

DIVERSITY AND BIOGEOGRAPHY OF NEOTROPICAL BAMBOOS (POACEAE: BAMBUSOIDEAE)

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RESUMO — O presente trabalho analisa a distribuição geográfica dos bambus do Novo Mundo. Por questões práticas, os bambus foram divididos em dois grupos: os bambus lenhosos e os herbáceos, essas categorias entretanto, nem sempre refletem relacionamentos filogenéticos, pois embora as Bambuseae incluam todos os bambus lenhosos, sendo portanto provavelmente monofiléticos, os bambus herbáceos são classificados em oito tribos. No Novo Mundo, (incluindo os taxa ainda não descritos) existem cerca de 45-46 gêneros e aproximadamente 515 espécies. Desses gêneros, apenas dois: *Arundinaria* e *Streptogyna* não são exclusivamente neotropicais. A área de maior endemismo e diversidade do grupo, está nas florestas costeiras da Bahia, Brasil. Nesta região são encontrados 22 gêneros, representando 48% de todos os gêneros neotropicais e desses, 5 são exclusivos desta região da Bahia.

Palavras-chave: bambus, Gramineae, neotropical, endemismo.

ABSTRACT — The present paper analyses the distribution of bamboos in New World. For convenience, bamboos are divided into two broad groups, the woody bamboos and the herbaceous bamboos. These categories do not necessarily reflect phylogenetic relationships among bamboo groups. The Bambuseae includes all of the woody bamboos and is probably monophyletic, whereas the herbaceous bamboos are classified into eight tribes. In the New World (including undescribed taxa), 45-46 genera and approximately 515 species are represented; only two genera: *Arundinaria* and *Streptogyna* are not exclusively neotropical. The area of greatest endemism and diversity is the humid coastal forests of Bahia, Brazil. 22 genera have been found in this relatively small area, representing 48% of all New World genera. Five of the 22 genera are endemic to the Bahia coastal forests.

Key-words: bamboos, Gramineae, neotropical, endemism.

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Introduction

The grasses (Poaceae) are the fourth largest family of flowering plants, with approximately 600-700 genera and 10,000 species (Campbell, 1985). In addition to their paramount importance as crop plants, grasses are numerous and widespread, occurring in virtually every terrestrial habitat. Diverse in every aspect, the grass family is currently divided into five subfamilies, each encompassing one or more major evolutionary lines. One of these subfamilies is the Bambusoideae, which includes the true bamboos, and probably rice (*Oryza* L.) and related genera as well.

Results and discussion

Bamboos are distinguished from other grasses by their perennial habit, well developed rhizomes, distinctive seedlings, often strongly lignified culms, pseudopetiolate leaves, special leaf-blade anatomy, nonseasonal flowering, frequently trimerous reproductive structures, and chromosome number (Calderón and Soderstrom, 1980). Worldwide, there are about 89 (-90) genera and 1035 species of bamboos (Table 1); New World bamboos account for approximately half of the total generic and specific bamboo diversity (Table 2). The fossil record for bamboos is virtually non-existent, so that any conclusions regarding their historical biogeography must be drawn from modern distribution patterns.

For convenience, bamboos are divided into two broad groups, the woody bamboos and the herbaceous bamboos (or herbaceous bambusoid grasses). These categories do not necessarily reflect phylogenetic relationships among bamboo groups. The Bambuseae includes all of the woody bamboos and is probably monophyletic, whereas the herbaceous bamboos are classified into eight tribes (Table 1). Woody bamboos have well developed, sometimes massive rhizomes, strongly lignified culms, new shoots bearing specialized culm leaves, complex branching, and usually cyclical, monocarpic flowering (Calderón and

Table 1. Diversity in the Bambusoideae s. s. (excluding rice and its allies).

Total diversity: 89 (-90) genera + \pm 1035 species

Bambuseae: Worldwide; \pm 65 genera; \pm 1000 species

Olyreae: Neotropical (1 species in Africa); 18 (-19) genera; 120 species

Phareae: Pantropical; 3 genera; 12 species

Streptochaeteae: Neotropical; 1 genus; 3 species

Streptogyneae: Pantropical; 1 genus; 2 species

Anomochloae: Neotropical; 1 genus; 1 species

Guaduelleae: Paletropical (Africa); 1 genus; 6 species

Puelieae: Paleotropical (Africa); 1 genus; 5 species

Buergersiochloae: Paleotropical (New Guinea); 1 genus; 1 species

Table 2. Biogeographic diversity of bamboos (including undescribed taxa).

