



## RESEARCH ARTICLE

## Determination of minimal age of five species of *Chusquea* bamboos through rhizome analysis as a tool to predict the flowering in southern Chile

Determinación de la edad mínima de cinco especies de *Chusquea* mediante el análisis de rizomas como un método para predecir las floraciones en el sur de Chile

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### ABSTRACT

Synchronous flowering and subsequent drying up of bamboos of the genus *Chusquea* are important processes in the dynamics and structure of many forest ecosystems. In southern South America, bamboo flowering and subsequent mast seeding trigger rodent outbreaks associated with zoonotic diseases. Predicting future flowering events requires knowledge of the age of bamboo stands together with species-specific periodicity in flowering. We explored whether it is possible to predict the minimum age in bamboo plants based on the features of their rhizomes. We studied bamboo stands of age known by the local people in 15 sites in the coastal and Andes Mountains as well as in the Central Valley of southern Chile (37° 48'–43° 58' S, from 12 to 1047 m.a.s.l.). For 164 individual plants, of five South American *Chusquea* bamboo species (*C. valdiviensis*, *C. uliginosa*, *C. culeou*, *C. montana*, and *C. macrostachya*), we collected and characterized the number and shape of divisions of whole rhizomes. For all species sampled there was a tight linear relationship between plant age and the number of rhizome divisions or rhizomes, accounting for 11–99 % of variation. In order to overcome constraints caused by the limited number of age cohorts available for individual species and to allow for prediction over a wider range of age, we also fitted a common linear model to species with similar age-rhizome relationships. We provide calibration relationships that can be used for retrospectively estimating the date of last flowering over large areas where bamboos form part of the understory and for predicting the future flowering events.

**Key words:** age determination, Bamboo, *Chusquea* spp., Hanta, seed masting, rhizome.

### RESUMEN

La floración y posterior desecamiento de la Bambúsea del género *Chusquea* son procesos importantes en la dinámica y estructura de muchos ecosistemas forestales. Además, en Sudamérica desencadenan grandes tamaños de poblaciones de roedores, “ratadas,” asociados con enfermedades zoonóticas. Para predecir futuros eventos de floraciones se requieren conocer la edad de los quilantos y los períodos en que ocurren. Exploramos la posibilidad de predecir la edad mínima de las plantas de quila a partir de las características de los rizomas en 5 especies de quila (*C. valdiviensis*, *C. uliginosa*, *C. culeou*, *C. montana* y *C. macrostachya*) de edad conocida por personas de la localidad en 15 sitios de la Cordillera de la Costa, de los Andes y Valle Central del sur de Chile (37° 48'–43° 52' S), desde los 12 a los 1047 m.s.n.m. En 164 plantas individuales colectamos y caracterizamos el número y forma de las divisiones del rizoma de plantas. Para cada especie se encontró una relación lineal entre la edad de la planta y el número de divisiones de rizomas o rizomas para plantas entre 6 y 42 años de edad, que dieron cuenta del 11 al 99 % de la variación. Con el fin de ampliar el limitado rango de edad disponible y el rango de edad de las predicciones, se ajustó un modelo lineal común a las especies con similar relación entre edad y rizoma. La relación de las calibraciones pueden ser así utilizadas en forma retrospectiva para estimar la última fecha de floración en una gran área donde *Chusquea* spp. forma parte del sotobosque y para predecir futuros eventos de floraciones.

**Palabras clave:** *Chusquea* spp., determinación de edad, Hanta, rizoma, semillación.

## INTRODUCTION

Bamboo is a plant of global interest because of their distinctive life form, the major role they play in forest ecosystem dynamics (Keeley & Bond 1999), and the wide range of uses and value they have for humans and wildlife species. Bamboos have a global distribution, ranging from 46° N to 47° S latitude, reaching elevations as high as 4000 m.a.s.l. and occurring in a wide range of ecosystems (Huberman 1959, McNeely 1996). In almost all Latin American habitats 64 bamboos from the genus *Chusquea* are found, which accounts for 50 % of the mountain species of Andean countries (Clark 1995, Matthei 1997, Judziwicz et al. 1999). In southern South America *Chusquea* colonizes evergreen forests and false beech (*Nothofagus* spp.) dominated forests of Chile and Argentina, from sea level to 1200 m.a.s.l. (Veblen 1979). *Chusquea* bamboo populations of the same lineage are characterized by synchronized blooming and subsequent death, occurring after variable, but not always well-known, periods of vegetative growth (Jaksic & Lima 2003). The *Chusquea* flowering phenomenon may occur over extensive geographic areas, as happened in Southern Chile during the 1990's, with more than 10000 km<sup>2</sup> of *C. valdiviensis* (E Desvieux 1854) involved in sequential flowering from 1991 to 1993 (Pacheco 1993, González & Donoso 1999). There are prior records of massive flowering of different *Chusquea* species including by *Ch. uliginosa* (R Philippi 1859) in 1962-1963, in 1977-1978 (*Chusquea* spp.) and in 2001 (*C. culeou* (E Desvieux 1854)) (Jaksic & Lima 2003).

