ago (van der Hammen & Cleef, 1983). Coevolution of both plants cannot be excluded completely, where the life cycles of Chusquea and Quercus could adjust with time. An analogous case is a meadow, where annuals and perennials coexist in a natural community. The difference between the forest and the meadow is the scale of space and time. Thus, the phenomenon of semelparity of a bamboo species in the forest is analogous to semelparity of an annual plant in a meadow of mainly perennial plants.

Bamboo species without flowering periodicity may have evolved outside the forest environment. Chusquea subtessellata is an example of a bamboo which grows outside the forest, in the páramo of the Cordillera
de Talamanca (above timberline), and flowers sporadically (sensu Campbell, 1985) without resultant mortality (Clark et al., 1989).

There are many evolutionary hypotheses to explain bamboo life cycle, semelparity and synchronism within the flowering population (Kawamura, 1927; Janzen, 1976; Uchimura, 1980; Campbell, 1985). The explanation that the flowering cycle of bamboo has evolved as a consequence of the forest environment needs further discussion after bamboos have been classified according to the ecosystem they originally belong to.

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SUMMARY

This thesis concerns aspects of the taxonomy and ecology of bamboos of the genus *Chusquea* in the *Quercus* forests of the Cordillera de Talamanca in Costa Rica. The study had five main objectives: 1. To describe three new species of *Chusquea*; 2. To characterise the environment and vegetation in the *Quercus-Chusquea* forest; 3. To compare aspects of the population dynamics of different *Chusquea* species; 4. To describe the distribution and flowering behaviour of various *Chusquea* species; 5. To describe the life history of *Chusquea* in relation to the forest environment.

In chapter 1 three new species of *Chusquea* from the Upper Montane forests of the Cordillera de Talamanca are described and illustrated. *C. tomentosa* and *C. subtilis* belong to *Chusquea* section *Longifoliae* and are closely related to *C. foliosa*. The third species, *C. talamancensis*, is a member of *Chusquea* section *Swallenochloa* and shows similarities to both *C. tonduzii* and *C. vulcanalis*. Revised keys to the species of section *Longifoliae* and section *Swallenochloa* in Costa Rica are provided.

Chapter 2 presents the results of a survey of the vegetation and soils of the oak forests on Cerros Cuercí and Cerro Abarca. The plots studied were selected to include one of the *Chusquea* species present in the area (*C. talamancensis*, *C. tomentosa* or *C. foliosa*) and to represent one of the types of canopy closure (closed canopy, intermediate canopy or gap). Based on a PCOA of the floristic data eight plant communities were recognized which can be associated with differences in topography, soil characteristics and canopy closure. The *Chusquea* species appear to be indicators for particular topographic situations and soil types. The data on size distribution of trees show the inhibitory effect upon tree growth of the dominance of bamboo in gaps.

Chapter 3 examines in more detail the soil conditions of *Chusquea talamancensis*, *C. tomentosa* and *C. foliosa*, and presents data on soil pH, organic content and concentrations of plant nutrients. The soils supporting the different species of *Chusquea* bamboos were mainly acidic (pH 3.3-6.0) and derived from volcanic ash. However, individual bamboo species appeared to have distinct requirements in terms of soil conditions. The soils carrying *C. talamancensis* were richer in organic matter, had a higher C:N ratio and were
more acidic than those with *C. tomentosa* or *C. foliosa*. *C. tomentosa* grew on more nutrient-rich soils than the other two species.

In chapter 4 the effect of canopy closure on the growth and spatial pattern of the three understory *Chusquea* species is described. Clumps of all species tend to be few and large under open conditions and numerous and small under more shady conditions. The smaller clump density in gaps implies that there is intraspecific competition and density-dependent mortality when bamboos become dominant under favourable light conditions. Species differ in their response to light conditions: *C. tomentosa* and *C. foliosa* had a higher degree of morphological plasticity than *C. talamancensis*, which in turn appeared to be more shade tolerant.