	New World		Old World	
	Genera	Species	Genera	Species
Woody	23*	± 380	40*	± 500
Herbaceous	23**	± 135	6**	18
Total	45(-46)	± 515)	46	± 520

* *Arundinaria* occurs in both hemispheres.
 ** *Streptogyne* occurs in both hemispheres

Soderstrom, 1980). Setting the limits for the subfamily as a whole, woody bamboos range in distribution from 46° N latitude to 47° N latitude, and in altitude from sea level to well over 4000 m elevation in equatorial highlands. Herbaceous bamboos have less well developed rhizomes, only slightly lignified culms, and very restricted branching. They lack specialized culm leaves, and flowering, while not strictly seasonal, is not known to be cyclical. Herbaceous bamboos occur between 29° N latitude and 34° S latitude, and are rarely found above 1000 m elevation (a very few species are exceptional in that they may occur at elevations of up to 2000 m in the Andes) (Calderón and Soderstrom, 1980).

Worldwide, 28 herbaceous and 61 woody genera are currently recognized (not including 2-3 as yet undescribed genera) (Table 2), representing approximately 10% of the diversity of the grass family. In the New World (including undescribed taxa), 45 (-46) genera and approximately 515 species are represented; only two genera, *Arundinaria* Michaux and *Streptogyne* Palisot de Beauvois, are not exclusively neotropical. At the generic level, diversity is almost evenly divided, with 22 (-23) herbaceous and 23 woody genera. But the neotropical woody bamboos (ca. 380) contribute over two and a half times as many species as do the herbaceous bamboos (ca. 135). About a third of the woody bamboo species belong to one genus, *Chusquea* Kunth. It is evident that South and Central America represent a major center of bamboo diversity. This is particularly striking in the case of herbaceous bamboos, in which 80% of total diversity is neotropical. Soderstrom et al. (1988) provide an annotated list of all neotropical bamboo genera, both woody and herbaceous, including estimates of species diversity and brief comments on distribution and habitat, as well as distribution maps for many of the genera. Since then, *Parodiolyra* Soderstrom & Zuloaga, a herbaceous genus with three species, has been described (Soderstrom and Zuloaga, 1989).

Members of various grass groups often form large associations such as prairies, savannas, and campos, where they are the dominant element. In contrast, bamboos are almost exclusively associated with woody vegetation (Soder-

strom and Calderón, 1979). In many regions, bamboos are an important, characteristic component of tropical and subtropical forests, although some taxa are adapted to other habitats (e.g., páramos, cerrado, or cliff faces near waterfalls). Within the forest, or even at higher elevations in the páramo, a few woody bamboo species (primarily of *Guadua* Kunth and *Chusquea*) can occur in extensive, almost pure stands known as "taquarais" (singular "taquaral"). The herbaceous bamboos are generally restricted to warm and humid tropical zones in the shady understory of rain forests. No truly aquatic bamboos are known, but some taxa are xerophytic.

Study of the biogeography of neotropical bamboos has been and continues to be limited by a lack of adequate collected material. The large and bulky woody bamboos are frequently ignored entirely, or if collected, specimens are usually incomplete. In addition, because woody bamboos usually flower cyclically, often at intervals of 10, 20, 30, or 50 or more years, there is the problem of lack of flowering material, making correct identification of species even more difficult. Herbaceous bamboos are much easier to collect but tend to be overlooked on the forest floor due to their small stature and inconspicuous inflorescences. In many instances, our knowledge of a species is based on only one or very few specimens. This obviously affects estimates of species variability and range, and consequently endemism. Nonetheless, our knowledge has increased greatly even within the last few years, and some reliable estimations of biogeographical patterns in neotropical bamboos have emerged, although many gaps remain.

The area of greatest endemism and diversity is the humid coastal forests of Bahia, Brazil. Twenty-two genera have been found in this relatively small area, representing 48% of all New World genera. Five of the 22 genera are endemic to the Bahian coastal forests (Table 3); these include the extremely rare herbaceous bamboo, *Anomochloa* Brongniart, and four woody bamboos: *Alvimia* Soderstrom & Londoño, *Atractantha* McClure, *Criciuma* Soderstrom & Londoño, and *Eremocaulon* Soderstrom & Londoño. About 62 bamboo species occur there, of which 27 are endemic. The other genera that occur in this region are not restricted to it, but show connections to other regions with the same or usually different species. These genera include *Arberella* Soderstrom & Calderón, *Athroostachys* Bentham, *Aulonemia* Goudot, *Chusquea*, *Cryptochloa* Swallen, *Diandrolyra* Stapf, *Eremitis* Doell, *Guadua*, *Merostachys* Sprengel, *Olyra* L., *Pariana* Fusée-Aublet, *Pharus* P. Brown, *Piresia* Swallen, *Raddia* A. Bertoloni, *Streptochaeta* Nees von Esenbeck, *Streptogyna*, and *Sucrea* Soderstrom.