These massive flowering events by bamboos of the genus *Chusquea* also trigger outbreaks of rodent populations, the so-called "ratadas" recorded since 1552 (Jaksic & Lima 2003). In southern Chile several cricetid rodents respond with outbreaks (Murúa et al. 1996, Gallardo & Mercado 1999, González et al. 2000), but one granivorous species, *Oligoryzomys longicaudatus* (Bennett, 1832) (OL), is epidemiologically important because it is a confirmed reservoir of a zoonotic diseases, Hantavirus (Medina et al. 2009). Outbreaks of OL seemingly, in turn, underpin variation in the prevalence of Hanta virus infections amongst humans (Toro et al. 1998).

Regeneration occurs during spring after a winter period of decomposition of dried biomass, thus beginning another period of

growth and development (Huberman 1959, McClure 1966, Janzen 1976, Sharma 1982, Franklin 2004). The plants of *Chusquea* are formed by an aerial part (culms, twigs and leaves) and a subterranean part (rhizome). The rhizomes are modified stems that support the aerial stems, storing foods and functioning as vegetative reproductive organs in woody bamboos. They are formed by repeated units including nodes, internodes, bud and roots (Hidalgo 2003). The rhizome of southern South American *Chusquea* are pachymorphic, with strong, thick and short ramified rhizomes, 5 to 15 cm long, each splitting in two or three new rhizomes every spring (Pearson et al. 1994, Watanabe et al. 1996, 1997). New rhizomes produce roots and culms yearly until they senesce. We hypothesized that the patterns of growth and division of rhizome would be related to the age of the plants.

Bamboo plants play an important ecological role fostering the regeneration of shade-intolerant species, such as *Fagus* in Japan (Abe et al. 2001), *Abies* and *Betula* spp. in south-western China (Taylor et al. 2004) and *Nothofagus* spp. in South America (Veblen 1979, Holtz & Veblen 2005). Forest disturbances affect light availability in the shrubs strata modifying germination and growth of other species (Valeria 1996). Also, the thick covering of the ground surface with dead leaves following a flowering event may affect the germination of understory plants (González & Donoso 1999).

Here we report on an investigation that combines knowledge of the growth pattern of *Chusquea* rhizomes and detailed examination of plants of known age in order to calibrate relationships that could be used to predict the likelihood of future flowering events and possibly the so called "ratadas" with the associated public health consequences.

## METHODS

We selected 15 sites, distributed between 37°30' and 43°50' S in both the coastal and Andes cordilleras and central valley of southern Chile which included 5 species of *Chusquea* (*C. valdiviensis*, *C. uliginosa*, *C. culeou*, *C. montana* (R Philippi 1864) and *C. macrostachya* (R Philippi 1864)). Samples were collected from January 2004 to March 2006. Individual plants of known age were selected by interviewing local people who witnessed the last flowering events and subsequent regeneration. The maximum age of individual plants was determined by

TABLE 1  
 Sampling site, geographical coordinates, altitude and eco region of sampling of individual plants. \*\* Plants collected in different years (2004, 2005 or 2006). \*\*\* Plants standing dead, dying post flowering recorded in 2002-2003.

Sitios de muestreos con las coordenadas geográficas, altitud y las ecoregiones donde se obtuvieron muestras de las plantas. \*\* Plantas colectadas en los años 2004, 2005 y 2006  
 \*\*\* Planta muertas en pie después del florecimiento los años 2002-2003.

Site name	Latitude (S)	Longitude (W)	Altitude (m)	Ecoregion	Species	Year of flowering	Type of flowering	Maximum plant age when sampled (year of sampling - year of flowering -2)
Nahuelbuta	37° 48' 57"	73° 00' 30"	1058	Coast Cordillera	C. culeou	1975	massive	29
Tolhuaca	38° 02' 23"	71° 50' 18"	974	Andes Cordillera	C. culeou	1982	massive	20, 21**
Malacahuello	38° 29' 51"	71° 38' 17"	1130	Andes Cordillera	C. macrostachya	1972	massive	30
					C. culeou	1982	massive	20, 21**
					C. valdiviensis	1991	massive	11, 12**
Conguillio	38° 47' 29"	71° 39' 48"	983	Andes Cordillera	C. culeou	1981	massive	22
					C. culeou	1982	massive	20, 21**
					C. valdiviensis	1992	massive	10, 11**
Huerquehue	39° 09' 59"	71° 43' 28"	734	Andes Cordillera	C. culeou	1975	massive	29
					C. macrostachya	1981	massive	23
San Martín	39° 38' 50"	73° 13' 20"	13	Central valley	C. uliginosa	1962	massive	39***
					C. uliginosa	1980	Isolated plants	24
					C. valdiviensis	1986	Isolated plants	17
					C. valdiviensis	1992	massive	10, 11**
Máfil	39° 43' 59"	72° 56' 36"	73	Central Valley	C. uliginosa	1962	massive	39***
					C. uliginosa	1972	massive	28***
Queule	39° 22' 05"	73° 13' 04"	21	Coast	C. uliginosa	1962	massive	39***
Follico	39° 50' 59"	72° 35' 05"	173	Central valley	C. uliginosa	1972	massive	28***
Hueicolla	40° 09' 41"	73° 39' 04"	58	Coast Cordillera	C. macrostachya	1995	Isolated plants	9
					C. montana	1993	massive	11
Alerce costero	40° 14' 65"	73° 21' 27"	746	Coast Cordillera	C. montana	1995	Isolated plants	9
Anticura	40° 43' 09"	72° 11' 45"	992	Andes Cordillera	C. montana	1987	Isolated plants	16
					C. montana	1991	massive	12
					C. valdiviensis	1991	massive	11, 12**
Puyehue	40° 31' 51"	71° 53' 30"	1132	Andes Cordillera	C. culeou	1976	massive	27
					C. macrostachya	1962	massive	42
					C. montana	1987	Isolated plants	16
					C. montana	1991	massive	12
					C. montana	1997	Isolated plants	6
Cucao	42° 37' 30"	74° 06' 39"	12	Coast	C. valdiviensis	1991	massive	11, 12**
La Junta	43° 58' 25"	72° 24' 18"	102	Andes Cordillera	C. valdiviensis	1992	massive	10, 11**