Chapter 5 describes the mass flowering of *C. talamancensis*, *C. tomentosa*, and *C. subtilis* between 1987 and 1990, followed by the death of all plants. The different phenological states were coupled with the seasonal pattern of rainfall. Flower formation, fruit formation and germination of seeds occurred in the rainy season, whereas pollination, fruit maturation and abscission occurred in the dry season. On population level different flowering phases of cohorts were recognized. There was no seed production when isolated plants flowered, indicating that reproductive success depends on cross-pollination.

Chapter 6 presents observations on the distribution and flowering of six *Chusquea* species in the northwestern Cordillera de Talamanca. The most abundant species of *Chusquea* bamboos (*C. foliosa, C. longifolia, C. patens, C. subtilis, C. talamancensis* and *C. tomentosa*) show an altitudinal zonation and distributional differences between the Atlantic and Pacific slopes. *C. longifolia* is associated with Lower Montane Forest, *C. patens* and *C. foliosa* with Lower and Upper Montane Forests, and *C. subtilis, C. talamancensis* and *C. tomentosa* with Upper Montane Forest. In the study area, the six species exhibited mass flowering with interspecific overlap of the flowering periods within a ten year period.

In the discussion it is concluded that *Chusquea* species have a major influence on the dynamics of the *Quercus* forests. The flowering and death of the bamboo is probably the most important type of disturbance in these forests, and tree regeneration is coupled with these events. Regarding the evolution of the bamboo life cycle, it is hypothesized that the forest environment may have been the driving force for the selection of periodic flowering in bamboos.
ZUSAMMENFASSUNG


Im Kapitel 1 werden drei neue *Chusquea*-Arten der oberen Gebirgswälder der Cordillera de Talamanca beschrieben und illustriert. *C. tomentosa* und *C. subtilis* gehören zu *Chusquea* Section *Longifoliae* und sind nahe verwandt mit *C. foliosa*. Die dritte Art, *C. talamancensis*, ist ein Mitglied der *Chusquea* section *Wallenochloa* und zeigt Ähnlichkeiten zu *C. tonduzii* und *C. vulcanalis*. Es werden überarbeitete Schlüssel der Arten aus der section *Longifoliae* und section *Wallenochloa* geliefert.


Im Kapitel 3 werden die Eigenschaften der Böden, auf denen *Chusquea talamancensis*, *C. tomentosa* und *C. foliosa* gedeihen, genauer untersucht, und Daten über Bodenazidität, organische Substanz und Konzentrationen von
Makroelementen gegeben. Die Böden, auf denen die verschiedenen Chusquea-Arten wachsen, waren überwiegend leicht bis stark sauer (pH 3.3-6.0) und hatten vulkanischen Ursprung. Man konnte feststellen, dass verschiedene Bambusarten auf spezifische Bodenbedingungen ansprachen. Die Böden mit *C. talamancensis* zeichneten sich aus durch einen höheren Gehalt an organischer Substanz, ein höheres C:N-Verhältnis und waren saurer als die Böden unter *C. tomentosa* oder *C. foliosa*. *C. tomentosa* wuchs auf nährstoffreicherer Böden als die beiden anderen Arten.


Im Kapitel 6 werden Beobachtungen über die Verbreitung und Blüte von sechs Chusquea-Arten in der nordwestlichen Cordillera de Talamanca vorgestellt. Die häufigsten Chusquea-Arten (*C. foliosa*, *C. longifolia*, *C. patens*, *C. subtilis*, *C. talamancensis* und *C. tomentosa*) zeigten eine spezifische Höhenverteilung und Unterschiede zwischen der atlantischen und pazifischen Gebirgsseite. *C. longifolia* befand sich im Unteren Gebirgswald, *C. patens* und *C. foliosa* im Unteren und Oberen Gebirgswald und *C. subtilis*, *C.
talamancensis und C. tomentosa im Oberen Gebirgswald. Im Untersuchungsgebiet kamen alle sechs Arten zu einer Massenblüte, mit interspezifischer Überlappung der Blühperioden in einem Zeitraum von zehn Jahren.

