BAMBOO SCIENCE & CULTURE

The Journal of the American Bamboo Society

Volume 19

BAMBOO SCIENCE
&
CULTURE
The Journal of the American Bamboo Society

is published by the
American Bamboo Society

ISSN 0197– 3789

Bamboo Science and Culture: The Journal of the American Bamboo Society
is the continuation of ***The Journal of the American Bamboo Society***

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On the cover: *Arundinaria gigantea* habit with leaf and branch complement insets, from the population described by Platt *et.al.* on pgs. 30-31 of this issue. Photo by G.F. Guala.

Bamboo Science and Culture:
The Journal of the American Bamboo Society 19(1): 1-4

Distribution of starch in the culms of *Bambusa bambos* (L.) Voss and its influence on borer damage

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Borer damage to bamboo culms both during storage and use is generally attributed to starch stored in the culm tissues. In order to elucidate the possible reasons for more severe tunneling by borers through the inner part of the culm wall than the outer part, the present study was conducted on five mature culms of *Bambusa bambos* (L.) Voss. The results indicated higher quantity of starch in the inner portion of the culm wall. It was also found that this portion had a lower proportion of fibrous tissue and a higher proportion of ground parenchyma which facilitates abundant starch storage.

Freshly felled bamboo culms are generally prone to damage from insect borers, which reduce the material into a powdery mass within a few weeks. Borer infestation is a serious problem in bamboo growing countries such as India. Due to this, an enormous quantity of raw material is lost every year. The common species of borer beetles causing serious damage are *Dinoderus brevis* Horn., *D. ocellaris* Steph. and *D. minutus* Fab. (Coleoptera: Bostrychidae) which are popularly known as *ghoon* borers in India (Beeson, 1941; Sen Sarma, 1977). Although there are various beliefs with regard to the susceptibility of bamboo to borer infestation, starch content is often regarded as a predisposing factor for the borer incidence and several studies have correlated the borer attack with the occurrence of starch in bamboo (Plank and Hageman, 1951, Joseph 1958, Nair *et al.* 1983, Dhamodaran *et al.* 1986, Liese 1980, Mathew and Nair 1994). More recent information on the variability of starch content in bamboo in relation to season and culm age is available from studies by Abd. Latif *et al.* (1994) and Liese (1998). Many of these studies have indicated a positive relationship between storage starch and borer damage and in some instances, suitable 'low starch periods' have been suggested for harvesting bamboos to minimize the borer problem (Beeson, 1941; Sulthoni,1987). The present study was conducted to understand the pattern of distribution of starch content across the culm wall and its relationship to borer infestation patterns in *Bambusa bambos* (L.) Voss. The study is based on the casual observation that the borer tunneling is generally more concentrated in the inner portion of the culm wall as compared to the outer layers (Fig.1).

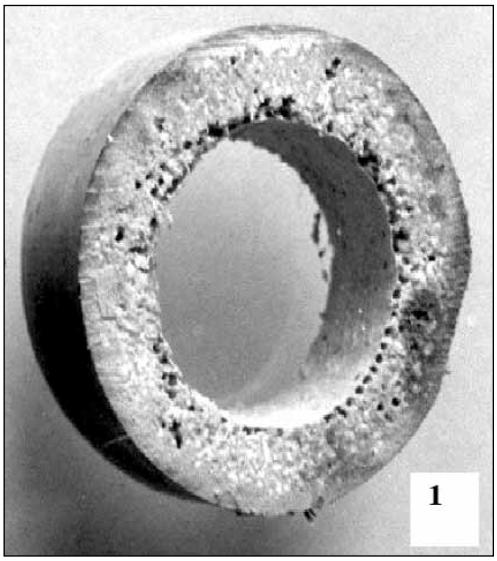

Figure 1. Cross sectional view of the culm internode showing the typical pattern of borer damage in the culm wall.

MATERIALS AND METHODS

Culm internodal samples of *B. bambos* were collected from different forest areas of Kerala. For quick verification of starch in culm samples, iodine-potassium iodide (I_2KI) was used. A 2 per cent solution of I_2KI was applied to the exposed longitudinal surface of the culm. A bluish coloration developed after the application indicated the presence of starch. The samples were stored for periodic observation on borer infestation. Selected portions of these samples were used for the analysis of starch content subsequently. Outer and inner portions of the culm wall from base, mid-height and top levels of the culms were analyzed separately. In order to examine the distribution of starch in culm tissues, microscopic study of sections was carried out.

Starch content was estimated using the technique of Humphreys and Kelly (1961). The samples were powdered in a Wiley mill and the material sieved through a 200-mesh sieve (B.S.S.) was used for the analysis. The powder was then treated with perchloric acid and centrifuged. An aliquot (10 ml) was placed in a 50 ml volumetric flask, and a solution was made alkaline with sodium hydroxide. Acetic acid was used for de-colorization and a further 2.5 ml was added according to the standard procedure. The colorless solution was allowed to react with potassium iodide and potassium iodate for 15 minutes and made up to volume (50 ml). The absorption and concentration of the solution was then measured by photoelectric colorimeter.

The proportions of fibro-vascular and parenchyma tissues were estimated by tracing the cross-sectional views on tracing film and measuring the area occupied by each tissue in a unit area.

RESULTS AND DISCUSSION

Part of a split culm of *B. bambos* tested for starch using iodine reagent is shown in Fig. 2. In contrast to the inner portion, the outer part of the culm wall was almost free of dark vertical striations indicative of starch containing cell strands. A photomicrograph of the inner portion of the culm wall (Fig.3) shows distribution of starch in ground parenchyma cells. The fibers were largely free of starch. Average values of starch content for outer and inner portions of the culm wall at different height levels is given in Table 1. Analysis of variance showed that the difference in starch content between the culms and that between height levels was not significant. However, there was a highly significant (1% level) difference in starch content between the outer and inner parts of the culm wall as shown by paired t-test of the data pooled together ($t = -4.232$).

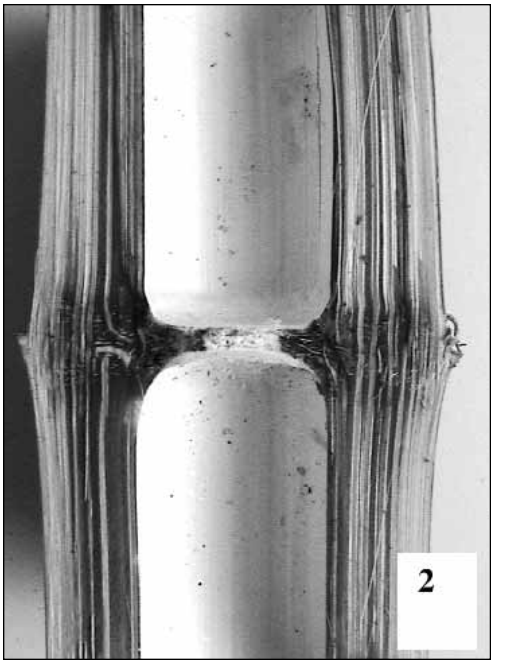

Figure 2. Part of a freshly felled split bamboo tested for starch; dark vertical striations indicate portions rich in starch.

The typical pattern of borer damage of the culm wall of *B. bambos* is shown in Fig.1. It was found that the damage was more intensive towards the inner portion of the culm wall that is rich in starch content. The outer portion remained nearly sound without much tunneling. This observation supports the findings of Plank (1951) that the inner portion of the culm

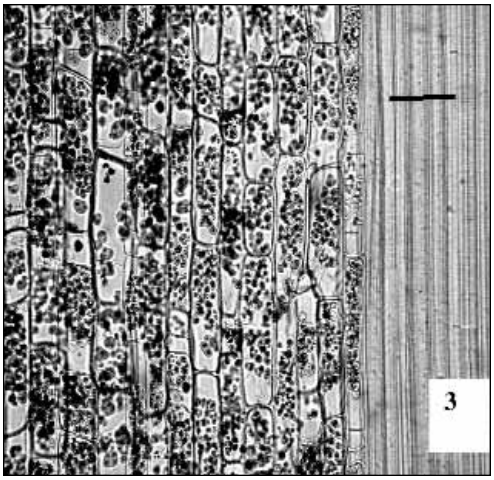

Figure 3 L.S. showing distribution of starch in parenchyma tissue in the inner portion of the culm wall. The scale bar is 55µm.

contains more starch and is more susceptible to borer damage. Evidently, the borers show a preference for 'starch-rich sites' probably for a more productive feeding.

The proportions of fibro-vascular and parenchyma tissues in different parts of the culms are given in the Table 1. The percentage of the fibro-vascular and parenchyma tissues varied widely across the culm wall. The outer portion of the culm wall had compactly arranged fibro-vascular bundles and lower proportion of parenchyma. In the inner portion of culm wall, the proportion of fibrous tissue was lower. Consequently, the proportion of parenchymatous tissue increased from outer to inner part of the culm wall. This trend of distribution of tissues was also observed at different height levels of the bamboo culm. Thus the proportion of ground parenchyma tissue responsible for storage was invariably greater in the inner portion, which favored accumulation of starch in this portion (Table 1). Maximum starch content was observed in the inner portion of the distal part of the culm. In contrast, it was lowest in the outer part of the basal portion of the culm.

The selective feeding behavior of the borers as observed in the present study is an indication of their preference for starch-rich sites. Abundant availability of starch seems to be a prerequisite for successful multiplication of borer population, and this turns out to be a reason for intensive damage to felled or stored culms. It has been previously reported that borer infestation occurs if the starch content in the material exceeds a certain total level (Beeson, 1941). This also implies that culms that escape borer damage are the ones with less or no starch.

ACKNOWLEDGEMENTS

The financial support from MoEF, Govt. of India to carry out this study is gratefully acknowledged. We are thankful to Dr. J.K. Sharma (Director, KFRI) for encouragement and Prof. Walter Liese (Germany) and Elizabeth Magel (University of Hamburg, Germany) for their help during the study.

Table 1. Starch content and tissue proportion in outer and inner portions of the culm wall at different height levels of *B. bambos* (mean value of five culms with standard deviation)

Portion of the culm	Starch content %		Parenchyma (%)		Fibro-vascular tissue	
	Outer	Inner	Outer	Inner	Outer	Inner
Base	1.5 (1.0)	5.2 (2.1)	56.0 (4.0)	73.0 (8.4)	44.0 (4.0)	27.0 (8.4)
Middle	4.8 (3.0)	6.6 (2.7)	53.4 (7.3)	67.6 (6.3)	46.5 (7.3)	32.4 (6.3)
Top	4.8 (4.6)	8.2 (8.0)	46.9 (7.4)	65.6 (3.9)	53.0 (7.4)	34.4 (3.9)

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Bamboo Science and Culture:
The Journal of the American Bamboo Society 19(1): 5-10

A new species of *Chusquea* sect. *Longifoliae* from Ecuador

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Chusquea robusta from Ecuador is described as new. It is illustrated and compared and contrasted with *Chusquea antioquensis* (from Colombia), the species to which it is most similar. *Chusquea robusta* is distinguished by its large size (culms up to 7 cm in diameter), for which it is named, and also by its relatively small culm leaf blades, more or less horizontal junction of the culm leaf sheath and blade, abaxially pilose foliage leaf blades with an excentric midrib, relatively large spikelets [(11-) 12-15.5 mm long], and lengths of glumes III and IV relative to the spikelet length. A majority of the spikelets exhibit an elongated rachilla internode between glumes I and II, a feature not observed in other species of *Chusquea*. Keys to the species of *Chusquea* sect. *Longifoliae*, to which the new species belongs, are presented.