subtracting 2 years from the flowering date of parent plants (González & Donoso 1999). Details of the sites studied are shown in Table 1.

One hundred and sixty four complete rhizomes, some larger than 3 m<sup>3</sup>, were excavated. Rhizomes were cut and cleaned in the laboratory. The shape, growth form, number of rhizomes, number of splitting events and the structure of the rhizomes were recorded (Figure 1). The older rhizome were identified and considered the starting point of a branching process, and each rhizome and splitting events were marked with different colored pins. Figure 1 shows details of a *Chusquea* plant and details of the propagation and the divisions in the rhizome underground.

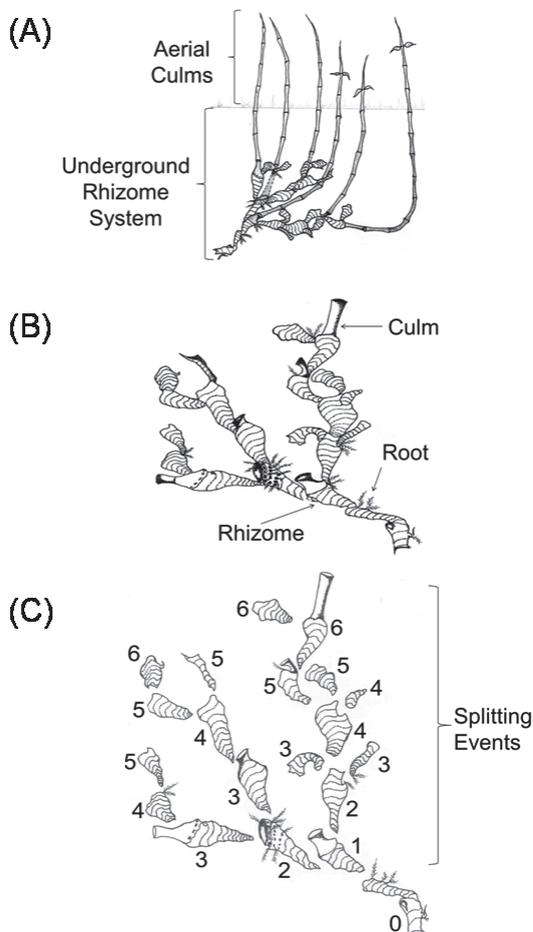


Fig. 1: Details of a *Chusquea* spp. A and B show the structure of *Chusquea* plant and its rhizome. C shows details of the pattern of splitting events and the rhizome divisions. The numbers refer to the sequence of splitting events, starting from the root (numbered 0).

Detalles de la planta *Chusquea* spp. A y B muestran la estructura de una planta *Chusquea* y su rizoma. Figura C muestra detalles del patrón de eventos de separación y las divisiones del rizoma. Los números se refieren a la secuencia los eventos de separación comenzando desde la raíz (identificada con el número 0).

Generalized linear models with a Gaussian error and identity link were fitted with age as dependent variable and the number of splitting events and rhizomes as predictors. Common models for all species (with species as covariates) were fitted, as well as single species models to overcome the limited range of age classes sampled for each species. GLMs were fitted using S-Plus 6.1 (Insightful Corp.). All means are reported with their standard error.