In der Diskussion wird dargelegt, inwieweit die Chusquea-Arten einen wichtigen Einfluss auf die Dynamik der Quercus-Wäldern haben. Die Blüte und das Absterben von Bambus ist möglicherweise die wichtigste Störungsart in diesen Wäldern, da die Baumverjüngung offensichtlich mit diesen Ereignissen gekoppelt ist. In bezug auf die Evolution des Lebenszyklus von Bambus wird die Hypothese aufgestellt, dass die Waldumgebung massgebend für die Selektion der periodischen Blüte von Bambus ist.
RESUMEN

Esta tesis trata de aspectos de la taxonomía y ecología de bambúes del género *Chusquea* en los bosques de altura de la Cordillera de Talamanca en Costa Rica. Esta investigación tuvo cinco objetivos principales: 1°) Describir tres nuevas especies del género *Chusquea*; 2°) Caracterizar la vegetación y suelos en los bosques *Quercus-Chusquea*; 3°) Comparar aspectos de la dinámica de población de diferentes especies de *Chusquea*; 4°) Describir la distribución y la floración de varias especies de *Chusquea*; 5°) Describir la historia de vida de *Chusquea* en relación al medio boscoso.

En el capítulo 1 se describen e ilustran tres nuevas especies de *Chusquea* del Bosque Montano Alto de la Cordillera de Talamanca. *C. tomentosa* y *C. subtilis* pertenecen a *Chusquea* section *Longifoliae* y están cercanamente emparentadas con *C. foliosa*. La tercer especie, *C. talamancensis*, es un miembro de *Chusquea* section *Swallenochloa* y demuestra tener similaridades con *C. tonduzii* y *C. vulcanalis*. Se ofrecen llaves revisadas de las especies de la section *Longifoliae* y la section *Swallenochloa* en Costa Rica.

En el capítulo 2 se presentan los resultados de un estudio de reconocimiento de la vegetación y los suelos en los Cerros Cuericí y en Cerro Abarca. Las parcelas de estudio debían contener una de las especies de *Chusquea* presentes en el área (*C. talamancensis*, *C. tomentosa* o *C. foliosa*) y representar uno de los diferentes tipos de cobertura del dosel arbóreo (dosel denso, dosel intermedio o claro). Con base en un análisis de coordenadas principales de los datos florísticos se reconocieron ocho comunidades vegetales que parecen estar asociadas a diferencias en la topografía, características de suelo y cobertura del dosel arbóreo. Las especies de *Chusquea* pueden ser indicadoras de situaciones topográficas y de tipos de suelo específicos. Los datos sobre la distribución del tamaño de árboles muestran que existe un efecto inhibitorio del bambú sobre el crecimiento de los árboles en los claros.

El capítulo 3 examina en mayor detalle las condiciones de suelo asociadas con *Chusquea talamancensis*, *C. tomentosa* y *C. foliosa*, y presenta datos sobre el pH del suelo, contenido de materia orgánica y concentraciones de macronutrientes. Los suelos que llevan las diferentes especies de *Chusquea* eran generalmente ácidos (pH 3.3-6.0) y son derivados de ceniza volcánica.
Sin embargo, especies de bambúes individuales tienen diferentes requerimientos en términos de condiciones de suelo. Los suelos con *C. talamancensis* eran más ricos en materia orgánica, tenían una mayor relación C:N y eran más ácidos que aquellos con *C. tomentosa* ó *C. foliosa*. *C. tomentosa* crecía en suelos más ricos en nutrimentos que las otras dos especies.

En el capítulo 4 se describe el efecto de la cobertura del dosel arbóreo sobre el crecimiento y la distribución espacial de las tres especies de *Chusquea*. Las macollas de todas las especies tienden a ser pocas y grandes en condiciones abiertas, y numerosas y pequeñas bajo condiciones de sombra. La menor densidad de macollas en claros implica que existe una mayor competencia intraespecífica y mortalidad dependiente de la densidad cuando los bambúes son dominantes bajo condiciones lumínicas favorables. Las especies se diferencian en su respuesta a las condiciones de luz: *C. tomentosa* y *C. foliosa* presentan un mayor grado de plasticidad morfológica comparadas con *C. talamancensis*, que por su lado, parece ser más tolerante a la sombra.