The Atlantic forest continues toward the south to Rio de Janeiro and São Paulo. There are four genera restricted to this zone. *Sucrea*, *Diandrolyra*, and *Eremitis* are herbaceous bamboos found only in the Brazilian Atlantic forests. *Athroostachys* is a woody bamboo from this area. *Raddia* is another herbaceous bamboo of this forest with additional species represented in the Guianan flora. *Piresia* has endemic species in Bahia with other distinct species in the Guianas

Table 3. Genera of bamboos endemic to Brazil.

Woody	Herbaceous
* <i>Alvimia</i>	* <i>Anomochloa</i>
<i>Apoclada</i>	<i>Diandrolyra</i>
<i>Athroostachys</i>	<i>Eremitis</i>
* <i>Atractantha</i>	<i>Reitzia</i>
<i>Colantheria</i>	<i>Sucrea</i>
* <i>Criciuma</i>	
* <i>Eremocaulon</i>	
<i>Glaziophyton</i>	
* Endemic to Bahia.	

and the Amazonian forests, showing a different type of floristic connection. Two herbaceous genera, *Pariana* and *Arberella*, extend as far as Central America. *Pariana* is more diverse in Amazonia, whereas *Arberella* is more diverse in Panama and Costa Rica than in Bahia where only one collection of a new species has been made. A number of the genera represented in Bahia and the Atlantic forest are widespread and exhibit no discernible special phytogeographic connections as in the above cases. These genera include: *Aulonemia* (Mexico to Rio Grande do Sul), *Chusquea* (Mexico to Argentina and Chile), *Cryptochloa* (Mexico and Central America to Ecuador with one species in Amazonia), *Guadua* (Mexico to Argentina), *Merostachys* (Guatemala, to Rio Grande do Sul), *Olyra* (Mexico to Argentina), *Pharus* (Mexico to Argentina), *Streptochaeta* (Mexico to southern Brazil), and *Streptogyna* (tropical America, Africa, and South Asia). Other widespread genera but with no species in Bahia include *Arthrostylidium* Ruprecht, *Elytostachys* McClure, *Lithachne* Palisot de Beauvois, and *Rhipidocladum* McClure.

There are three genera (two woody and one herbaceous) endemic to the south of Brazil, in the Serra do Mar from Rio de Janeiro to Santa Catarina. *Colantheria* McClure & E. W. Smith, with seven species, is related to *Arthrostylidium* and probably replaces it in this zone. The other, *Glaziophyton* Franchet, is a very strange, monotypic genus, known only from the misty summits of two morros in the Serra dos Órgãos. *Reitzia* Swallen, a monotypic herbaceous genus, occurs at the base of the mountains in humid forests along streams in the states of São Paulo and Santa Catarina.

Two genera of herbaceous bamboos, *Froesiochloa* G. A. Black and *Rehia* Fijten, are endemic to the Guianas. *Myriocladus* Swallen, a woody bamboo of ca. 20 species, is endemic to the tepuis. There are two herbaceous genera endemic to Cuba, and *Arthrostylidium* has more or less 10 species endemic to the Caribbean islands. Mexico possesses moderate diversity, with eight genera (two endemic) and 32 species of woody bamboos as well as several herbaceous species. Southern Central America (Costa Rica and Panama) has 21 genera and

approximately 65 species of bamboos, giving it the most diverse bamboo flora outside of Atlantic Brazil.

The Andes of South America are extremely rich in woody bamboo species, and represent the center of diversity for the speciose genera *Chusquea* and *Aulonemia*. *Neurolepis* Meisner is important in the páramos, and *Guadua* is well represented at lower elevations. The Chocó region is relatively poor in bamboos. It is interesting that the Amazon basin is relatively poor with respect to the woody bamboos, with a few species of *Guadua* and possibly *Arthrostylidium*, although it has a moderate diversity of herbaceous bamboos, and is the center of diversity for *Pariana* and *Olyra*.

Although the data are far from complete, some general patterns are evident. (1) The Bahian coastal moist forest has the highest degree of bamboo diversity and endemism in the New World, and it corresponds to proposed refugia. However, in neither Bahia nor elsewhere can we find a concentration of recognizably primitive genera or species as was postulated by Soderstrom and Calderón (1974); further studies of the anatomy and morphology of putatively primitive groups such as *Anomochloa* and *Streptochaeta* have revealed them to be in fact specialized taxa. (2) Southern Mesoamerica (Costa Rica/Panama) approaches the Bahian area in generic diversity and probably surpasses it in species diversity but does not have the same level of endemism, although there is one endemic genus and a number of endemic species. (3) At least for herbaceous bamboos, which are better known taxonomically than woody genera, greatest species diversity and endemism is found at approximately 10-15° on either side of the equator, and diversity diminishes noticeably near the equator (Figure 1).