Se describe *Chusquea robusta* del Ecuador. *Chusquea robusta* se ilustra y compara con *C. antioquensis*, la especie mas parecida. *Chusquea robusta* está nombrado por su gran tamaño (culmos hasta de 7 cm de diametro) y se le distingue ademas por sus láminas de la hoja caulinar relativamente cortas, la articulación más o menos horizontal entre la lámina y la vaina de la hoja caulinar, láminas de las hojas de follaje abaxialmente pilosas y con un nervio central excentrico, espiguillas relativamente largas [(11-) 12-15.5 mm de largo) y las proporciones de las glumas III y IV comparadas con la largura de la espiguilla. Una mayoria de las espiguillas presentan el entrenudo de la raquilla elongado entre glumas I y II, una característica no observada en otras especies de *Chusquea*. Se presentan claves a las especies de *Chusquea* secc. *Longifoliae*, a la cual pertenece *C. robusta.*

An estimated 30 species of *Chusquea*, including representatives of both *Chusquea* subg. *Swallen*ochloa (McClure) L. G. Clark and *Chusquea* subg. *Chusquea*, are known from Ecuador. One of these is described in this paper as part of work toward a treatment of the bamboo diversity of Ecuador for the Flora of Ecuador.

The most notable feature of this new species is its size. When the senior author first saw this species in 1982, it appeared to be a *Guadua* Kunth from a distance. Upon closer examination, it became obvious that it was instead a *Chusquea* Kunth, but one with culms as much as 7 cm in diameter. To date, the largest described species of *Chusquea* are *C. pittieri* Hack. and *C. antioquensis* L. G. Clark & Londoño, both of which can reach 5.5 cm in diameter, but this new bamboo species is now the record-holder.

Further study of herbarium specimens of this new bamboo revealed several features that placed it unambiguously in *Chusquea* sect. *Longifoliae* L. G. Clark: infravaginal branching; numerous constellate subsidiary buds/branches; long, narrow foliage leaves; reduced glumes I and II; and shortly awn-tipped glumes III, IV, and lemmas (Clark 1989). Within sect. *Longifoliae*, however, these Ecuadorean specimens did not match any described species, although they were most similar to the Colombian *C. antioquensis.* We therefore describe and illustrate *C. robusta* as a new species. We provide a revised key to the species of sect. *Longifoliae* and a morphological comparison of *C. robusta* and its presumed sister species, *C. antioquensis.* Two Mexican species, *C. aperta* L. G. Clark and *C. nelsonii* Scribn. & J. G. Sm., were placed in this section in Judziewicz et al. (1999), but further study is required to establish their true affinities, so they are not included in the keys presented here.

TAXONOMIC TREATMENT

Key to the Species of Chusquea Sect. Longifoliae
(based on vegetative specimens)

1a. 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* (Costa Rica)

1b. 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 abaxially distinctly tomentose or pilose.

3a. Foliage leaf blades abaxially tomentose, 15-27 cm long; culm leaf sheaths abaxially glabrous; culms 6-9 m tall, 1.3-4 cm in diameter.....*C. tomentosa* (Costa Rica)

3b. Foliage leaf blades abaxially pilose, 8-21 cm long; culm leaf sheaths abaxially pubescent or pubescent only basally and scabrid to glabrous apically; culms (5-) 7-12 m tall, 3-7 cm in diameter .....*C. robusta* (Ecuador)

2b. Foliage leaf blades abaxially glabrous or sometimes with sparse, scattered hairs.

4a. Foliage leaf blades 0.6-1.3 cm wide and subsidiary branches 18-30 per node; base of culm leaf blade cordate .....*C. longifolia* (Panama to Chiapas, Mexico)

4b. Foliage leaf blades 0.3-1.4 cm wide and subsidiary branches 24-80 (-100) per node; base of culm leaf blade linear.

5a. Foliage leaf blades (0.5-) 0.7-1.4 cm wide, L:W = 11-27; internodes terete.....*C. grandiflora* (Colombia, Panama)

5b. Foliage leaf blades 0.3-0.9 cm wide, L:W = 18-55 (-65); internodes flattened or shallowly sulcate above the bud/branch complement.

6a. Juncture of culm leaf sheath and blade an inverted “V”; culm leaf blades 9.7-21 cm long, the base as wide as the sheath apex.....*C. antioquensis* (Colombia)

6b. Juncture of culm leaf sheath and blade a more or less horizontal line, sometimes slightly convex; culm leaf blades 2.6-12 cm long, the base narrower than the sheath apex.

7a. Subsidiary branches 24-65 per node; inner ligules of foliage leaves 0.5-4 mm long.....*C. patens* (Costa Rica, Panama)

7b. Subsidiary branches 50-80 (-100) per node; inner ligules of foliage leaves to 1.5 mm long.

8a. 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* (Costa Rica)

8b. 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* (Costa Rica, Mexico)

Key to the Species of Chusquea sect. Longifoliae
(based on flowering and vegetative specimens)

1a. Synflorescences open, primary branches strongly spreading, sometimes deflexed.

2a. Glumes I and II no more than 1/10 the spikelet length; spikelets 6.9-11.2 mm long; foliage leaf blades 0.4-0.9 cm wide, L:W = 18-48 .....*C. patens* (Costa Rica, Panama)

2b. Glume I ca. 1/5 and glume II ca. 1/3 the spikelet length; spikelets 9.7-12.6 mm long; foliage leaf blades (0.5-) 0.7-1.4 cm wide, L:W = 11-27 .....*C. grandiflora* (Panama, Colombia)

1b. Synflorescences contracted, primary branches appressed or ascending.
3a. Spikelets 10.4-20.6 mm long.
4a. Glume III 1/3-1/2 and glume IV 1/2-2/3 the spikelet length; a majority of the spikelets with an elongated rachilla internode between glumes I and II; foliage leaf blades abaxially pilose.....*C. robusta* (Ecuador)
4b. Glume III 1/2-2/3 and glume IV 4/5 to equal the spikelet length; rachilla internode between glumes I and II always short (0.1-0.2 mm); foliage leaf blades abaxially tomentose or glabrous (but sometimes with sparse, scattered hairs).
5a. Foliage leaf blades 0.3-0.7 (-1.1) cm wide, abaxially tomentose; fertile lemma subulate .....*C. tomentosa* (Costa Rica)
5b. Foliage leaf blades 0.6-1.3 cm wide, abaxially glabrous or sometimes with sparse, scattered hairs; fertile lemma awned.....*C. longifolia* (Panama to Mexico
3b. Spikelets 7-11 (-12) mm long.
6a. Spikelets 7-9.4 mm long; thin, curly, leafless fibrillar branchlets interspersed with the leafy subsidiary branches; internodes scabrous.....*C. scabra* (Costa Rica)
6b. Spikelets (7.9-) 8.4-11.8 mm long; fibrillar branchlets absent; internodes usually smooth, rarely scabrous just below the nodes.
7a. Glume IV and fertile lemma awned; glume III 2/3-3/4 the spikelet length.....*C. subtilis* (Costa Rica)
7b. Glume IV and fertile lemma subulate or awn-tipped; glume III 1/2-2/3 (-3/4) the spikelet length.
8a. Foliage leaf blades with L:W = 20-40 (-45); culm leaf blades with the base narrower than the sheath apex; juncture of culm leaf sheath and blade a more or less horizontal line .....*C. foliosa* (Costa Rica, Mexico)
8b. Foliage leaf blades with L:W = 31-55 (-65); culm leaf blades with the base as wide as the sheath apex; juncture of culm leaf sheath and blade an inverted “V”.....*C. antioquensis* (Colombia)

Chusquea robusta L.G. Clark & Losure, sp nov. TYPE: Ecuador. Pichincha: Saloya river valley NE of Hacienda La Favorita, 11 Nov 1945 (fl), *F.A. McClure 21431* (holotype, QCA!; isotypes, ISC!, US!, AAU). Fig. 1.

Culmi (5-) 7-12 m alti, 3-7 cm diam. Internodia 22-32 cm longa, glabra, sulcata. Folia culmorum 15-37 (-40) cm longa, 1-1.5-plo longiores quam internodam; vaginae 13.5-31 cm longae, (2.3-) 4-11 (-13)-plo longiores quam laminam, abaxialiter pubescentes ad basim, scabridae vel glabrae ad apicem, junctura cujusvagina laminae linearis; cingulum ca. 3 mm latum, pubescentes; laminae 3-6 (-12) mm longae, triangularae, persistentes, glabrae vel scabridae, apice acuminati. Ramificatio infravaginalis; rami subsidiarii cujusquisque nodi 40-60, 15-45 cm longi. Folia cujusquisque complementi 2-5; vaginae striatae, marginibus ciliis, apicibus prolongatis; laminae 8-21 cm longae, 0.3-0.7 cm latae, long./lat. = (16-)21-38(-41), adaxialiter scabridae, abaxialiter pilosae, costae excentricae. Synflorescentia 6-16 cm longa, paniculata, angusta. Spiculae (11-)12-15.5 mm longae; gluma I 0.5 mm longa, internoda rachillorum inter gluma I et II saepe elongata 0.5-2 mm longa; gluma II 1-1.5 mm longa, purpurea, cupulata; gluma III (4.5-) 5-7 mm longa, 1/3-1/2 longior quam spiculam, breviter aristata; gluma IV 7-10 mm longa, 1/2-2/3 longior quam spiculam, breviter aristata; lemma 12-15 mm longum; palea 9-11 mm longa.

Woody Bamboo. *Culms* (5-) 7-12 m tall, 3-7 cm diam; *internodes* 22-32 cm long, glabrous, sulcate above the bud/branch complement. *Culm leaves* 15-37 (-40) cm long, persistent, 1-1.5 times as long as the internodes, juncture of the sheath and blade horizontal to slightly convex; *sheaths* 13.5-31 cm long, (2.3-) 4-11 (-13) times as long as the blade, abaxially densely to sparsely pubescent basally and scabrid/glabrous apically, margins ciliate; *girdle* ca. 3 mm wide, pubescent; *inner ligule* ca. 2-3