El capítulo 5 trata de la floración en masa de *C. talamancensis*, *C. tomentosa*, y *C. subtilis* entre 1987 and 1990, seguida por la muerte de todas las plantas. Los diferentes estadios fenológicos estaban asociados al patrón de precipitaciones estacionales. La formación de la flor, del fruto y la germinación de las semillas ocurrieron en la estación lluviosa, mientras que la polinización, la maduración del fruto y la caída del fruto acontecieron en la estación seca. A nivel de la población se observaron diferentes fases de la floración en cohortas. No hubo producción de semillas cuando florecían plantas aisladas, lo que indica que el éxito reproductivo es dependiente de la polinización cruzada.

El capítulo 6 presenta observaciones sobre la distribución y la floración de seis especies de *Chusquea* en el noroeste de la Cordillera de Talamanca. Las especies más abundantes de bambúes *Chusquea* (*C. foliosa, C. longifolia, C. patens, C. subtilis, C. talamancensis* y *C. tomentosa*) muestran una zonación altitudinal y diferencias en la distribución entre la vertiente atlántica y la pacífica. *C. longifolia* está asociada al Bosque Montano Bajo, *C. foliosa* y *C. patens* a los Bosques Montano Bajo y Alto. *C. subtilis*, *C. talamancensis* y *C. tomentosa* están asociadas al Bosque Montano Alto. En el área de estudio florecieron en masa las seis especies con traslape interespecífico de los periodos de floración en un período de diez años.
En la discusión se concluye que las especies de *Chusquea* tienen una gran influencia en la dinámica de los bosques de *Quercus*. La floración y la muerte del bambú es probablemente el tipo de perturbación más importante en estos bosques y la regeneración arbórea está acoplada a estos eventos. Con respecto a la evolución del ciclo de vida de los bambúes, se hipotetiza que el medio boscoso habrá sido la fuerza motriz para la selección de la floración periódica de los bambúes.
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APPENDIX
Table 1. List of the fifty-four 500 m² plots selected upon 'Chusquea species' and 'canopy closure' with the parameters altitude, aspect and slope angle. Soil types were classified based on soil description (see Chapter 2; N.D. not described). Soil samples are referred to in Chapter 3.

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<th>Aspect</th>
<th>Slope [°]</th>
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Table II. List of plant species recorded in the study area. The vernacular names are those used by the local field assistants. Species not fully identified are shown with the numbers of herbarium specimens (HN: Herbario Nacional de Costa Rica, HZH: Zürich Herbarium, NY: Herbarium New York Botanical Garden). Species with * were not in the study plots.

**MAGNOLIOPHYTA: DYCOTYLEDONEAE**

**Apiaceae**
- *Hydrocotyle pusilla* A. Rich
- *Hydrocotyle ribifolia* Rose & Standl.

**Aquifoliaceae**
- *Ilex lamprophylla* Standley
- *Ilex pâlida* Standley
- *Ilex sp. N° 600HN*
- *Ilex tristis* Standley

**Araliaceae**
- *Oreopanax capitatus* Decné & Planchón
- *Oreopanax echinops* (Schdl. & Cham) Decné & Planchón
- *Oreopanax xalapense* (Kunth) Decné & Planchón
- *Schefflera aff. styrilasa* (Donn.Sm.) Viquier
- *Schefflera pittieri* (Marchal) Frodin

**Asteraceae**
- *Ageratina subcordata* (Benth.) R. King & H. Robinson
- *Cirsium subcoriaceum* (Less.) Petr.
- *Clibadium? N° 111HN*
- *Asteraceae? N° 317HN*
- *Asteraceae? N° 323HN*
- *Asteraceae N° 325HN*
- *Asteraceae N° 334HN*
- *Asteraceae N° 341HN*
- *Erectites cf. valerianifolia* (Wolf) DC.
- *Gnaphalium sp. N° 219KW*
- *Jungia ferruginea* L.F.
- *Liabum sp. N° 320HN*
- *Mikania ilicissii* R.King H.Robins
- *Mikania sp. N° 875HN*
- *Munnozia aff. seneciodinis* Benth.
- *Senecio copeynsis* Greenm.
- *Senecio heterogamus* (Benth.) Hemsley
- *Senecio multivenius* Benth.
- *Senecio? N° 720HN*
- *Sigesbeckia jorullensis* Kunth