## RESULTS

In twenty two samples out of 33, we were able to sample bamboos from one species from a single age cohort, whereas in nine sample sites, two age cohorts of a species were sampled. This reflects both the availability of plants of known age as well as the likely dominance of one or more age cohorts at each site. Bamboo plant age, according to local witnesses, ranged from 6 to 42 years old and resulted from either massive flowering or of flowering by isolated plants (Table 1). Simple linear regressions with the number of splitting events as a linear predictor of age were significant for all species and explained 78-98 % of variance in age (*C. culeou*:  $F_{2,34} = 118.7$ ;  $P < 0.001$ ); *C. macrostachya*:  $F_{2,28} = 1210$ ,  $P < 0.001$ ; *C. montana*:  $F_{2,34} = 189.3$ ,  $P < 0.001$ ; *C. uliginosa*:  $F_{2,17} = 897.3$ ,  $P < 0.001$ ; *C. valdiviensis*  $F_{2,41} = 184.2$ ,  $P < 0.001$ ) (Table 2). Whereas intercept estimates fluctuated widely and values were not biologically meaningful, reflecting our use of linear models and the paucity of data at low age. Estimates of the number of splitting events per year (slopes) were rather consistent, ranging from 0.85 to 1.27, except for *Ch. uliginosa* that had a low estimate of 0.62.

Simple linear regressions using the number of rhizomes as a linear predictor of age were also significant, although with lower coefficient of determination than for the number of splitting events, (*C. culeou*  $F_{2,34} = 8.248$ ,  $P < 0.001$ ; *C. macrostachya*  $F_{2,28} = 164.5$ ,  $P < 0.001$ ; *C. montana*  $F_{2,34} = 24.7$ ,  $P < 0.001$ ; *C. uliginosa*  $F_{2,17} = 276.5$ ,  $P < 0.001$ , *C. valdiviensis*  $F_{2,41} = 4.85$ ,  $P < 0.03$ ). Even though the natural logarithm of the number of rhizome should better reflect the multiplicative nature of the rhizome multiplication process, models predicting age based on natural logarithm of number of rhizome only improved fit relative to untransformed values for one of 5 species (*C. uliginosa*  $F_{2,17} = 276.5$ ,  $P < 0.001$ ,  $R^2 = 0.94$ ). The best linear regression for this species was

TABLE 2

Parameters (standard errors) and coefficient of determination of *Chusquea* species specific linear regressions predicting plant age with the number of splitting events and numbers of rhizomes to estimate age by each one of the five species of *Chusquea*. The regressions were not forced through the origin.

Parámetros (error estándar) y coeficientes de determinación de las regresiones especie específicas de *Chusquea* para estimar la edad de la planta, el número de eventos de separación ocurridos y el número de rizomas en las cinco especies de *Chusquea*. Las regresiones no se forzaron a pasar por el origen.

Species	Splitting events		Rhizomes	
	Equation	R <sup>2</sup>	Equation	R <sup>2</sup>
<i>C. culeou</i> n = 36	age ~ 2.12(2.49) + 1.27(0.12)* splitting event	0.78	age ~ 0.14(0.37)+ 1.03(0.02)*rhizomes	0.39
<i>C. macrostachya</i> n = 30	age ~ 2.18(0.91) + 1.07(0.03)* splitting event	0.98	age ~ 2.43(2.43) + 0.68(0.05)*rhizomes	0.85
<i>C. montana</i> n = 36	age ~ 3.23(0.7) + 0.96(0.07)* splitting event	0.85	age ~ 3.77(1.79) + 0.46(0.09)*rhizomes	0.42
<i>C. uliginosa</i> n = 19	age ~ 16.52(0.6) + 0.62(0.02)* splitting event	0.98	age ~ 22.5(0.73) + 0.13(0.01)*rhizomes	0.92
<i>C. valdiviensis</i> n = 43	age ~ 2.64(0.64) + 0.85(0.06)* splitting event	0.82	age ~ 8.91(1.02) + 0.125(0.06)*rhizomes	0.11

TABLE 3

Parameter estimates of General linear Models considering the number of splitting events as predictor of age in five species of *Chusquea*.

Parámetros estimados del Modelo Lineal Generalizado considerando el número de eventos de separación ocurridos como predictor de edad en las cinco especies de *Chusquea*.

Age~Propagations	Coefficient	Standard Error	P-value
Intercept	4.49	0.51	0.000
splitting events	0.95	0.03	0.000
<i>C. culeou</i>	2.15	0.99	0.031
<i>C. macrostachya</i>	1.07	0.43	0.014
<i>C. montana</i>	3.85	0.29	0.000
<i>C. uliginosa</i>	-0.46	0.23	0.047
splitting event * <i>C. culeou</i>	-0.1	0.04	0.026
splitting event * <i>C. macrostachya</i>	-0.07	0.03	0.035
splitting event * <i>C. montana</i>	-0.12	0.013	0.000
splitting event * <i>C. uliginosa</i>	-0.024	0.02	0.238

thus: age ~ 2.05(1.92) + 7.46(0.45)\*ln(rhizomes). Figures 2a to 2e shows linear regression for each species. The fit of the linear regression for *C. valdiviensis* was poor, even if significant, when using number of rhizomes as predictor of age.