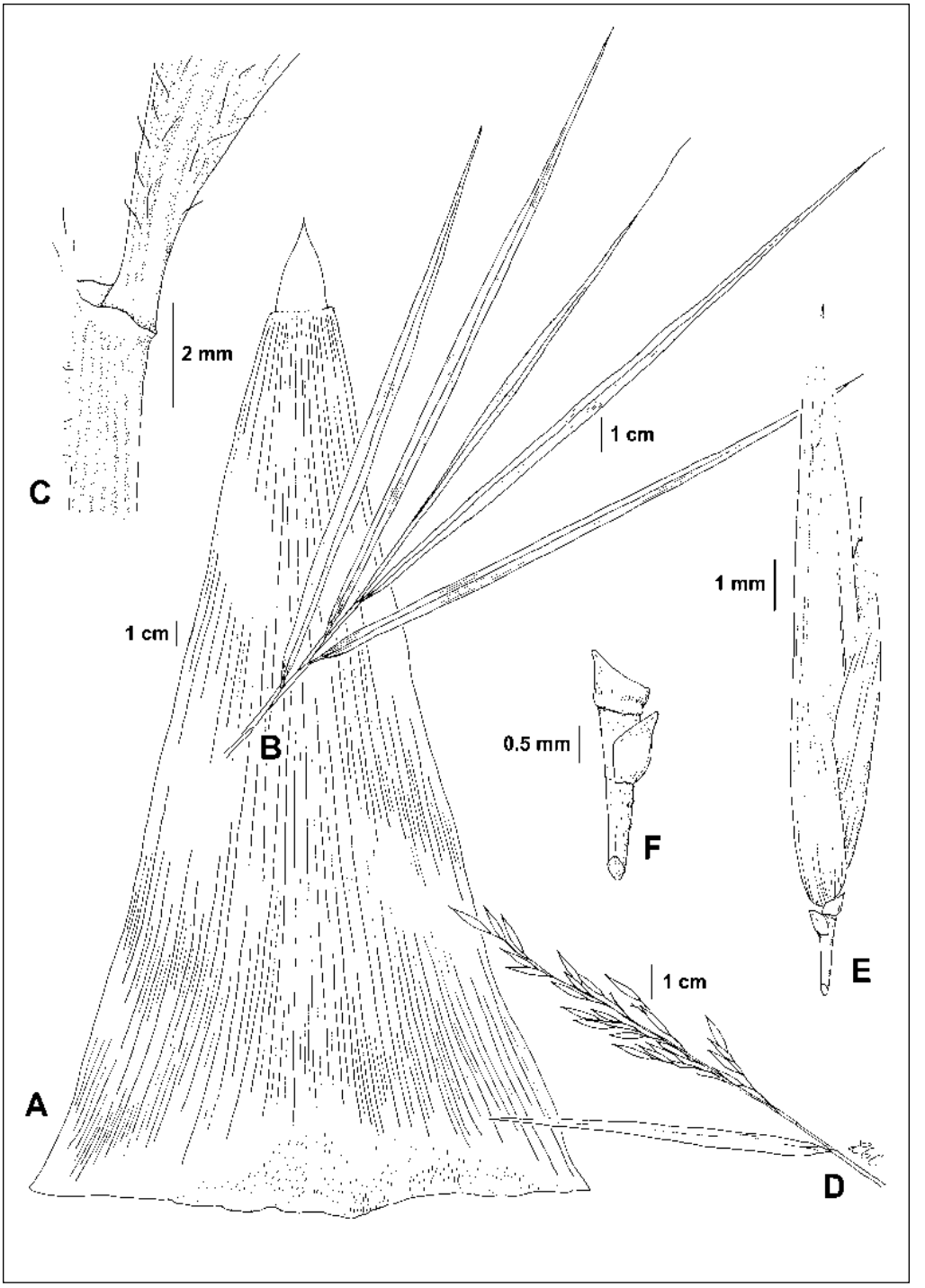

Figure 1. *Chusquea robusta.* A. Culm leaf, abaxial view. B. Foliage leaf complement. C. Foliage leaf, ligular area. D. Synflorescence. E. Spikelet. F. Glumes I and II, closeup showing the elongated rachilla internode. (A, C-F based on *McClure* 21431; B based on *Young 90*)

mm, entire to very shortly ciliate; *blades* 3-6 (-12) cm long, triangular, persistent, abaxially glabrous to scabrid, adaxially longitudinally furrowed, pubescent, apex acuminate, often broken off in pressed specimens. *Nodes* with one triangular central bud subtended by numerous subsidiary buds in several rows in a crescent arrangement; nodal line horizontal, dipping below the bud/branch complement; supranodal ridge pronounced, 4-8 mm above the nodal line. *Branching* infravaginal; leafy subsidiary branches 40-60 per node, 15-45 cm long, not re-branching. *Foliage leaves* 2-6 per complement; *sheaths* striate, margins ciliate, apex prolonged and bearing villous hairs; outer ligule ca. 0.5 mm, glabrous, rounded; inner ligule ca. 0.7 mm, brown-purplish, pubescent; pseudopetiole 1-2 mm long; *blades* 8-21 cm long , 0.3-0.7 cm wide, L:W = (16-) 21-38 (-41), linear-lanceolate, adaxially retorsely scabrid, abaxially pilose, midrib clearly offset from leaf center, prominent abaxially, margins serrulate, + cartilaginous, base attenuate, apex acuminate to shortly aristate. *Synflorescences* 6-16 cm long, narrow, paniculate, subtended by a pale bract 1.5-5mm long, or arising from the foliage leaf sheaths; rachis angular, twisted, scabrid; pedicels 2-10 (-15) mm long, angled. *Spikelets* (11-) 12-15.5 mm long; glume I reduced to a 0.5 mm long brown-purplish bract, 60-70% of spikelets with a rachilla internode 0.5-2 mm long between glumes I and II, the internode 0.1-0.2 mm long in the remainder; glume II 1-1.5 mm long, brown-purple, scabrous, cup-shaped; glumes III and IV navicular, awn-tipped, abaxially scabrid, sparsely ciliate along the apical margins, 7-9 nerved; glume III (4.5-) 5-7 mm long, 1/3-1/2 the spikelet length; glume IV 7-10 mm long, ca. 1/2-2/3 the spikelet length; lemma 12-15 mm long, awn-tipped, 7-9 nerved, abaxially scabrid; palea 9-11 mm long, 2-keeled, faintly 7-9 nerved. Flowers not seen. Fruit not seen.

Chusquea robusta is named for its robust culms and general aspect. The elongated rachilla internode found between glumes I and II in 60-70% of the spikelets is a highly unusual character in *Chusquea*. The two flowering collections in which this feature appears are almost certainly from the same population; given that it is not uniformly present in the spikelets of this population, additional flowering material from other populations is needed to confirm whether this is characteristic of *C. robusta*. For the present, this character, as well as spikelet size and the ratio of glume III and IV length to spikelet length, clearly differentiate flowering specimens of *C. robusta* from the closely allied species *C. antioquensis*, which is known from the same mountain range as *C. robusta* but from further north in Colombia. Vegetatively the two are quite similar, but can be distinguished by the horizontal junction of the culm leaf sheath and blade, as well as the excentric midrib of the foliage leaf and the abaxially pilose foliage leaf blades, in *C. robusta* (Table 1).

Table 1. Morphological comparison of C. robusta and C. antioquensis.

Character	*C. robusta*	*C. antioquensis*
spikelet length	(11—)12—15.5 mm	(7.9—) 8.6—10 (—11) mm
0.5-2 mm long internode between glumes I and II	present in 60—70% of spikelets	absent
ratio of glume III length to total spikelet length	1/3—1/2	1/2—2/3
ratio of glume IV length to total spikelet length	1/2—2/3	ca. 4/5
juncture of culm leaf sheath and blade	linear	distinctly notched or v'd
culm leaf length	15—37 cm	38—65 cm
foliage leaf midrib	excentric	centric
foliage leaf blade pubescence	pilose	glabrous

This species is known from four collections in the mountainous region of northern Ecuador. The two collections for which the location is known precisely were both from disturbed cloud forest habitats at elevations between 2000 and 2100 m.

Chusquea robusta was first collected in flower in 1945. Another flowering collection was made in 1982. Since the two collections appear to be from the same population, this could indicate a 37-year flowering cycle, which would be typical for species of *Chusquea* (Judziewicz et al. 1999). However, further observation of the species will be necessary to confirm this.

One vegetative collection from northern Ecuador, *S.M. Young* 90, was examined and used in defining the species concept of *C. robusta*. Other vegetative collections from southern Ecuador examined, *P. Lozano 927* (ISC, LOJA) and *L.G. Clark, R. Townsend & P. Lozano 1626* (ISC, LOJA, QCA) clearly belonged to *Chusquea* sect. *Longifoliae*, but could not be determined as either *C. robusta* or *C. antioquensis*. Although these specimens, from the province of Zamora-Chinchipe, closely resemble both *C. robusta* and *C. antioquensis*, they do not have sulcate internodes and their foliage leaves are wider than those observed in either named species. Until flowering material or collections from other southern populations are available, we refer these specimens to an entity called *C.* aff. *robusta*.

Additional specimens examined. ECUADOR. Pichincha: Old Quito-Sto. Domingo road, 54-55 km from Quito, 4.9 km west of Chiriboga, western slope, 2100 m, 27 Aug 1982 (fl), L. Clark, C. Calderon & E. Asanza 312 (ISC, QCA, US); old road from Quito to Santo Domingo, about 55 km from Quito, W of Chiriboga, 1850 m, 7 Jun 1992, L. Clark 1132 (AAU, ISC, MO, QCA, US). Napo: 36 km south of Baeza on the road to Tena, 2070 m, 28 Mar 1980, S. M. Young 90 (QCA, US).

ACKNOWLEDGMENTS

Travel to Ecuador by Clark was supported by a Foreign Travel Grant from Iowa State University. Fieldwork was conducted under the auspices of the Pontifícia Universidad Católica del Ecuador (Herbario QCA) and a grant to Simon Laegaard from the Danish National Science Foundation. Clark thanks Simon Laegaard (AAU), Benjamin Øllgaard (AAU) and Pablo Lozano (LOJA) for valuable assistance with the fieldwork and the Gonzalo Alcivar family for their hospitality in Ecuador. Anna Gardner assisted with final preparation of the line drawing.

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Bamboo Science and Culture:
The Journal of the American Bamboo Society 19(1): 11-15

Aulonemia dinirensis (Poaceae: Bambusoideae: Bambuseae) a new dwarf Venezuelan species from the easternmost Andean páramos

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The new species *Aulonemia dinirensis* Judz. & Riina is described from the Páramo de Cendé, the easternmost páramo of the Andean Cordillera, in the state of Lara, Venezuela. A dwarf species 0.4-0.8 m tall known only from elevations of 2700 m in subpáramo vegetation on sandstone, its most closely related congener may be *A. trianae*, which is a much more robust plant with smaller spikelets.

Una nueva especie, *Aulonemia dinirensis* Judz. & Riina, es descrita del páramo de Cendé, uno de los páramos más orientales de la Cordillera de los Andes, en el Estado de Lara, Venezuela. Se trata de un bambú enano 0.4-0.8 m alto, solo conocido de elevaciones de 2700 m en vegetación de subpáramo sobre areniscas. La especie[s] está más relacionada con su congénere *A. trianae*, la cual es mucho más robusta con espiguillas más pequeñas.

A floristic inventory of the páramos and subpáramos of the Parque Nacional Dinira (Lara, Trujillo, and Portuguesa states, Venezuela) by the second author resulted in the collection of several botanical novelties, including a new dwarf bamboo species in the genus *Aulonemia* (Poaceae: Bambusoideae: Bambuseae: Arthrostyliidinae):

Aulonemia dinirensis Judz. & Riina *sp nov.* (Fig. 1). TYPE: VENEZUELA. Lara: Parque Nacional Dinira, vertiente hacia El Tocuyo, sector “La Lajita”, camino hacia “La Lajita”, 9°32'47"N, 70°05'38"W, 2700 m, vegetación herbácea con arbustos dispersos o agrupados en pequeñas islas, bambusillo de 1 m alto, espiguillas verde-grisáceas, frecuente en ladera, 15 Aug 1999, R. Riina, R. Duno, R. Ghinaglia & R. Gonto 713 (HOLOTYPE: VEN; ISOTYPES: ISC!, MO!, SI!).

Culmi 3-4 mm diametro, 0.4-0.8 m alti, cespitosi, erecti. Vagina foliorum glabrescens, striata, nonauriculata; fimbriae nulliae; lamina foliorum 7-10 cm longa, 1-2.3 cm lata, reflexa, puberulenta. Inflorescentia paniculatam 20-25 cm longa. Spiculae 25-35 mm longae, puberulentes, 8-10 flosculos fertiles continentes; glumae 2, acutae; gluma I 2-2.5 mm longa, gluma II 5.5-7 mm longa; lemma 8-10 mm longa, apiculata.