**Begoniaceae**
- *Begonia usysylvestris* C. DC.

**Berberidaceae**
- *Mahonia sp. N° 324HN*

**Caprifoliaceae**
- *Viburnum costaricanum* (Oersted.) Hemsley
- *Viburnum sp. N° 333HN*

**Caryophyllaceae**
- *Arenaria lanuginosa* (Hichx.) Rohrb.
Stellaria cuspidata Willd.

Celastraceae
Crossoptetalum tonduzii (Loes.) Lundell

Chloranthaceae
Hedwosnum bonplandianum Kunth

Clethraceae
Clethra gelida Standley
*Clethra molinae Standley & L.O. Williams

Clusiaceae
*Clusia sp. N° 266NY

Cornaceae
Cornus disciflora Mociño & Sessé

Cruciferae
Cardamine ovata Benth.

Cunoniaceae
Weinmannia pinnata L.
Weinmannia trianea Wedd. var. sulcata (Engl.) Cuatrecasas

Ericaceae
*Cavendishia bracteata (R.L. & P. ex J.St.Hil.) Hoer
*Cavendishia cf. crassifolia (Benth) Hemsl.
*Distigma homboldtii (Kl.) Nied.
*Gaultheria odorata Willd.
Macleania rupestris (Kunth) A.C. Smith
*Pernettya prostrata (Cav.) D.C.
*Satyraria warsewieszii Klotzsch
*Sphyrospermum cordifolium Benth.
Vaccinium consanguineum Klotzsch

Fagaceae
Quercus copeyensis Corn. Mueller
Quercus costaricensis Liebm.
*Quercus seemanii Liebm.
Quercus sp.

Flacourtiaceae
Abatia parviflora Ruiz López & Pavón

Gesneriaceae
Alloplectus ichtyoderma Hanst.
Gesneriaceae N° 81HN

Grossulariaceae
*Escallonía myrtilloides L.f.

Hydrangeaceae
Hydrangea asterolasia Diels

Labiatae
Salvia iodochroa Briq.

Lauraceae
Nectandra aff. salicifolia (Kunth) Nees
Ocotea austini Allen
Ocotea calphylla Mez.
Ocotea pittieri (Mez) van der Werff
Persea vesticula Standley & Steyerm.

Loasaceae
Loasa speciosa Donn. Sm.

Loranthaceae
Gaiadendron punctatum (R.L. & P.) Don.

Magnoliaceae
Magnolia sororum Seib.

Melastomataceae
Miconia aff. sterilis Gleason

berrito corazón
copado
agüilla
madroño hoja grande, nance
nance
azahar bejucos, azahar
lloró
arracachillo
arrayán
arrayán blanco
tornillo
tornillo
escarchado
ericácea epífita
cabezón
madroño (escarchadillo)
tornillo
huponcílllo
madroño
roble
encino
encino colorado
caragreira, puposo
lanita
bejucos redondo
carnitoro, escarchado
bejucos resina
chicoria
aguacatillo
íra rosa
yema huevo
quizarra amarillo, íra amarillo
ascá
ortiga
bejucos morado
magnolia
uña de gato
Miconia carnea Cogn.
*Miconia schnelli Wurd.
Miconia sp. 1 N° 112HN
Miconia sp. 2 N° 639HN
Miconia sp. 3 N° 651HN
Miconia sp. 4 N° 596HN
Miconia sp. 5 N° 240HN
Miconia tonduzii Cogn.

Myrsinaceae
Ardisia compressa Kunth
Ardisia glandulosos-marginata Oersted
Grammadenia myricoides (Schdl.) Lundell
pellucido-punctata (Oersted.) Mez
Myrsine pittieri (Mez) Lundell

Myrthaceae
Myrcianthes fragans (Sw.) DC.
Myrcianthes storkii (Standley) McVaugh

Onagraceae
Fuchsia arborescens Sims
Fuchsia microphylla H.B.K.
Fuchsia paniculata Lindley

Oxalidaceae
Oxalis vulcanicola Donn.Sm.