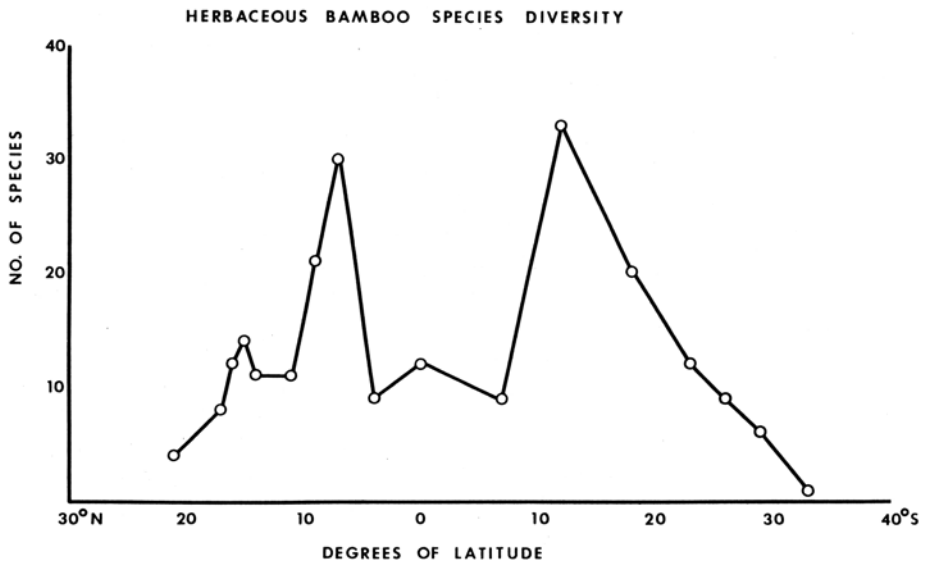


Figure 1.

(4) Particularly in woody bamboos, much of the diversity is associated with radiation into montane habitats, primarily along the Andean range, but secondarily in the mountains of Central America, the tepuis, and the Serra do Mar of Brazil. The diversity of endemic woody genera in lowland Bahia does, however, provide an exception to this generalization. (5) The forests of the Amazon Basin are relatively poor in bamboos, especially in woody taxa, as are the wet forests along the Pacific coast of Colombia, although the latter area is undercollected.

According to my best estimate, 36 genera (17 woody and 19 herbaceous) and about 187 species (100 woody and 87 herbaceous) of bamboos occur in Brazil. Thus, 80% of the genera and 36% of the species of neotropical bamboos are found in Brazil, a rich diversity indeed. Thirteen, or nearly one third, of the genera are endemic to Brazil (Table 3); data for species is less precise, but probably at least 50 of the 187 species are endemic. With the exception of the Atlantic forest endemics, woody bamboo diversity in Brazil is more or less comparable to that found in the northern Andes or in Costa Rica/Panama, especially at the species level (75% of the genera, 26% of the species). Most striking is the fact that 80% of herbaceous bamboo genera and 64% of herbaceous bamboo species occur in the humid forests of Brazil.

Thanks to the efforts of T. R. Soderstrom, C. E. Calderón, E. J. Judziewicz, F. Zuloaga, and V. Hollowell, the taxonomy of the herbaceous bamboos in Brazil and elsewhere is relatively complete, but still lacking are much fundamental data on the basic biology of these plants, especially ecology and reproductive biology. Their long flowering cycles, complex morphology, and lack of good collections in general have caused basic systematic studies in the woody bamboos to lag far behind those in other grass groups, including the herbaceous bamboos. No monographs for any of the major genera are available, and there are many undescribed species. As with the herbaceous bamboos, little ecological data relating specifically to woody bamboos has been published, although studies are underway in Costa Rica and Ecuador. In Brazil, Soderstrom and Calderón did much over the last 20 years to upgrade collection quality, but the basic taxonomic work remains to be done.

Anomochloa marantoidea Brongniart is known from only two wild populations, and is certainly endangered and now possibly extinct in the wild. We do not have enough data about the other bamboos to assess their current status, but virtually all taxa, particularly those of the Bahian coastal forest, are threatened or endangered due to habitat destruction. For any group, not just bamboos, obviously the highest priority belongs to habitat preservation, not only of rainforests but montane forests, cerrado, and campo rupestre and others as well. Unfortunately, such efforts will be too late for some areas, but others may still be preserved.

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