Cespitose woody bamboo. *Culms* glabrous, smooth, non-maculate, hollow (the lumen about one-third the diameter of the culm), 0.4-0.8 m tall and 3-4 mm in diameter; buds or branches one per node; branches several to many, erect. *Culm leaves* not seen, perhaps not differentiated from foliage leaves. *Foliage leaves* 4-5 per complement; sheaths glabrous, striate throughout, stramineous (at least when

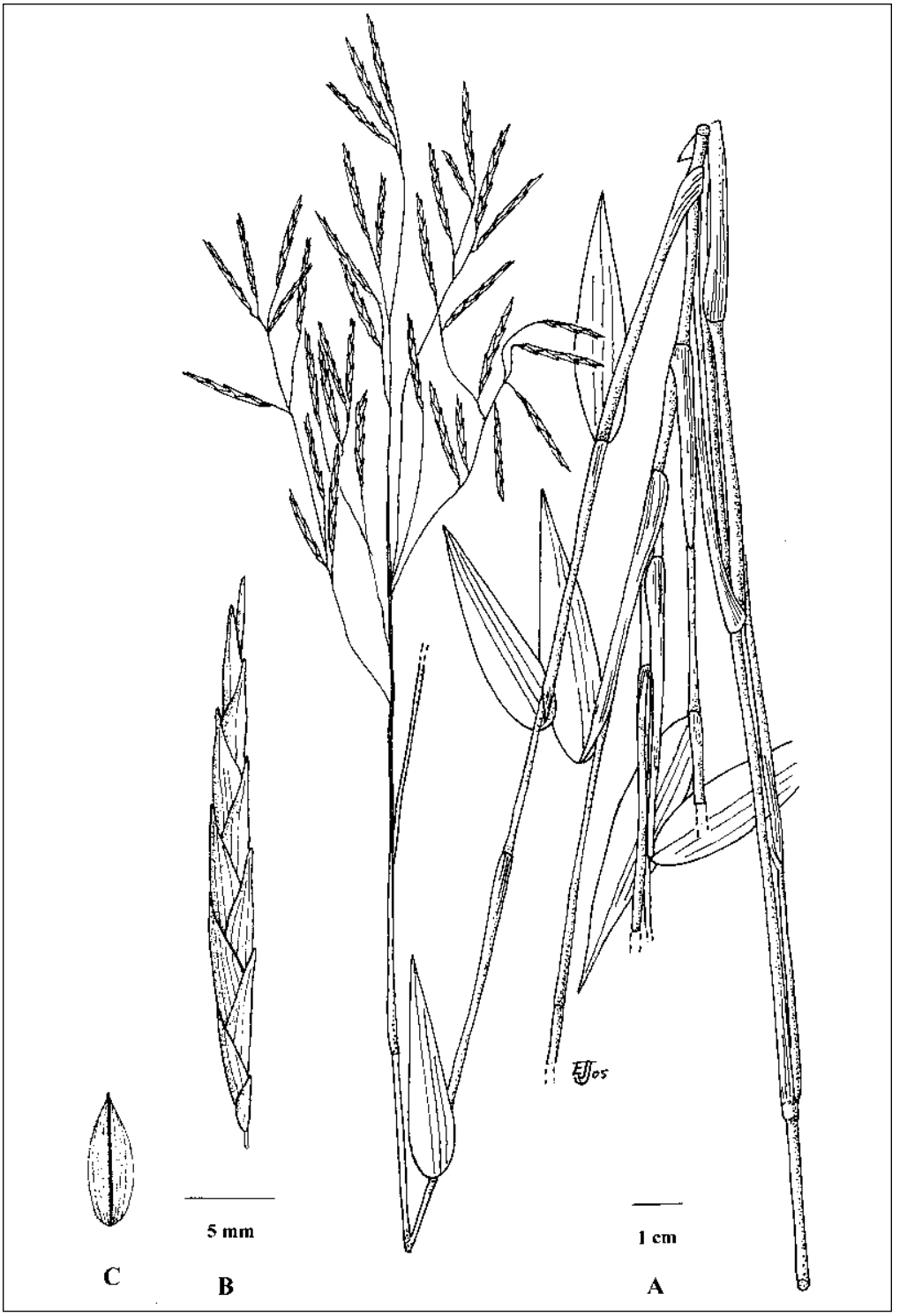

Figure 1. *Aulonemia dinirensis.* A. Habit. B. Spikelet, profile view. C. Lemma, dorsal view. I llustration by E. Judziewicz. (Based on *Riina et al.* 713, MO).

dried), not keeled, non-maculate, lacking auricles; *fimbriae* not evident on sheath margins or summit (but, if present, could have fallen from the available mature collections); *outer ligules* 0.2-0.3 mm long, indurate, rim-like; *inner ligules* 0.4-0.6 mm long, membranous; *pseudopetioles* 1-2 mm long, pale, glabrous; *blades* lanceolate, strongly reflexed, deciduous, 7-10 x 1-2.3 cm, acuminate at the apex, rounded at the base, finely puberulent on both surfaces. *Inflorescences* 20-25 x 8-10 cm, open panicles with loosely erect, glabrous, smooth, capillary branches. *Spikelets* 25-35 mm long, 1.5-2.7 mm wide, linear, grayish-stramineous (at least when dried), finely puberulent throughout, 8-10-flowered; *lower glume* 2-2.5 mm long, ovate-lanceolate, acute, 1-3-nerved; *upper glume* 5.5-7 mm long, lanceolate, acute, 3-5-nerved; *lemmas* 8-10 mm long, lanceolate, apiculate, 7-9-nerved; *paleas* 6.5-7.5 mm long, 2-nerved, obtuse at the apex; *stamens* with anthers ca. 3 mm long; *fruits* not seen.

Aulonemia dinirensis grows on sandstone substrates in periodically burnt subpáramos at elevations of 2700 meters on the northeastern slopes of the Páramo de Cendé, in the Andes of northwestern Venezuela (Fig. 2). This is the easternmost páramo in the Andean cordillera reaching its maximum altitude at the summit of the Páramo de Cendé (ca. 3350 m). The species is not common and is apparently restricted to a small area of the Parque Nacional Dinira in the state of Lara. Associates include the endemic sundew *Drosera cendeensis* Tamayo & Croizat (Droseraceae); the endemic asteraceous species Ruilopezia emmanuelis Cuatrec., *Ruilopezia floccosa* (Standl.) Cuatrec., *R. jabonensis* (Cuatrec.) Cuatrec., *R. vergarae* Cuatrec. & López and *Monticalia rigidifolia* (V.M. Badillo) C. Jeffrey; various grasses (*Festuca* sp., *Agrostis humboldtiana* Steud., *Chusquea angustifolia* (Soderstr. & C. Calderón) L.G. Clark, and *Danthonia secundiflora* J. Presl.); the bromeliad *Puya aristeguietae* L.B. Sm.; the fern *Blechnum obtusum* R.C. Moran & A.R. Sm. (Moran & Smith 2005); and *Dendrophthora meridana* Kuijt (Viscaceae).

Figure 2. Subpáramo habitat of *Aulonemia dinirensis*, el. 2700 m, Parque Nacional Dinira, state of Lara, Venezuela, 15 Aug. 1999. Photograph by R. Riina.

The specific epithet refers to the name of the park (Parque Nacional Dinira). The word "dinira", of arawak-caquetio origin, was used in the description of the city of El Tocuyo (Lara state) in 1578, published by Arellano Moreno (1964). The report (translated) indicates that "El Tocuyo was founded between two mountain ranges, Dintas to the east and Dinira to the west". The meaning of "dini" is breast and refers to conical shape of some mountains, and "ira" means liquid, so the meaning of "dinira" for the caquetio amerindians was probably "mountain where the river (the Tocuyo river) comes from" (B. Manara, pers. com.).

Aulonemia is a genus of 45-50 species of bamboos (Judziewicz et al. 1999, 2000), with many undescribed narrowly endemic species in Andean South America. The new species is clearly referable to *Aulonemia* based on its branching habit (one branch per node), reflexed leaf blades, paniculate inflorescence, and spikelet structure.

Aulonemia dinirensis is a dwarf species probably most closely related to *A. trianae* (Munro) McClure (Table 1; Clark & Londoño 1990, Clark et al. 1997), an Andean species found in northern Colombia and the adjacent state of Táchira, Venezuela. Both taxa share efimbriate or sparsely fimbriate leaf sheath summits; an absence of sheath auricles; and spikelets with awnless, apiculate lemmas. However, *A. dinirensis* is a shorter, more slender species than *A. trianae* and differs in its longer, more floriferous spikelets (Table 1).

A collection of an Aulonemia species by the second author (Parque Nacional Dinira, ladera del Páramo de Jabón, vertiente hacia El Tocuyo, sector "Los Charquitos", 9°34'26"N, 70°06'03"W, 2800-2900 m, 15 Aug 1999, *R. Riina* et al. *680*, VEN) made just 3 km by air from the type locality of *A. dinirensis* is tentatively referred to *A. trianae*. It differs from *A. dinirensis* in its more numerous (7 or more), crowded leaf complements; prominent 2 cm long, dark, erect, leaf sheath summit fimbriae; smaller panicles with just a few stout branches; and shorter (ca. 15-20 mm long) spikelets with fewer (5-6) florets.

Two other dwarf (1 m tall or less) species of *Aulonemia* occur in the northern Andes: *A. bogotensis* L.G. Clark, Londoño & M. Kobayashi (Clark et al. 1997) in central Colombia and *A. pumila* L.G. Clark & Londoño (1990) in southwestern Colombia. *Aulonemia dinirensis* differs from *A. bogotensis* in its much larger leaf blades (7-10 x 1-2.3 cm vs. 2-4.2 x 0.3-0.5 cm) and longer (25-35 vs. 9.7-13 mm long) spikelets with more florets (8-10 vs. 3-5). *Aulonemia dinirensis* differs from *A. pumila* in its larger spikelets (25-35 vs. 8.4-12.6 mm long) with awnless, apiculate (not subulate-aristate to aristate) spikelet bracts, and more (8-10 vs. 2-3(-4)) florets per spikelet.

Aulonemia dinirensis does not appear to be conspecific with any congeners occurring in the Guayana Highlands (Judziewicz 2004, 2005); in this region, *A. dinirensis* would key most closely to the dwarf species "*Aulonemia* sp. C" from Cerro Marahuaka, Venezuela – but the latter undescribed species differs in its significantly smaller leaf blades (4 x 0.7 cm) and purplish rather than grayish-stramineous spikelets. If the leaf blades of *Aulonemia dinirensis* are truly efimbriate (it is difficult to be certain with the late-fruiting-stage collections available; fimbriae are sometimes deciduous in

Table 1. Comparison of *Aulonemia dinirensis* Judz. & Riina with *A. trianae* (Munro) Mc Clure.

Character	A. dinirensis	A. trianae
Distribution	Venezuela (Lara)	Colombia (northern half), Venezuela (Táchira)
Elevation (m)	2700	2500-3150
Plant height (m)	0.4-0.8	1-2.5(-6)
Culm diameter (mm)	3-4	5-10
Leaf blade length (cm)	7-10	6-15
Spikelet length (mm)	25-35	10-18
Florets per spikelet	8-10	5-6(-8)

the genus), then the species might appear to have some affinities with the Bolivian endemic *A. tremula* Renvoize (Renvoize 1998). However, that species has a scandent, pendant habit with culms up to 10 m long and smaller (10-22 mm long), fewer-flowered (4-5) spikelets than *A. dinirensis*.