Passifloraceae
*Passiflora membranacea Benth

Phytolaccaceae
Phytolaca rugosa Braun & Bouché

Piperaceae
Peperomia alata R. & P.
Peperomia cf. elata C.D.C.
Peperomia dotana Trel.
Peperomia esperanzae Trel.
Peperomia galioides Kunth
Peperomia hispidula (Swartz) A.Dietr.
*Peperomia lancifolia Hooker
Peperomia reptabunda Trel.
Peperomia salicina H.B.K.
Peperomia tetraphylla (Forst.) Hooker & Arnott
Piper lacunosum Trel.
Piper pittieri C. DC.

Polygalaceae
Monnina crepinii Chodat
*Monnina zalapensis Kunth

Polygonaceae
Muehlenbeckia thammifolia (Kunth) Meissner

Rhamnaceae
Rhamnus oreodendron L.O. Williams

Rosaceae
*Prunus cornifolia Kochne
Rubus adnotrichus Schlecht.

Rubiaceae
Borreria sp. N° 347HN
Borreria sp. N° 203HN
Nertera granadensis (Mutis ex L.f.) Druce
Palicourea adusta Standley
Palicourea salicifolia Standley

Rutaceae
Zanthoxylum chiriquinum Standley
Zanthoxylum melanostictum Schldl. & Cham
Zanthoxylum scheryi Lundell

Sabiaceae
Meliosma glabrata (Liebm.) Urban.

Saurauiaceae
Saurauia rubiformis Vatky

Scrophulariaceae
*Calceolaria irazuensis J.D. Sm.
*Calceolaria mexicana Benth
*Castilleja sp. N° 217HN

Solanaceae
Cestrum irazuense Kuntze
Deprea orinoeensis (Kunth) Raf.
*LYcianthes sp. N° 355HN
*Solanandra bractealax Kuntze
Solanum sp. N° 377HN
Solanum vacciniflorum Standley & L.O. Williams
Solanum trizygum Bitter
Witheringia solanacea L'Hér.
Witheringia sp. N° 110HN

Styracaceae
Styrax argentus Presl.

Symplocaceae
Symplocos austin-smithii Standley
Symplocos serrulata Kunth
Symplocos sp. N° 148HN
*Symplocos sp. N° 374HN
Symplocos sp. N° 369HN

Theaceae
Cleyera theaeoides (Sw.) Choisy

Tropaeolaceae
Tropaeolum emarginatum Turcz.

Urticaceae
*Phenax sp. N° 798HN
*Pilea angustifolia Killip.
Pilea cornutocucullata Cufodontis
Pilea dauciodora Wedd.
Pilea gracilipes Killip.

Verbenaceae
Aegiphila odontotphila J.D. Smith
Verbenaceae? N° 372HN

Violaceae
Hybanthus aff. attenuatus (Humb. & Bonpl.) Schultze
Viola nannei Pollak
Viola scandens Willd.

Winteraceae
Drimys granadensis L.f.

Unknown
*Unknown tree N° 638HN
*Unknown herb N° 149HN

MAGNOLIOPHYTA: MONOCOTYLEDONEAE

Alstroemeriaceae
Bomarea acutifolia (Link & Otto) Herb.

lagartillo
urucu
lagartillo
omegá
anonillo, nance hoja grande
gesni
falso chiberrillo
herba ciprés
zorriho hoja menuda
chilillo
codo largo
cabezon peludo
ozo
zorriho
tomatiho
sulfato
codo
resina
anonillo
cuerillo
piquete
anonillo hoja peluda
nance
tífora
recta
volcancito
cerrito flor blanca
serruchito
rosadita
rosadita larga
salvia
fenicera
serrucho sin v
v-corazón
cornaza
chilemuela
azullillo hoja mediana
base ancha
papa venado
Araceae

*Anthurium concinnatum* Schott.

Arecaceae

*Chamaedorea parviflora* Burret

Bromeliaceae

*Greigia sylvicola* Standley

*Guzmania* sp. N° 100HN

*Vriesea williamsii* L.B.Smith

Campanulaceae

*Burmeistera* sp. N° 329HN

*Centropogon costaricensis* (Vatke) McVaugh

*Centropogon* sp. N° 186HN

*Centropogon valerii* Standley

Commelinaceae

*Callisia* aff. *repens* (Jacq.) L.