In order to overcome the limited age range available for individual species and to widen the

range of age predictions for species with similar age-rhizome relationships, we also fitted GLM (analysis of covariance), with species identity as factor and splitting events as linear predictor of age. The model was highly significant ( $F_{2,154} = 9743$ ;  $P < 0.00001$ ) and accounted for 98 % of the variance in age (null deviance: 19108.65 on 163

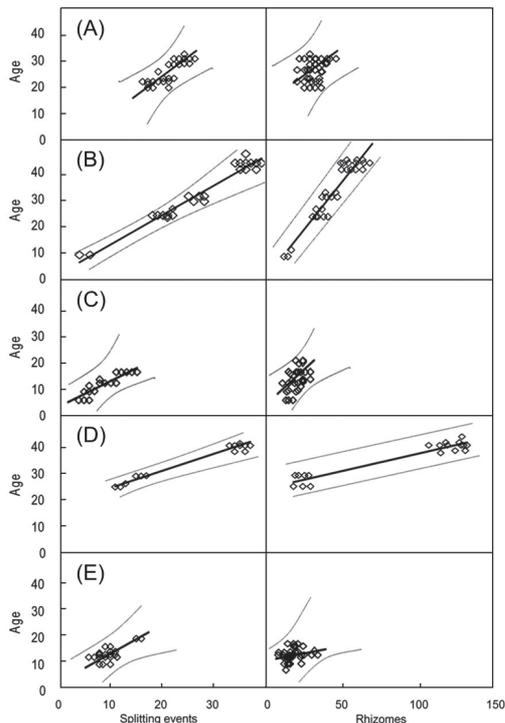


Fig. 2: Single regression for five species of *Chusquea* using splitting events and rhizomes to predict age. A *C. culeou*, B *C. macrostachya*, C *C. montana*, D *C. Uliginosa*, E *C. valdiviensis*.

Regresiones simples para predecir la edad usando los eventos de separación y rizoma en cinco especies de *Chusquea*. A, *C. culeou*, B, *C. macrostachya*, C, *C. montana*, D, *C. uliginosa* E *C. valdiviensis*.

df, residual deviance: 287.99 on 154 df). There was statistical support for different intercepts ( $F_{5,154} = 46.3, P < 0.00001$ ) and different slopes (interaction splitting event\*species  $F_{10,154} = 36.6, P < 0.0001$ ). We found no support for a common slope for *C. valdiviensis* and *C. uliginosa* when we fitted an ANCOVA model for those two species ( $F_{1,58} = 12.82, P = 0.0007$ ). On the other hand, a model for the other three species (*C. culeou*, *C. macrostachya* and *C. montana*) gave support for common slopes ( $F_{2,98} = 0.083, P = 0.92$ ) and intercepts ( $F_{2,96} = 2.53, P = 0.085$ ). Thus a common linear regression, accounting for 97.6 % of variance for those three species is  $Age \sim 2.21(0.35) + 1.064(0.016) * \text{splitting event}$  (Fig. 3).

A similar GLM with rhizome as linear predictor was also significant ( $F_{2,162} = 1284, P < 0.00001$ ), accounting for 95.3 % of the variance in age significant variation in different intercepts and slopes between species ( $F_{5,162} = 148.5, P < 0.00001$ ;  $F_{10,162} = 53.9, P < 0.0001$ ) respectively. The difference in slopes here stemmed from *C. valdiviensis* producing more rhizomes per year than *C. culeou*, *C. montana*, *C. macrostachya* and *C. uliginosa*.

*C. valdiviensis* and *C. uliginosa* had undistinguishable slopes ( $F_{1,58} = 0.000, P = 0.996$ ), but different intercept. The model for *C. valdiviensis* was:  $Age \sim (15.7(0.51) - 6.8(0.39)$

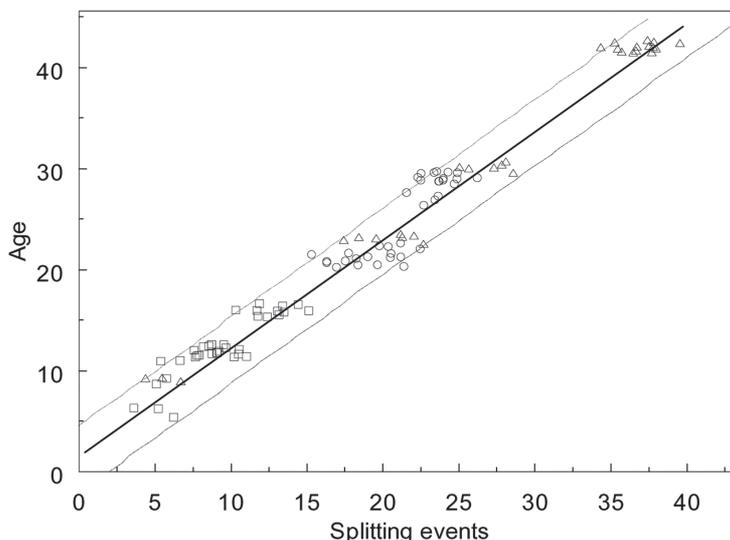


Fig. 3: Common regression for *C. culeou* (□), *C. macrostachya* (Δ) and *C. montana* (○) using the number of splitting events as predictor of age.

Regresión usando los eventos de separación como predictor de la edad en *C. culeou* (□), *C. macrostachya* (Δ) y *C. montana* (○).