ACKNOWLEDGMENTS

We thank Gerrit Davidse (MO) for the loan of the specimens, Lynn Clark for encouraging us to publish this new species, Bruno Manara for his contribution to the etymology of the species name, Ismael Capote and Carlos Reyes from the Herbario Nacional de Venezuela, and the Fauna & Flora Preservation Society and Fundación Instituto Botánico de Venezuela for helping to fund the second author's fieldwork.

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Bamboo Science and Culture:
The Journal of the American Bamboo Society 19(1): 16-22

Developmental anatomy of the fiber in *Phyllostachys edulis* culm

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With several methods of microscopy, the differentiation and development of fibers in the middle third of *Phyllostachys edulis* culm walls were systematically studied. The development of fibers could be divided into three stages: the formation of fiber initials, primary wall and secondary wall. Fibers originated from the same procambium as the vascular bundle elements like vessels and sieve tubes, but their differentiation is later. Fibers centrifugally underwent differentiation and development outwards from a vascular bundle. During primary wall formation, most fibers were bi-nucleate or multi-nucleate contributing to their elongation, which might be related to amitosis. During secondary wall formation, fiber wall underwent dominant thickening during the first 4 years, and then the degree of wall thickening decreased gradually. With the thickening of secondary wall, fiber nucleus persisted for many years in the culms investigated. The plasmodesmata and transfer vesicles were also persistent in the pits between the fibers and their adjacent cells. The results demonstrated that the fiber in the middle third of *Phyllostachys edulis* culm walls is a kind of long-living cell. The persistence of fiber nucleus and plasmodesmata and transfer vesicles is closely related to the thickening of secondary wall with aging.

Phyllostachys edulis (Carr.) H. De Lehaie has the largest distribution area and the highest economical value in China. Because of the high fiber content of 38% (Grosser & Liese, 1974), it is widely used for making furniture, construction, pulp and other industries in China. The variation in the structure and properties of fibers with aging has a decisive impact on the property of bamboo culms, and in turn, dramatically affect culm utilization. The morphology, chemical components and tissue ratio of fibers in *Phyllostachys edulis* culm were studied by Parameswarn and Liese (1976) and Xiong et al. (1980b). Some anatomical changes during the development of fibers were also reported (Xiong et al., 1980a; Liese and Weiner, 1997; Murphy and Alvin, 1997; He et al., 2000). Little is known about systematic anatomical studies of fiber development so far.

In this paper, further studies of the origin and developmental anatomy, as well as the long-living character of fiber in *Phyllostachys edulis* culms were reported in detail. Due to the difference of the position of the vascular bundles and the location of the fibers within, the developmental pattern among fibers across a culm wall is different (Liese, 1998). Only the fibers in the middle third of the culm wall were investigated in this work.

MATERIALS AND METHODS

Materials

Young shoots and culms of 1 to 16 year old *Phyllostachys edulis* were harvested in April 2001 at the Bamboo Garden and the experimental forestry farm of Nanjing Forestry University. Young shoots with heights of 60 cm, 80 cm, 120 cm and 700 cm were collected, and samples about one-cm3 from the middle third of the culm wall in the middle part of every internode of the young shoots taken. For 1 to 16-year-old culms blocks about one-cm^3

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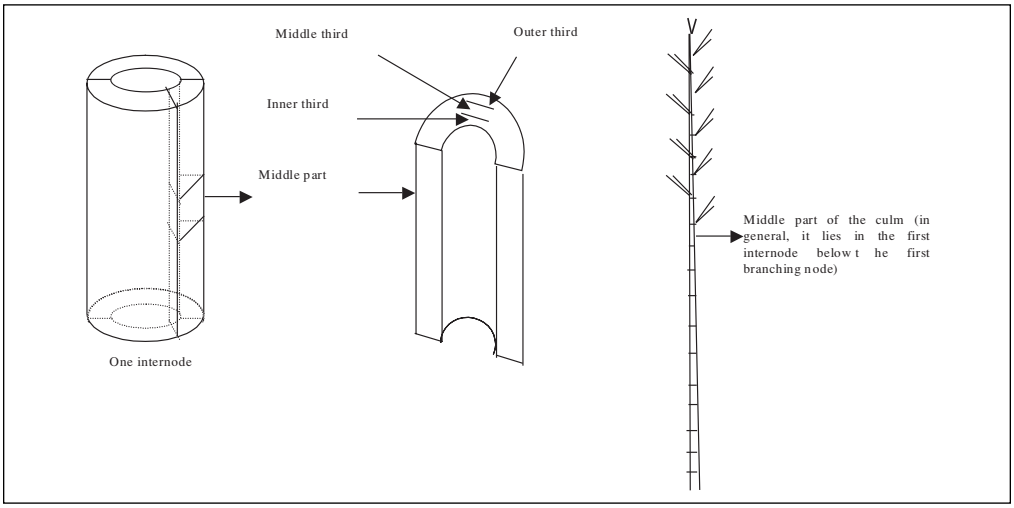

Figure. 1 Schematic figure of material collection

were sampled only from the middle third of culm wall in the middle part of internodes in the middle part of the culms. (Fig. 1)

Methods

Preparation for light microscope

The blocks from young shoots were immediately fixed in FAA (formalin, acetic acid and ethyl alcohol) with 50 % alcohol, and the blocks from 1 to 16-year-old culms in FAA with 70% alcohol. Transverse and longitudinal sections of young shoots were made with a routine paraffin method and stained with safranin-fast green. For the 1 to 16 years old culms, sections were made with GMA (glycol methacrylate) or PEG (polyethylenglycol) 2000 method, and stained with safranin-alstrablue, crystal violet, or acridin orange. All sections were examined and photographed with a biological optical microscope (OLYMPUS, Japan).

Preparation for scanning electron microscope

Blocks of approximately one-cm3 from 1 to 16-year-old culms were treated with FAA, and cooked at 1.2 bars in an autoclave for 4 hours. Later the surface of the transverse samples was cleaned with a sharp blade. Following dehydration with serial gradient alcohol from 50 to 100%, the samples were dried with the critical point method. All samples were examined and photographed with a JSM-6300 scanning electron microscope.

Preparation for transmission electron microscope

Blocks of approximately one-mm^3 from 1 to 16-year-old culms were fixed in 2.5% glutaraldehyde (in 0.025 mol/l phosphate buffer, pH7.0) for 4 hours. After washing with the same buffer, the samples were post-fixed in 1% OsO_4 (also in the same buffer) for 3 hours. Followed by a further washing with the buffer, the specimens were dehydrated in a graded ethanol series and embeded in Spurr's resin. After cutting with a diamond knife on a LKB-V ultramicrotome, ultrathin sections were stained with saturated aqueous uranyl acetate for 5 min, followed by 5 min in lead citrate. Finally all sections were examined and photographed with a H-600 transmission electron microscope (TEM).

RESULTS

The successive development of bamboo fibers could be divided into three stages: formation of fiber initials, primary wall and secondary wall.

Fiber initials formation

The terminal meristem in longitudinal sections consists of tunica and corpus from where the primary meristem was derived (Fig. 2, a). With further development and differentiation, some cells elongated in axial direction forming procambium(Fig.2, b). These cells were much

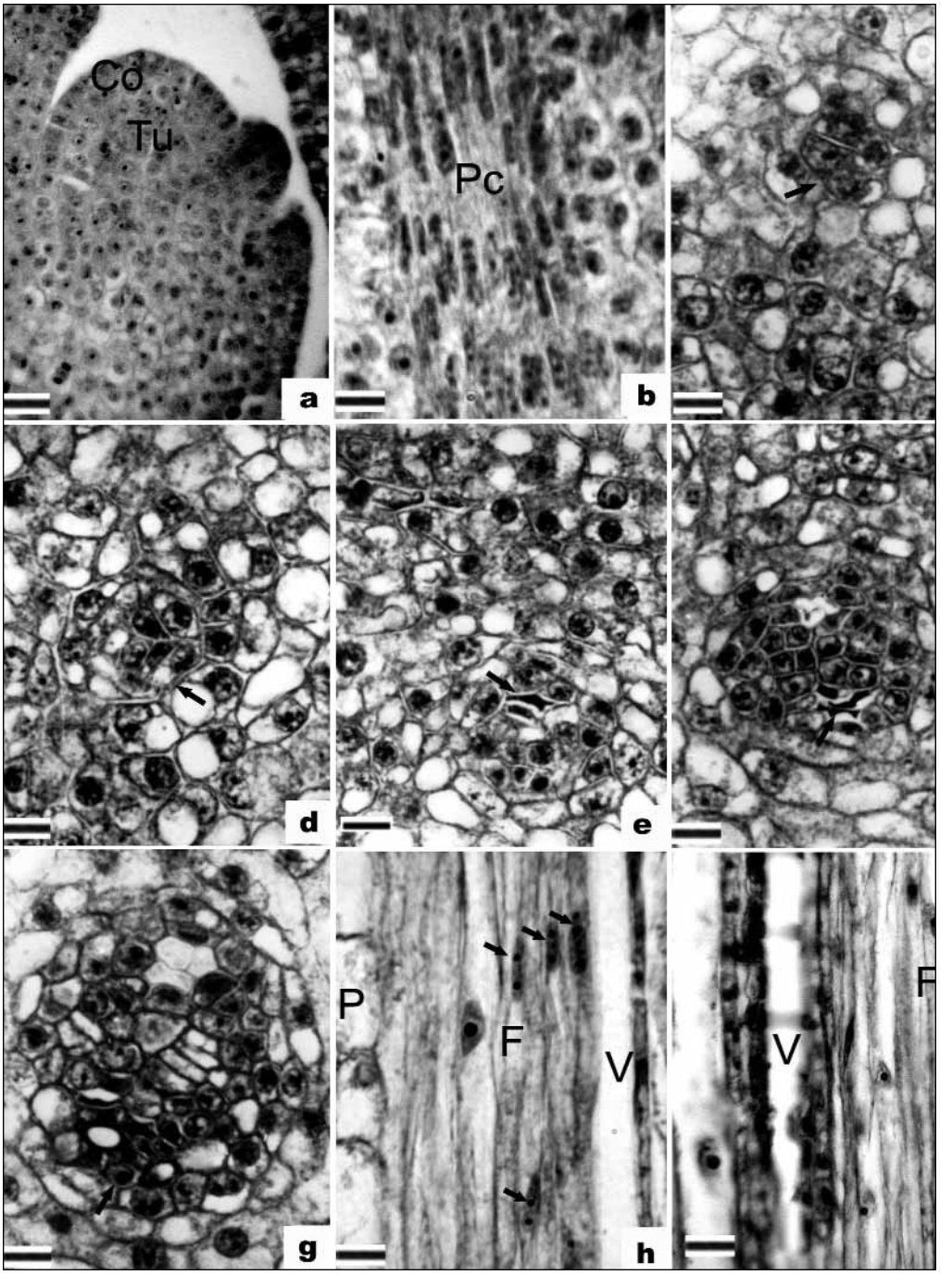

Figure .2. a: the structure of shoot apex, showing tunica, corpus, LS; b: the procambium with diffuse chromatin, LS; c: the early procambium strands with four cells (arrowheads), TS; d: procambium strands with a cluster of cells (arrowheads), TS; e: the formation of prophloem sieve tube (arrowheads), TS; f: the formation of protoxylem vessel (arrowheads), TS; g: the formation of fiber initials (arrowheads), TS; h: the fibers during co-development with vascular bundle, showing bi-nuclei or multi-nuclei phenomenon(arrowheads), LS; i: the fibers during intrusive growth, showing only a nucleus, LS. (Co, corpus; F, fiber; Pc, procambium; Tu, tunica; V, vessel). – Scale bar for a, c, d, e- i = 10µm, for b =100µm

longer than the neighboring ones and appeared deeply stained with safranin.