*Tradescantia poelliae* D.R. Hunt

Convallariaceae

*Maianthemum* sp. N° 871HN

*Maianthemum paniculatum* (Martens & Galeotti) La Frankie

Cyperaceae

*Carex bonplandiana /distachya*

*Cyperaceae* N° 160HN

*Rhynchospora aristata* Boeck.

*Uncinia hamata* (Sw.) L'Her.

Orchidaceae

*Epidendrum* sp. N° 704HN

*Erythodes secunda* Ames

*Goodyera striata* Rchb.f.

*Malaxis* sp. N° 855HN

*Orchidacea* N° 703HN

*Orchidacea* N° 758HN

*Pelexia funckiana* (Rich. & Gal.) Schltr.

Poaceae

*Chusquea foliosa* Clark

*Chusquea longifolia* Swallen

*Chusquea patens* Clark

*Chusquea talamancensis* Widmer & L.G.Clark

*Chusquea tomentosa* Widmer & L.G.Clark

*Chusquea subtessellata* Hitchcock

*Chusquea subtilis* Widmer & L.G.Clark

Smilacaceae

*Smilax* sp. N° 688HN

*Smilax* sp. N° 352HN

PYNOPHYTA

Podocarpaceae

*Podocarpus macrostachyus* Parl.

*Prumnopitys standleyi* (Buchholz & N. Gray) Laubef.

PTERIDOPHYTA

Aspleniaceae

*Asplenium castaneum* Schlechtend & Cham.

*Asplenium cuspidatum var.foeniculaceum* (HBK) Morton & Lell.

*Asplenium luteum* (L.) Sw.

*Asplenium trichomanes* L.
Asplenium harpeodes Kunze
Asplenium miradorense Liebm.
Asplenium monanthcs L.
Asplenium polyphyllum Bertol.
Asplenium serra Langsd. & Fischer
Asplenium sessilifolium Desv.
*Asplenium squamosum L.
Blechnaceae
Blechnum falciforme (Liebm.) C.Chr.
Blechnum fragile (Liebm.) Morton & Lellinger
*Blechnum maxonii (Broadhurst) C.Chr.
Cyatheaceae
Cyathea divergens Kunze
Cyathea cf. suprastrigosa (H.Christ) Maxon
Dennstaedtiaceae
Histiopteris incisa (Thunb.) J. Smith
Hypolepis N° 13HZH
Paesia anfractuosa (Christ.) C.Chr.
Pteridium aquilinum (L.) Kuhn
Dicksoniaceae
Culcita conifolia (Hooker) Maxon
Cibotium sp. N° 301HN
Dryopteridaceae
*Arachnioides denticulata (Swartz) Ching
Dryopteris parallelogram (Kunze) Alston
Polystichum sp. N° 10HZH
Grammitidaceae
Grammitis moniliformis (Sw.) Proctor
Hymenophyllaceae
Hymenophyllum polyanthos (Swartz) Swartz
Lomariopsidaceae
*Elaphoglossum biollevii Christ
*Elaphoglossum erinaceum (Fée) Moore
Elaphoglossum eximium (Mett.) Christ
Elaphoglossum furruraceum (Mett. ex Kuhn) Christ
Elaphoglossum hoffmannii (Mett. ex Kuhn) Christ
Elaphoglossum latifolium (Sw.) J.Smith
Elaphoglossum muscosum (Sw.) Moore
Elaphoglossum paleaceum (Hook. & Grev.) Sledge
Elaphoglossum papillosum (Baker) Christ
Elaphoglossum tondzii (Christ) Christ
Plagiogyriaceae
Plagiogyria costaricensis (Presl.) Christ
Plagiogyria semicordata (Presl.) Christ
Polypodiaceae
Campyloneuron amphostenon (Kunze ex Kl.) Fée
Campyloneuron multipunctatum (Christ.) Lell.
*Campyloneuron sp. N° 418HZH
Campyloneuron wercklei (Christ.) Lellinger
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.
=Polypodium lanceolatum
Polypodium eurybasis C.Chr.
Polypodium loricatum L.
Polypodium montigenum Maxon
Polypodium myriolepis Christ
Polypodium sp. N° 70HN
Pteridaceae
**Cheilantes chaerophylla** Kunze  
**Eriosorus flexuosus** (HBK) cord.  
**Eriosorus villosulus** (Maxon) Scamman