TABLE 4

General linear Models considering number of rhizomes to estimate age in five species of *Chusquea*.

Parámetros del Modelo lineal Generalizado considerando los rizomas para estimar la edad en cinco especies de *Chusquea*.

Age~Rhizomes	Coefficient	Standard Error	P-value
Intercept	7.55	0.78	0.000
Rhizome	0.48	0.03	0.000
<i>C. culeou</i>	1.14	1.48	0.441
<i>C. macrostachya</i>	0.83	0.81	0.307
<i>C. montana</i>	5.09	0.41	0.000
<i>C. uliginosa</i>	-0.34	0.32	0.282
Rhizome * <i>C. culeou</i>	-0.18	0.06	0.002
Rhizome * <i>C. macrostachya</i>	-0.13	0.04	0.007
Rhizome * <i>C. montana</i>	-0.14	0.01	0.000
Rhizome * <i>C. uliginosa</i>	-0.08	0.02	0.000

+ 0.13(0.01)\*rhizomes and for *C. uliginosa*: Age  $\sim 15.7(0.51) + 0.13(0.01)*\text{rhizomes}$  ( $R^2 = 0.974$ ). Finally, a GLM including the 3 other species (*C. culeou*, *C. macrostachya* and *C. montana*) had species-specific slopes ( $F_{2,98} = 103.4$ ,  $P < 0.000$ ) and intercepts ( $F_{2,96} = 6.13$ ,  $P = 0.003$ ).

#### DISCUSSION

We found that simple linear model gave an often excellent fit to the relationship between the age of *Chusquea* bamboo plants aged 5 to 50 years and the number of splitting events or rhizomes. This was made possible by our

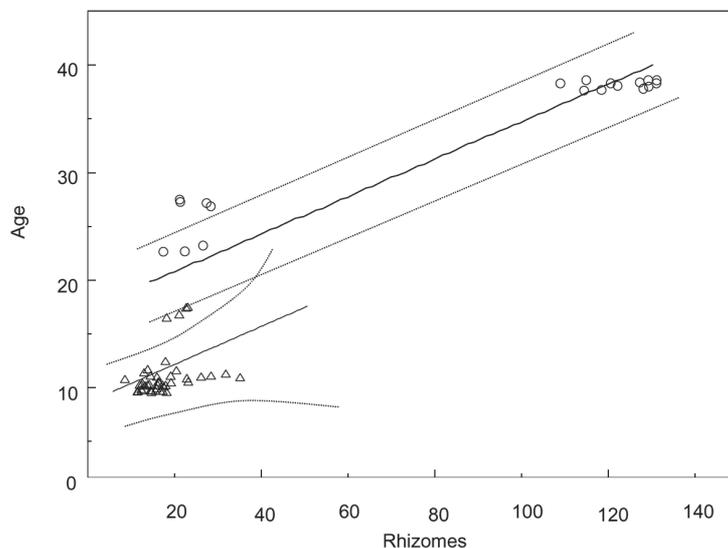


Fig. 4: Common regression for *C. uliginosa* (○) and *C. valdiviensis* (Δ) using the number of rhizomes as predictor of age.

Regresión usando el número de rizomas como predictor de la edad en *C. uliginosa* (○) y *C. valdiviensis* (Δ)

use of local knowledge of individual plants by the local inhabitants we interviewed. Overall, a linear relationship between plant age and the number of splitting events provided a superior predictive ability than a relationship involving the number of rhizomes. A log linear relationship expected from the multiplicative nature of the rhizome expansion process only gave a better fit than a linear model for *C. uliginosa*. This would suggest that rhizomes of this species senesce more slowly than those of other species.

Despite our large scale sampling effort, each species was represented by one or two, always adjacent, cohorts at each site and by a small number of cohorts throughout our sampling area. For *C. valdiviensis* in particular, the overall range of age encountered was small, and this greatly reduces the predictive power of the relationships for this species. As our intent was to produce a pragmatic relationship that could be used for predicting future bamboo flowering events and the associated Hanta virus epizootic risk to humans, we chose to overcome this constraint inherent to the biology of the species by deriving common relationships for bamboo species that had similar growth patterns. Here, we found that *C. culeou*, *C. macrostachya* and *C. montana* had similar growth rates for both propagation and rhizomes, and *C. uliginosa* and *C. valdiviensis* seemingly have similar growth rates, lower than those of the other three species considered. Clearly, given the limited age range available for *C. valdiviensis*, any inference and estimation of age from root structure should be made with caution.

While we are well aware that bamboos do not grow linearly, we deliberately restricted ourselves to linear relationships that gave more than satisfactory fit over the range of ages considered. Fitting more biologically realistic non-linear growth curves must await more data on growth patterns in the early years of growth. Thus, while the intercept of the relationships derived have no biological meaning, the estimated growth rate of one propagation per year has useful practical applications. The overall linear regression can be used for estimating plant age in an area. Indeed, *Chusquea* bamboo flowering is followed by massive seed production and this notoriously triggers outbreaks of the Sigmodontinae reservoir of the Andes Hanta

virus, *Oligoryzomys longicaudatus* (González et al. 1989, Murúa & Padula 2004, Murúa & Briones 2005) with Hantavirus prevalence on both side of the Andes Mountains (Murua et al. 2003, Piudo et al. 2005). There is a clear public health need to predict the likely occurrence of these outbreaks, and excavation of bamboo plants in a 241 wide range of area could provide a useful indicator of the flowering probability.