Transversely, the vascular bundles were to differentiate from procambium cells with the culm elongation. The procambium strands had only four cells formed early (Fig.2, c), and then divided into a cluster (Fig.2, d). With further development, protophloem sieve tubes from the outer layers of procambium appeared (Fig.2, e). Afterwards, the first protoxylem vessel, the annular vessel, developed from the inner layers of procambium (Fig.2, f). With internodal elongation of the culm, metaxylem vessels from the lateral cells of procambium and vascular bundle parenchyma from the middle ones gradually differentiated. Nevertheless, a layer of procambium cells to form the culm fibers was still around the vascular bundle elements as fiber initials (Fig. 2, g).

Primary wall formation

During primary wall formation, a fiber successively exhibits co-growth with vascular elements and intrusive growth.

At this stage, fiber maintained its cylinder form and partly elongated coupled with radial extension and elongation of vessel elements. Bi-nuclei or multinuclei cells were observed with a dense protoplast and smaller vacuole (Fig.2, h). Following, fibers with bi-nuclei or multinuclei were gradually vacuolated and in parallel way arranged.

culm, TS; f : a one-year-old inflorescence fiber, showing the agglutinated nucleus, LS; g: a one-year-old inflorescence fiber, showing the normal nucleus(arrow), LS; h: the fiber in the eight-year-old culm, showing the persistence of nucleus (arrow), TS; i: the plasmdesmata and transfer vesicles (arrow) between fiber and its adjacent cells in four-year-old culm, TS. (F, fiber; FC, fiber cap; MV, metaxylem vessel; N, nucleus; Pa, parenchyma; Pd, plasmodesmata; Ph, phloem; SW, secondary wall). – Scale bar for a,f,g = 10μm, for b =100μm, for c- e =5μm, for h,i = 1μm

When the co-growth of fiber terminated, fibers longitudinally arranged in stagger way were fusiform, indicating the beginning of intrusive growth. At this stage, a central large vacuole and only a single nucleus with distinct nucleolus were seen (Fig. 2, i). When fiber walls were stained red by safranin due to lignification, primary wall formation came to an end.

During primary wall formation, fiber underwent centrifugally differentiaton and development transversely. Earlier only a layer initials surrounded the vascular bundle. Later they radially divided into two daughter cells. Thereafter, the outer ones maintained its meristematic character, while the inner ones increasingly vacuolated and elongated until the end of fiber primary wall formation (Fig.3, a). Similarly, fiber cap formed increasingly (Fig.3, b).

Secondary wall formation

During secondary wall formation, fiber walls lignified and thickened with aging. During the first 4 years, a dominant thickening of fiber wall was observed (Fig.3, c-e). Later, the degree of thickening decreased gradually.

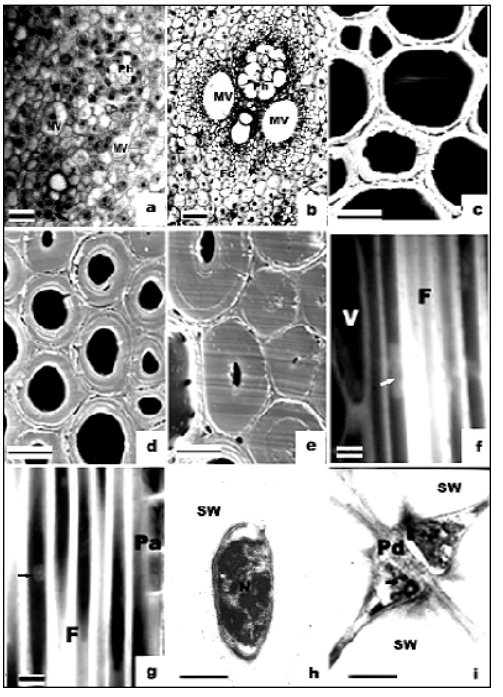

Figure.3. a: the fiber cap during development (arrow), TS; b: the fiber cap finishing development, TS; c: the fiber wall in the culm of one year old, TS; d: the fiber wall in the two-year-old culm, e; 15: the fiber wall in the four-year-old

Fiber wall is characterized by a regular alternation of broad and narrow lamellae during thickening, as also observed by Parameswaran & Liese (1976, 1980).

With the formation of secondary wall, fiber nuclei underwent a series of changes. Almost all fiber nuclei with distinct nucleoli in one-year-old culms were fusiform and unevenly stained (Fig.3, g). In contrast, the nuclei in the fibers adjacent to the vascular bundle were evenly stained with crystal violet, due to the agglutination of chromatin (Fig.3, f). With the continuous thickening of fiber wall, the nuclei became strip-formed and evenly stained. , They were persistent for eight years (Fig.3, h).

Ultrastructural investigations showed the plasmodesmata persistent in the border pit pairs between fibers and their adjacent cells during secondary wall formation. A great number of transfer vesicles were also seen in the pit channels (Fig.3, i).

DISCUSSION

The origin of fibers

The fibers in the culm of *Phyllostachys edulis* around a vascular bundle form a fiber cap or fiber sheath, but their origin is still controversial. Fahn (1982) considered that the inner cells of the fiber cap originated from procambium, but the outer ones from ground meristem. According to Xiong et al. (1980b), procambium cells first differentiated into parenchyma just around the vascular elements, and then differentiated into fiber cells, so that fibers originate from parenchyma around vascular bundle. In this research, fiber cells differentiated later than vascular tissue. With the formation of vascular bundle elements, the cells just around can become fiber initials. Subsequently, they underwent differentiation and development centrifugally outwards from vascular bundle resulting in the formation of fiber caps. Whereby the development degree of fiber in a fiber cap decreased outwards, and the wall thickness of inner cell was thinner than at the outer part. Accordingly, fiber cells originate from the same procambium strand as vascular bundle elements.

The bi-nucleate or multi-nucleate phenomenon of fibers during primary wall formation

During primary wall formation, fiber cells were bi-nucleate or multi-nucleate, while the phenomenon disappeared with secondary wall formation. Bi-nuclei or multi-nuclei were first reported by Esau (1943) in the development of the primary phloem fibers of *Nicotiana* and *Linum*, and also by Xi and Bao (1997) in the fusiform initial cell and ray initial cell of *Camptothea acuminate* cambium. Hu and Zhu (2000) thought that bi-nucleate or multi-nucleate occurrence is related to amitosis, which enables faster gene amplification in a cell. The bi-nuclei or multi-nuclei can provide more nutrients for the development of the pollen strengthening the metabolism. Xiong et al. (1980a) discovered the phenomenon of amitosis in internodes elongation, but did not discuss the relationship between amitosis and the bi-nucleate or multi-nucleate phenomenon. During the growth of *Phyllostachys edulis* culm, internodal elongation attributed to amitosis leading to the occurence of bi-nuclei or multinuclei. Fiber primary wall formation and elongation is consistent with the internodal elongation of culms. We presume that the bi-nuclei or multi-nuclei of a fiber can strengthen its metabolism to meet the demands of fiber elongation. When fiber elongation came to an end, amitosis was unnecessary as shown in the disappearance of bi-nuclei or multinuclei. How the bi-nuclei or multi-nuclei phenomenon of fiber disappeared was not investigated in this paper. The mechanism of nucleus change in bamboo fiber has to be studied further during fiber development.

The variation of fiber wall

The variation of fiber wall was largely reported to date. Fujii (1985), reported that larger fibers of *Pleioblastus chino* continued thickening late into the second year. Alvin and Murphy (1988) found that fiber walls in *Sinobambusa tootsik* were to go on thickening into the third year. Murphy and Alvin (1992) discovered that fiber walls in the 3-5 years old culms of *Phyllostachys viridi-glaucescens* had a polylamellate structure. Liese and Weiner (1996), in a valuable view of ageing in bamboo

culms, showed that the culm of *Phyllostachys viridi-glaucesens* underwent aging processes involving fiber wall thickening. While in their research (Liese & Weiner 1997), fiber wall thickness of the same bamboo was observed to increase during the maturation period, but also up to the investigated 12 years. Most recently, Lybeer and Koch (2005) investigated the lignification during ageing of bamboo culm. However, the variation law of fiber wall with aging was unclear as yet.

The result in our investigation just indicated the variation law of fiber walls during development: the fiber wall underwent a fast thickening in the first 4 years, and then the degree of thickening decreased. The variation of fiber wall is consistent with the growth of bamboo culms (Zhou, 1998): in the first 4 years, the growth of bamboo culms was dominant, and then the degree of culm growth gradually decreased with aging. That means the fibers of *Phyllostachys edulis* culms underwent co-development with the culm growth. Only the variation of fiber wall was qualitatively analyzed in our research. Further studies about quantitative investigation of wall variation and physiological analysis during fiber development will help us to reveal the variation mechanism of fiber wall.

The persistence of the fiber nucleus and plasmodesmata

In this study, almost all fibers in the middle third of a one-year-old culm wall of *Phyllostachys edulis* still had nuclei with a distinct nucleolus, and then their nucleoli gradually disappeared, while the nuclei of fibers persisted for up to eight years. In addition, the persistence of plasmodesmata and transfer vesicles could guarantee intercellular linkage between the fibers and their adjacent cells. The results showed that the fibers in the middle third of *Phyllostachys edulis* culm walls kept their living protoplast for a long time after lignification and wall thickening. Generally, a mature fiber is considered a dead cell without protoplast, whereby bamboo fibers can maintain their protoplast for many years (Liese, 1998). In addition, it was reported that the xylem fibers of *Tamarix aphylla* kept alive for 20 years (Fahn, 1982). Due to secondary growth of woody dicotyledons, new secondary xylem will form and become sapwood instead of old secondary xylem. Fibers with living protoplast are usually in sapwood, and have functions in sustaining and storing (Gu et al., 1993), while those in heartwood, losing their protoplast, become dead cells. Different from other woody plants, bamboo in its absence of secondary growth depends mainly on its primary vascular system during the whole life of a culm. Once differentiating from procambium, bamboo fibers as an important component of primary vascular system will remain alive for many years. The persistence of nuclei and intercellular linkage attributes to continuous thickening of fiber secondary wall. This obviously shows that the fiber studied in this research is a special long-living cell, quite different from fibers in dicotyledons.