### Tectariaceae
- *Ctenitis* sp. N° 41HZH  
- *Ctenitis* sp. N° 49HZH  
- *Ctenitis* sp. N° 42HZH  
- *Ctenitis* sp. N° 48HZH

### Thelypteridaceae
- *Thelypteris delasotae* A.R. Smith & Lellinger  
- *Thelypteris frigida* A.R. Smith & Lellinger  
- *Thelypteris gomeziana* A.R. Smith & Lellinger

### Vittariaceae
- *Vittaria graminifolia* Kaulf.

### Woodsiaceae
- *Athyrium dombevii* Desv.  
- *Displazium* sp. N° 305HN

### Unknown ferns
- *Pteridophyta* N° 306HZH  
- *Pteridophyta* N° 386HZH  
- *Pteridophyta* N° 471HZH  
- *Pteridophyta* N° 476HZH  
- *Pteridophyta* N° 494HZH

### STENOPHYTA

#### Equisetaceae
- *Equisetum aff. bogotense* Kunth

#### LYCOPHYTA

#### Selaginellaceae
- *Selaginella cf. flagellata* Spring

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- **bordeado**  
- **pulpo**  
- **chumico**  
- **chumico escamoso**  
- **chumico opuesto**  
- **chumico picudo**  
- **chumico dedo**  
- **chumico pegado**  
- **denteado**  
- **tubito**  
- **manita, pinchito**  
- **entreverado**  
- **recto**  
- **chumico**  
- **benjamín**  
- **puñio**  
- **chumico**  
- **palitos**

- **ciprés rastrero**
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<th>Israel I</th>
<th>Israel II</th>
<th>Abundance</th>
<th>Gavriel I</th>
<th>Gavriel II</th>
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Table III. Presence-absence vegetation table of the study plots in the Cedroillas de Talavera.
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<th>Presence/absence table of the study plots in the Condatina de Tulumarca.</th>
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<td>Parthenium argentatum</td>
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<td>154</td>
<td>Falloperis salina</td>
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<td>Parthenium capitatum</td>
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<td>Raphiolepis celtoides</td>
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<td>Pericloom capitatum</td>
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<td>Myrtus communis</td>
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</table>
CURRICULUM VITAE

February 22, 1959  Born in Cali, Colombia
Citizen of Dietikon (ZH) and Tägerwilen (TG);

1966 - 1972  Primary School in Buenos Aires, Argentina (Goethe Schule) and Caracas, Venezuela (Humboldt Schule);

1973 - 1978  Secondary School in Buenos Aires, Argentina (Goethe Schule);

1979 - 1984  Study of Biology, University of Zürich
Diploma in Botany on 'Leaf temperatures and cold night sky: a comparison of growth forms of succulent dwarf shrubs' (in German);

1982 - 1984  Teaching assistant in general biology courses at Zürich University;

1984 - 1987  Language teacher at the Bénédict School, Zürich;

1985 - 1986  Postgraduate Course for Developing Countries (NADEL) at the Swiss Federal Institute of Technology Zürich, four month practical experience in Costa Rica;

1986  Beginning of the dissertation at the Geobotanical Institute, Swiss Federal Institute of Technology Zürich (ETHZ);

1986 - 1987  Teaching assistant in ecology courses at the ETHZ;

1987 - 1990  Field work for the dissertation at the Silviculture of Natural Forests Project (SBN) in the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Costa Rica;
Supporting teaching staff in the Natural Forest Management course at CATIE;
Part-time responsible for the Herbarium of the SBN at CATIE;

1989 - 1990  Master thesis advisor of Freddy Rodríguez Quirós at the Instituto Tecnológico de Costa Rica (ITCR);
Scientific advisor to the Costa Rican National Bamboo Project;

1991 - 1996  Teaching assistant in terrestrial ecology at the ETHZ.
OTHER PUBLICATIONS ON BAMBOO NOT INCLUDED IN THE THESIS


UNPUBLISHED REPORTS ON BAMBOO