Even though our sampling scheme was not random with respect to the age of plants (indeed, we only sampled plants that were known by local residents), the fact that we only encountered one or, at most two, age cohorts at a given site is strongly indicative that the age structure of bamboo is uni-modal, such that a surveillance program based on even a limited sampling effort at each location would yield highly valuable information on bamboo age structure. Furthermore, once implemented, such surveillance effort would not have to be repeated and would yield critical information on the size of areas with similar bamboo age structure and thus likely to be affected synchronously by a rice rat outbreak.

While knowing the age of bamboo plants would be most useful as a public health tool, in conjunction with precise knowledge of the age at flowering of each bamboo plant, the available information on the age of bamboo at flowering is not un-ambiguous and free of controversy (Jaksic & Lima 2003). Specifically, it is not absolutely clear whether each bamboo species has a fixed flowering age or whether a deterministic ontogenic component to the probability of flowering is modified by environmental conditions. The interval between flowering events has been reported as 61 years for a given *C. culeou* southern Argentinean population and as 50 to 70 years for *C. valdiviensis* for a population in southern Chile (González & Donoso 1999). However, for most bamboo species worldwide, neither the age nor any environmental trigger of flowering is well-known (Clark 1995, Bystriakova et al. 2004). In most cases, the information available in the literature often goes no further than reporting the intervals between flowering events in an area, without explicit reference to the interval between flowering of plants and their progeny. For instance, while Jaksic & Lima (2003) concluded from their review that *C. culeou* flowers every 14 years, we encountered

numerous plants that were 20-29 years old. It is thus important to clearly specify the spatial scale considered, as well as ensuring the same population actually flowered repeatedly when reporting flowering intervals. Clearly, there is a need to obtain more information on the determinants of bamboo masting strategies. Even in the absence of such information, the presence of cohorts of bamboo that are 30-40 years old (*C. uliginosa* and *C. macrostachya*) must be at least indicative of heightened risk for areas where those species prevail. Indeed, the probability of flowering certainly increases with age. We observed a relationship between the ages recorded by processing the rhizomes in all the species and past flowering recorded by several authors previously (Veblen 1982, Veblen & Schlegel 1982, Veblen et al. 1979, Pacheco 1993, Schlegel 1993, Pearson 1994, Valeria 1996, Jaksic & Lima 2003). There were four cohorts that could be linked to massive flowering events (*C. uliginosa* and *C. macrostachya*: 1962-1964; *C. uliginosa*, *C. macrostachya* and *C. culeou*: 1972 -1976 and 1980 -1982 and *Ch. valdiviensis* and *C. montana*: 1991 -1995) and two cohorts that could be traced back to isolated plants flowering (*C. valdiviensis* and *C. montana*: 1986 -1987 and *C. montana* 1997) (Table 1). None of the sampled plants seemed to be part of the flowering event of 1977-1978 (Murúa et al. 1986, Anonymous 1994, González & Donoso 1999, cited in Jaksic & Lima 2003).

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#### LITERATURE CITED

ABE M, H MIGUCHI & T NAKASHIZUKA (2001) An interactive effect of simultaneous dead of dwarf bamboo, canopy gap, beach regeneration. *Oecologia* 127: 281-286.

BYSTRIAKOVA N, V KAPOŠ & I LYSENKO (2004) Bamboo biodiversity. UNEP-WCMC/INBAR, USA.

CLARK L (1995) Diversity and distribution of andean woody bamboos. In: Churchill SP, H Balsley, E Forero & JL Luteyin (eds) Biodiversity and

conservation of neotropical montane forests: 501-512. New York Botanical Garden, New York USA.

FRANKLIN D (2004) Synchrony and asynchrony: observations and hypotheses for the flowering wave in a long-lived semelparous bamboo. *Journal of Biogeography* 31: 773.

GALLARDO M & C MERCADO (1999) Mast seeding of bamboo shrubs and mouse outbreaks in Southern Chile. *Mastozoología Neotropical (Argentina)* 6: 103-111.

GONZÁLEZ M & DONOSO C (1999) Producción de semillas y hojarasca en *Chusquea quila* (Poaceae: Bambusoideae), posterior a su floración sincrónica en la zona centro-sur de Chile. *Revista Chilena de Historia Natural* 72: 169-180.

GONZÁLEZ L, R MURÚA & C JOFRÉ (1989) The effect of seed availability on population density of *Orizomys* in Southern Chile. *Journal of Mammalogy* 70:401-403.

GONZÁLEZ L, MURÚA R & C JOFRÉ (2000) Habitat utilization of two muroid species in relation to population outbreaks in southern temperate forests of Chile. *Revista Chilena de Historia Natural* 73: 489-495.