ACKNOWLEDGEMENTS

We are grateful to Prof. Dr. Walter Liese for valuable advices and Mr. Richard Morton for checking the English text of this manuscript. This work supported by the National Natural Science Fund of China (30271064)

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Bamboo Science and Culture:
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Soluble carbohydrates and acid invertases involved in the rapid growth of developing culms in *Sasa palmata* (Bean) Camus

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Developing bamboo culms reach their final height of several meters (5-20) within a very short period of two to four months This rapid extension growth of bamboo is not well understood and no information about the physiological and molecular processes underlying this phenomenon exist. Extension growth is generally turgor-dependent and in many cases is regulated by invertases, either alone or in combination with sugars and plant hormones. Therefore, we investigated the pool sizes of the non-structural carbohydrates (glucose, fructose, sucrose, and starch) and the catalytic activities of acid invertases (soluble and cell wall bound) in the growing culm, in mature culms of different age-classes, and in the rhizome of bamboo, *Sasa palmata*. Our data show, that cell wall invertases (AIcw) dominate in the growing culm, where high catalytic activities of AIcw create a strong sink for sucrose. In the rapidly growing culm, high activities of cell wall and acid soluble invertases, together with the resulting high hexose (glucose, fructose) contents correlate with cell elongation and expansion, possibly by modulating osmotic pressure and cell turgor. The high availability of hexoses could also be the basis for maintaining a high mitotic activity. The findings thus give evidence that invertases are involved in the provision of organic solutes, necessary for elongation growth in bamboo culms.

The growth of a bamboo culm is still a mystery and not well understood. Only a few investigations have focused on limited aspects of this growth phenomenon. The culm grows by expanding its internodes, whereby cellular reorganization has been preformed in the buds (McClure 1997). The rate of daily expansion varies among species with an average of 5-20 cm (up to 60-80 cm), until a final length of several meters (up to 20-25 m) has been reached. Some of the bigger bamboos, such as *Guadua angustifolia*, produce about 500 cm^3 wall substance per day (Liese 2004), amounting to a total of about 0.1 m^3 biomass for the entire culm. This high quantity of biomass is produced within the growing season of about 3-5 months. There is no other plant with a comparable biomass production. Therefore, bamboos are considered highly suitable for biomass sequestration plantations, and are discussed with regard to the Kyoto protocol.

It has to be noted that the growing culm hardly contributes by itself to the biomass accumulation: as photosynthetically active leaves do not develop before full culm expansion (Nath et al. 2004). During expansion, the culm itself is covered by a dense layer of culm sheaths with hardly any net rate of assimilation. In the late stages of growth this cover is shed, enabling positive autotrophic carbon gain by the culm (Judziewicz et al. 1999). Consequently, the biomass production of an expanding culm has to be facilitated by internal supplies of carbon, which are reallocated from storage tissues of the rhizome and of older, previous years' culms.

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Non-structural carbohydrates are not only prominent in carbon storage (starch), but also provide transport of carbon (sucrose), or nutrient carbon substances in plants. Carbohydrates also function as metabolic signals and regulatory molecules, and thus affect the expression of different classes of genes (Koch 1996, Roitsch and Gonzalez 2004). Moreover, it is not just the presence of the carbohydrates that is of importance, but also the capacity of the tissues to use them in metabolic processes or facilitate their import and export that is just as significant. Sucrose, and the products of its hydrolysis, glucose and fructose are in this context of central importance. Hydrolysis of sucrose is mediated by invertases. In plants, three types of invertases are present. They are located in the apoplast, the vacuole and the cytoplasm. Besides their subcellular localization, they are characterized by their solubility, pH-optima and isoelectric points. Alone or in combination with sugars and plant hormones, invertases regulate many aspects of growth and development of plants (Sturm and Tang 1999, Roitsch and Gonzalez 2004).

In order to gather information about the regulation of growth in new bamboo shoots, we investigated the seasonal changes in pool sizes of these sugars, and of the levels of activity of soluble (vacuolar) and cell wall acid invertases in the rhizome, one-, and two-years-old, as well as the developing culms of *Sasa palmata*. *Sasa palmata* (Bean) Camus was chosen for this investigation as it is small and therefore easy to handle and study. The results, however, can be extended to the large bamboos.

MATERIALS AND METHODS

Plant material

Sasa palmata plants were investigated between March 2004 until February 2005. Specimens of the rhizome, of one-year-old culms, of two-years-old culms, and current year culms were harvested in the field near Hamburg, Germany. In order to follow the development of the emerging culm in detail, harvest took place in a weekly course from March 2004 until May 2004 (March 18th, March 25th, April 2nd, April 13th, April 20th, April 27th, May 2nd, May 10th). During this time, the diameter of the harvested developing culms were about 10 mm, whereas the length extended from 25 cm (April 13th), 70 cm (April 20th), 120 cm (April 27th), 170 cm (May 2nd), and 220 cm (May 10th), respectively. Additionally, specimen were collected in summer (June 15th), fall (October 18th), and winter (February 3rd, 2005) from fully developed, current-year culms. For analysis of mature culms (e.g. one-year-old and two-years-old culms), material of the 6th internode was used. Immediately after harvest, the specimen were quickly frozen. After freeze-drying, the material was homogenized to a fine powder and kept under vacuum at -30°C until use.

Determination of starch, glucose, fructose, and sucrose

Identification of the dominating soluble carbohydrates was done by thinlayer chromatography (Magel and Höll 1993). As it turned out that glucose, fructose, and sucrose dominated by far, their amounts, as well as the amounts of starch, were quantified enzymatically as described in Magel et al. (2001). After denaturing endogenous hydrolytic catalytic activities by heat treatment, non-structural carbohydrates were extracted from 6 mg plant material in 750 µl of double or doubly (see below) distilled water. For quantification, micro plate reader assays in 96-well micro plates (300 µl cavity volume; Greiner, Nürtingen, Germany) in a Spectra Thermo micro plate reader (Tecan, Crailsheim, Germany) were used.

Preparations of crude extracts for enzyme assays

Fifteen mg of lyophilized plant material was mixed with 20 mg of insoluble polyvinylpolypyrrolidone (MW 360000, Polyclar AT, Serva). Soluble invertases (AIsol) were extracted by adding 750 µl of ice-cold Tris/borate/2-mercaptoethanol buffer (100/300/2 mM, pH 7.2; extraction medium I), under occasional vortexing for 15 min on ice. After centrifugation (10000g, 10 min, 4°C), aliquots of the supernatants were taken for ammonium sulphate mediated protein-precipitation (Li et al. 2003). The precipitated protein was collected by

centrifugation, redissolved in extraction medium I, and desalted on a Sephadex G-25 PD-10 column (Amersham Pharmacia biotech, Sweden; extract I). Ten-µl-aliquots of the cooled filtrate were used for determination of the enzyme activities.

Extraction of ionically cell wall bound invertases (AIicw) was done by re-extraction of the pellet with buffer of high ionic strength (extraction buffer supplemented with 2 M NaCl; extract II). For the measurements of covalently cell wall bound (insoluble) invertases (AIccw), the pellet was resuspended with extraction medium I and the homogenate was used in the assays.

Assays of enzyme activities

The assays of the enzyme activities were based on the published micro plate reader assays for pine (Uggla et al. 2001) and walnut tissue (Magel et al. 2001), and were adapted to the specific requirements of bamboo tissues.

Activities of AIsol and AIicw were assayed by quantifying the amounts of glucose and fructose formed from sucrose in the specific step (total volume of 70 µl, pH 7.0, 150 mM Hepes-buffer, containing 3 mM $MgSO_4$, 1.55 mM NADP, 4.07 mM ATP, phosphoglucose-isomerase [4.3 U ml^{-1}], glc6P-dehydrogenase [2.2 U ml-1], hexokinase [9.2 U ml^{-1}]). For the assay of AIsol and AIicw, 10 µl of extract I or II respectively were incubated in a total volume of 55 µl at pH 4.0 (68 mM citrate/86 mM phosphate) containing 220 mM sucrose. For the measurement of the activities of AIccw the specific step was performed with the homogenate, at pH 4.0 and 200 mM sucrose. Termination of the reaction was achieved by adjusting the pH to 7.5 and centrifugation, and then amounts of glucose and fructose formed were quantified in the supernatant (see above).

Blanks were run either with inactivated enzyme extracts (10min, 98°C), double or doubly (see above) distilled water and with sample-free extraction buffer instead of the specific substrate (sucrose).

Protein determination

The protein content of the extracts (I and II) was determined in a micro plate assay using the BIO-Rad (BioRad, Munich) reagens according to the manufacturer's protocol.

RESULTS AND DISCUSSION

In the bamboo *Sasa palmata*, like other photoautotrophic and heterotrophic plant tissues, glucose, fructose and sucrose constitute the major soluble carbohydrate fraction. Together with starch these sugars represent the non-structural carbohydrates of this bamboo species. In mature above-ground organs such as one-year-old and two-years-old culms, the monosaccharides glucose and fructose dominate the soluble carbohydrate fraction during the cold season (February, March), and reach values of up to 120 nmol/mg dw. The high contents of monosaccharides and of sucrose (up to 100 nmol/mg dw; Figs: 1 b, c) together with low amounts of starch (down to less than 10 nmol starch-bound hexoses/mg dw; Figs: 1 b, c) during this period can be taken as an indication of cryoprotection. This has also been reported for other perennial plant organs, such as branches or stems of trees (Magel et al. 1994, Sauter and Marquardt 1966, Sauter and Wellenkamp 1998, Sauter et al. 1996). Starting with higher temperatures towards the end of March, sucrose becomes the dominating sugar fraction and starch accumulates in the parenchyma cells. This is most probably due to a surplus of photoassimilated products, resulting in highest amounts of starch in early summer (for example in conifers see Egger et al. 1996). In samples of one-year-old and two-years-old culms collected on April 20th, this steady starch increase is retarded. During autumn and winter, starch pools are low in mature culms (Figs. 1b, c).

In the bamboo under-ground organ, the rhizome, cryoprotection of the tissue during wintertime is also characterized by higher contents of soluble carbohydrates and decreased pools of starch (Fig. 1a). Contrasting to overwintering, one-year-old and two-years-old bamboo culms, rhizones contain sucrose as the preponderant component of the soluble carbohydrate fraction throughout the year. Starch contents in the rhizome peak in early spring (end of March; Fig. 1a) and then later on during early summer (May, June). Thus, the rapid spring growth of the new shoots, leads to reduced total amounts of non-structural

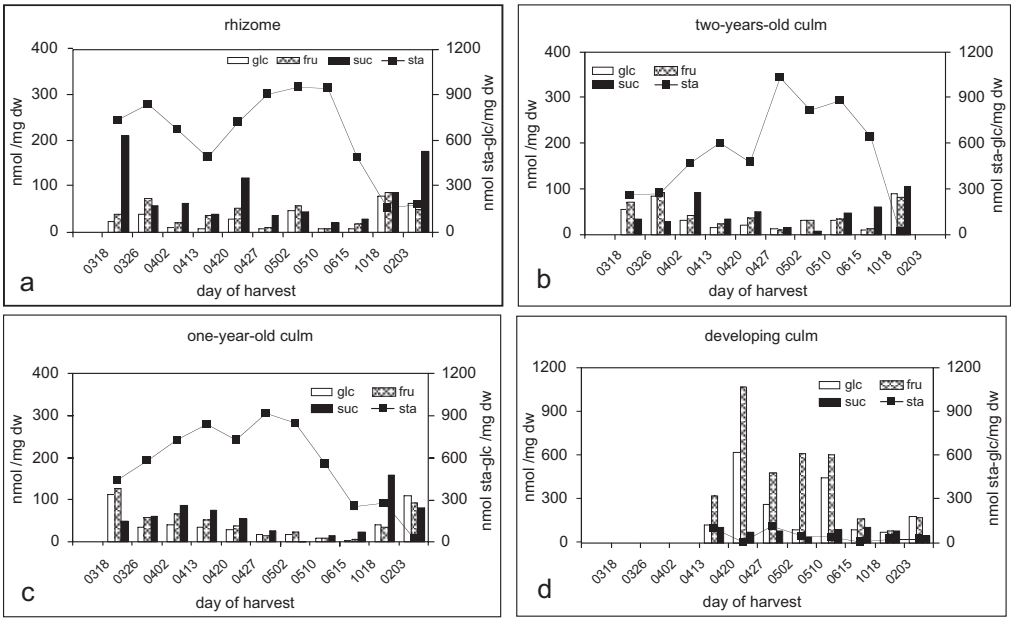

Figure1. Seasonal course of contents of glucose (glc, open bars; nmol/mg dw), fructose (fru, grey bars; nmol/mg dw), sucrose (suc, losed bars; nmol/mg dw), and starch (sta, closed squares; nmol sta-glc(mg dw) in the rhizome (a), one-year-old (b), two-years-old (c), and the developing (d) culm of *Sasa palmata* from March 18th, 2004 (0318), until February 3rd, 2005 (0203). The first two digits identify the month, the second two the day. Values given are means of three replicates. As standard deviations were lower 5% no SD is given.

carbohydrates in the rhizome (Li et al. 1998). It is noteworthy, that both the rhizome and the mature culms exhibit starch levels of up to 1 µmol starch-bound hexoses/mg dw, and thus starch constitutes more than 20 % of the dry weight.

Between April 2nd and April 13th, the current year's culms emerged (Fig. 1d). On April 13th, this new shoot was about 25 cm in length. A constant daily growth rate of about 7 cm was maintained until the final height of about 220 cm was reached on May 10th. During this growth period, starch contents were negligible and soluble carbohydrates reached amounts up to 1.8 µmol hexoses/mg dw (Fig. 1d); thus sugars constituted more than 30 % of the dry weight (for comparison sugar content of the phloem sap and of sugar storing tissues of sugar cane and sugar beet is about 15%). Moreover, hexose-contents found in the elongating tissue of bamboo culms are 5 fold higher than those present in the zone of enlarging tracheids within the cambial differentiation zone of pine trees (Uggla et al. 2001) and up to 10 fold higher than in the apical meristem of developing conifer seedlings (Einig et al. 1999). In vigorous growing culms, fructose contents exceed by far the contents of glucose and/or sucrose (Fig. 1d). This implies, that in the developing culm like in the dividing and expanding tissues of the cambial region of pine trees, glucose is faster consumed in metabolic and/or biosynthetic pathways (Uggla et al. 2001).

Based on these findings, we concluded that highest concentrations of osmotically active components in the vigorous growing culm, such as the monomeric and dimeric carbohydrates, glucose, fructose, and sucrose, enable the elongation of the bamboo tissue, which appears to be driven, at least partly, by changes in the solute potential (Cosgrove 1986, Hoffmann-Benning et al. 1997).

In rapidly elongating tissues, such as internodes, fibrous roots, early stages of fruit expansion, young sink leaves or expanding cambial cells increased amounts of monomeric

sugars are associated with high catalytic activities of soluble acid invertase (Morris and Arthur 1985, Quick and Schaffer 1986, Uggla et al. 2001). Soluble acid invertases are located in the vacuole. They control sugar composition in fruits or storage organs, respond to environmental stresses or wounding, and are involved in osmoregulation and cell enlargement (Roitsch and Gonzalez 2004). This pivotal role of acid invertase for cell elongation was also shown in transgenic tobacco plants, expressing a yeast-derived invertase in the vacuole (Hoffmann-Benning et al. 1997). In elongating bamboo culms, like in tissues which undergo rapid cell expansion (Tymowska-Lalanne and Kreis 1998), highest contents of monomeric sugars coincide in time and tissue distribution with the highest catalytic activities of acid soluble invertases, both when calculated on a dry weight or protein basis (Fig. 2). This can be taken as further proof that expansion and elongation of the cellular organization of the culm, which has been preformed within the buds, is at least partly controlled by osmotic pressure and cell turgor.

During these developmental processes, the heterotrophically growing culm depends on carbon supply from other tissues. Sharp decreases in starch pools in the rhizome during times of the early growing period of the new culm (April 13th), as well as lower starch accumulation in the mature culms (April 20th), indicate a reallocation of stored carbon from these tissues towards the developing culm. In addition, current photoassimilates of the older culms appear to be translocated to the rapidly growing new culm (Koyama and Ogawa 1993).

In most plant species, carbon is transported from source to sink tissues in the form of sucrose. At the sink area, sucrose is exported or leaked from the translocation path (e.g. sieve elements) into the apoplast. Here, cell wall located invertases hydrolyse sucrose into glucose and fructose. The hexoses are then taken up into the sink cells by hexose transporters (Roitsch and Gonzalez 2004). In the rapidly elongating culm (until May 2nd), high catalytic activities of cell wall invertases could facilitate such an import of sucrose into this sink tissue, and thus indicate apoplastic unloading in the expanding bamboo culm (Fig. 3). Ionically bound cell wall invertases dominate this developmental stage.

After cessation of the growth in height (June 15th) of the new culm, pools of soluble carbohydrates, and catalytic activities of the vacuolar (AIsol) and cell wall (AIicw, AIccw) invertases were similar to those of mature culms, whereas starch contents remained low.

In summary we conclude, that cell wall invertases play an important role in sucrose partitioning towards the growing culm, and hydrolysis of sucrose by cell wall invertases (AIcw) contribute to establishing sink strength (Sturm and Tang 1999). The correlation between high activities of AIcw and AIsol, and

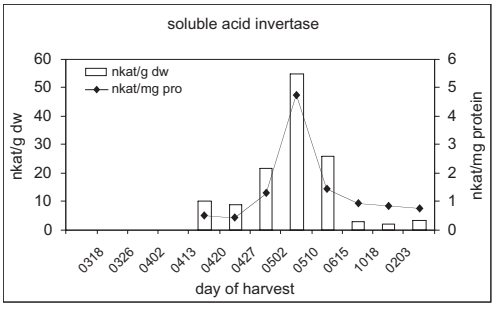

Figure 2. Catalytic activities of soluble, vacuolar acid invertase calculated on a dry weight (open bars; nkat/g dw) and protein (closed rectangles; nkat/mg pro) basis in the developing culm of *Sasa palmata.* Values given are means of three replicates. As standard deviations were lower 5% no SD is given.

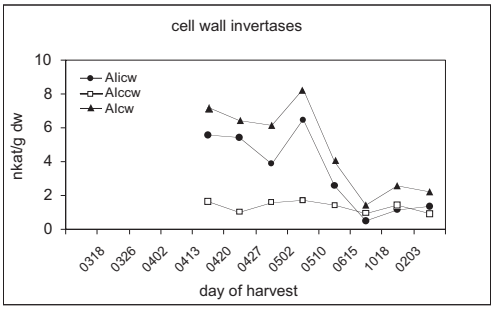

Figure 3. Catalytic activities of ionically (AIicw; closed circles; nkat/g dw), covalently (AIccw; open squares; nkat/g dw), and total (sum of AIicw plus AIccw; closed triangles; nkat/g dw) cell wall invertases in the developing culm of *Sasa palmata.* Values given are means of three replicates. As standard deviations were lower 5% no SD is given.

the high resulting hexose contents, control cell elongation and expansion by modulating osmotic pressure and cell turgor. Most probably, these sugar supplies are also important for maintaining high mitotic activity in the growing culm (Roitsch and Gonzales 2004). Our findings give evidence that invertases in combination with sugars regulate growth and elongation of developing bamboo culms. The biochemical and genetic regulation of the phenomenon of rapid growth and elongation of developing bamboo culms will be the focus of future work.

ACKNOWLEDGEMENTS

The authors thank Prof. Dr. Rüdiger Hampp (University of Tübingen) for helpful suggestions and critical reading of the manuscript and Dennis Wilstermann for assistance in sample preparation and protein determination.

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The Journal of the American Bamboo Society 19(1): 30-31

Bamboo Notes[1]

Contemporary size maxima of *Arundinaria gigantea* (Walt.) Muhl.

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Cane, *Arundinaria gigantea* (Walter) Muhl., is a monopodial bamboo with erect culms bearing evergreen foliage, occurring throughout much of the southeastern United States (Marsh 1977; Platt and Brantley 1997). In the past, culms were frequently reported as growing to 12 m tall and up to 10 cm in diameter (Michaux 1793-1796; Stoddard 1812; Lyell 1849; McWilliams 1981). Dunbar (1749-1810) reported culms the "size of a mans leg or more", Lawson (1714) stated that a single culm segment could "hold above a pint of liquor" and Bartram (in Van Doren 1928) described culms "as thick as a mans arm". The tallest culm recorded was 47 ft (~ 11.4 m) from the third node to the terminus (Romans 1775; Platt and Brantley 1997). Culms of the size described by these early writers apparently no longer exist (Harper 1928). The largest culms Meanley (1972) encountered in many years of searching were 4.5 to 6.0 m tall and 3.1 cm in diameter. Likewise, the largest culm measured by Marsh (1977) was 8.2 m tall and 2.5 cm in diameter. Here we describe a natural stand of cane containing culms that exceed the maximum size parameters previously reported by modern researchers.

We found the stand (30°23.91' N; 91° 08.28' W) on 29 December 2002 along Bayou Duplantier, approximately 1.5 km downstream from the bridge at Lee Drive, Baton Rouge, East Baton Rouge Parish, Louisiana. The culms are growing sparsely along a 30 m segment of a man-made embankment bordering an extensive *Taxodium distichum* swamp. Although the swamp is subject to frequent flooding, the cane is sufficiently elevated to avoid inundation. The embankment supports a second-growth forest comprised of *Celtis laevigata, Liquidambar styraciflua, Acer negundo,* and *Platanus occidentalis,* and we estimate canopy coverage above the cane to be 50%. Understory vegetation associated with the cane includes *Ligustrum sinense, Ligustrum japonicum, Sambucus canadensis, Lonicera japonica,* and *Lygodium japonicum.* The age of the stand is uncertain, but the embankment on which it is growing was constructed when Bayou Duplantier was dredged for flood control between 1953 and 1957 (US Army Corps of Engineers 1995).

The stand is composed of 38 living, 17 decadent (declining but at least one branch with living foliage), and 17 dead culms. We measured the diameter breast height (dbh) of each culm using tree calipers, and found eight living and two dead culms with a dbh greater than 3.1 cm. The largest was a dead culm with a dbh of 4.1 cm, which we severed at ground level and determined its height to be 882 cm.

[1]***Bamboo notes*** are communications of brief and generally self-evident data not requiring extensive discussion or explanation.

The basal portion of this culm and branches with foliage from an adjacent living culm were deposited as vouchers in the Clemson University Herbarium, Clemson, South Carolina, USA (CLEMS 61611 and 61612). To our knowledge, this culm represents the contemporary size maxima for uncultivated *Arundinaria gigantea*.

ACKNOWLEDGEMENTS

We thank Mike Leggio and Lucas Jackson for field assistance, Patrick McMillan for vouchering specimens, and the librarians at Clemson University and Louisiana State University for help in locating obscure references.

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F.A. McClure's photos of the type collection of *Chusquea robusta*

Chusquea robusta: top, habit; bottom, shoot internode showing culm leaf and branch initiation. Photos taken by F. A. McClure as part of the type collection (McClure 21431) of this species. From the research archives of the U. S. National Herbarium, Smithsonian Institution, Department of Botany.

See the article by Clark and Losure on pages 5-10 of this issue. Scans provided by Lynn Clark.

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