HIDALGO O (2003) Bamboo: The gift of the God. Kindle Amazon Inc. Columbia (USA).

HOLTZ A & T T VELEN (2005) Tree regeneration responses to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern andes. *Journal of Vegetation Science* 17:19-28.

HUBERMAN M (1959) Bamboo silviculture. *Unasylva, U. Nations (USA)* 13: 36-43.

JAKSIC F & M LIMA (2003) Myths and facts on ratadas: Bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecology* 28: 227-236

JANZEN D H (1976) Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7: 347-391.

JUDZIEWICZ E J, L G CLARK, X LONDOÑO & M J STERN (1999) American bamboos. Smithsonian Institution, Press, Washington DC.

KEELEY J & W BOND (1999) Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *The American Naturalist* 154: 383-391.

MATTHEI O (1997) Las especies del Género *Chusquea* Kunth (Poaceae: Bambusoideae), que crecen en la X región, Chile. *Gayana Botanica* 54: 199-220.

MCCLURE F A (1966) The bamboos, a fresh perspective. Harvard University Press, Cambridge, UK.

MCNEELY J A (1996) Bamboo, biodiversity and conservation in Asia. In: Ramanatha RV & RIV Ramanuja (eds) Biodiversity and genetic conservation: 6-19. New Delhi, India.

MURUA R & P PADULA (2004) Ecology and evolution of hantavirus in the Southern Cone of America. *Archivos de Medicina Veterinaria (Chile)* 36: 1-20.

MURÚA R & M BRIONES (2005) Abundance of the sigmodont mouse *Oligoryzomys longicaudatus* and patterns of tree seeding in Chilean temperate forest. *Mammalian Biology* 70: 321-325.

MURÚA R, M NAVARRETE, R CADIZ, R FIGUEROA, P PADULA et al. (2003) Hantavirus pulmonary syndrome: current situation among rodent reservoirs and human population in the 10th Region. *Revista Médica de Chile* 131: 169-176.

MURÚA R, L GONZÁLEZ, M GONZÁLEZ & C JOFRÉ (1996) Efectos del florecimiento del arbusto *Chusquea quila* Kunth (Poaceae) sobre

- la demografía de poblaciones de roedores de los bosques templados fríos del sur chileno. Boletín Sociedad de Biología de Concepción (Chile) 67: 37-42.
- PACHECO N (1993) Floración de las quilas. Flora fauna áreas silvestres FAO-PNUMA (Italia) 17: 34-35.
- PEARSON A, O PEARSON & I GOMEZ (1994) Biology of the bamboo *Chusquea coleou* (Poaceae: Bambusoideae) in southern Argentina. Vegetatio 111: 93-126.
- PIUDO L, M MONTEVERDE, S GONZÁLEZ-CAPRIA, P PADULA & P CARMANCHAHI (2005) Distribution and abundance of sigmodontine rodents in relation to hantavirus in Neuquén, Argentina. Journal of Vector Ecology 30:119-125.
- SHARMA Y (1982) Some aspects of bamboos in Asia and the Pacific. Food and Agriculture Organization, Bangkok, Thailand.
- SCHLEGEL F (1993) Quila: el problema de la floración. Chile Forestal (Chile) 206: 35-37.
- TAYLOR A J Y HUANG Z S QUIANG (2004) Canopy tree development and underground bamboo dynamics in old growth *Abies-Betula* forest in southwestern China: a 12-year study. Forest Ecology and Management 200: 345-360.
- TORO J J, A VEGA, S KHAN, J N MILLS, P PADULA et al. (1998) An outbreak of hantavirus pulmonary syndrome, Chile. Emerging Infection Diseases 4: 687-694.
- VALERIA L (1996) Influencia de la floración sincrónica de *Chusquea quila* (Kunth) y de condiciones microclimáticas asociadas, en la dinámica regenerativa de bosques remanentes originales en la provincia de Valdivia, Tesis Ingeniero Forestal. Facultad de Ingeniería Forestal, Universidad Austral de Chile, Valdivia.
- VEBLEN T T (1979) Structure and dynamics of *Nothofagus* forests near timberline in South-Central Chile. Ecology 60: 937-945.
- VEBLEN T, S SCHLEGEL & R ESCOBAR (1979) Biomasa y producción primaria de *Chusquea coleou* Desv, y *Chusquea tenuiflora* Phil, en el sur de Chile, Bosque 3: 47-56.
- VEBLEN T & F SCHLEGEL (1982) Reseña ecológica de los bosques del sur de Chile. Bosque 4: 73-116
- VEBLEN T T (1982) Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influence in forest dynamics. Bulletin Torrey Botany Club (USA) 109: 474-487
- WATANABE M A ZUNINO G KAHLER & C QUEZADA (1996). Ecological characteristics of *Chusquea quila* Kunth from Central-South Chile. INFOR (Chile) 94: 25-26.
- WATANABE M A ZUNINO G KAHLER & C QUEZADA (1997) Ecological characteristics of *Chusquea quila* Kunth from Central-South Chile. Bamboo Journal (Japan) 14: 01-14.

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