Applied Vegetation Science 7: 103-110, 2004

Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands

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Abstract. In recent decades, cattle ranchers of the Pantanal of Mato Grosso, Brazil, have pointed to the accelerated spread of several herbaceous and woody plant species that invade natural and artificial pastures (*campos*). It has been speculated that overgrazing by an increasing number of cattle, lack of grazing in abandoned areas, or large-scale changes in environmental conditions may be the reason for this invasion. This study focuses on ecological and ecophysiological aspects of *Vochysia divergens* (*cambará*), a flood-tolerant tree that began spreading in the Pantanal during the last 30 years and is considered a very aggressive invasive plant. The study shows that the spread of *cambará* can be related to natural multi-years wet periods. During multi-years dry periods the species is reduced by the increasing impact of fires in the Pantanal. This points to the great importance of multi-years climatic events on the vegetation cover of the Pantanal and indicates a very dynamic development in plant communities.

Keywords: Brazil; Floodplain; Flood pulse; Invasive tree; *Vochysia divergens*.

Nomenclature: Pott & Pott (1994).

Introduction

The Pantanal of Mato Grosso is a 140 000 km^2 floodplain in the southwestern part of Brazil bordering Bolivia and Paraguay. Since the beginning of the 18th century, the area has been used for cattle ranching. In 1970 about 30% of the beef produced in the states of Mato Grosso and Mato Grosso do Sul came from the Pantanal (Allen & Valls 1987). The existence of large pasture areas, locally called *campos,* is the economic basis for cattle ranching. These *campos* are covered with a large variety of herbaceous plants, with the frequent occurrence of *Paspalum almum* and *P. plicatulum*, which are considered valuable forage for cattle. Increasing competition with cattle ranches on non-flooded artificial *cerrado* pastures forces ranchers in the Pantanal to increase beef production. Quality, size, and availability of the pastures during the hydrological cycle are becoming limiting factors for the economy of the ranches. Ranchers increase pasture area by clearing periodically flooded shrubland (*campos sujos)* by means of fire, machetes and axes.

According to observations of the ranchers the spread of invasive plants started since the large floods of the early seventies including *Vochysia divergens, Licania parvifolia, Combretum lanceolatum, C. laxum, Byrsonima orbignyana* and *Ipomoea fistulosa*. Although they are native, these species are called invasive species (Anon. 1974; Pott 1982; Allen & Valls 1987). Of special importance is *Vochysia divergens*, *Vochysiaceae* (*cambará*), which vigorously spreads into pastures and can form monospecific stands locally called *cambarazais*.

Several authors mention the occurrence of *Vochysia* in the Pantanal (Veloso 1947, 1972; Almeida & Lima 1959; Prance & Schaller 1982; Rizzini 1979). According to Anon. (1982) *Vochysia* spreads from the riverine forests of the upper Cuiabá and São Lourenço rivers into the periodically flooded areas of the Pantanal. The first study about floristic composition and structure of a *cambarazal* was made by Nascimento & Nunes da Cunha (1989). Haase & Haase (1995) present data on litter production. Faßnacht (1995) used Landsat-TM-data to make maps of the distribution of *Vochysia* in the area near Poconé.

The unexpected spread of plants may point to large-scale changes in environmental conditions in this wetland of international importance with multiple far-reaching consequences for the ecosystem and its management. The following paper presents data on biology and ecology of *Vochysia* and offers explanations for its spread.

Study area

The study was undertaken in the Pirizal ecoregion in the northeast of the Pantanal of Poconé (Adámoli 1982) (Fig. 1) (16°15' 24" S, 56°36' 24" W). The climate is characterized by a pronounced dry season from May to September and a rainy season from October to April.

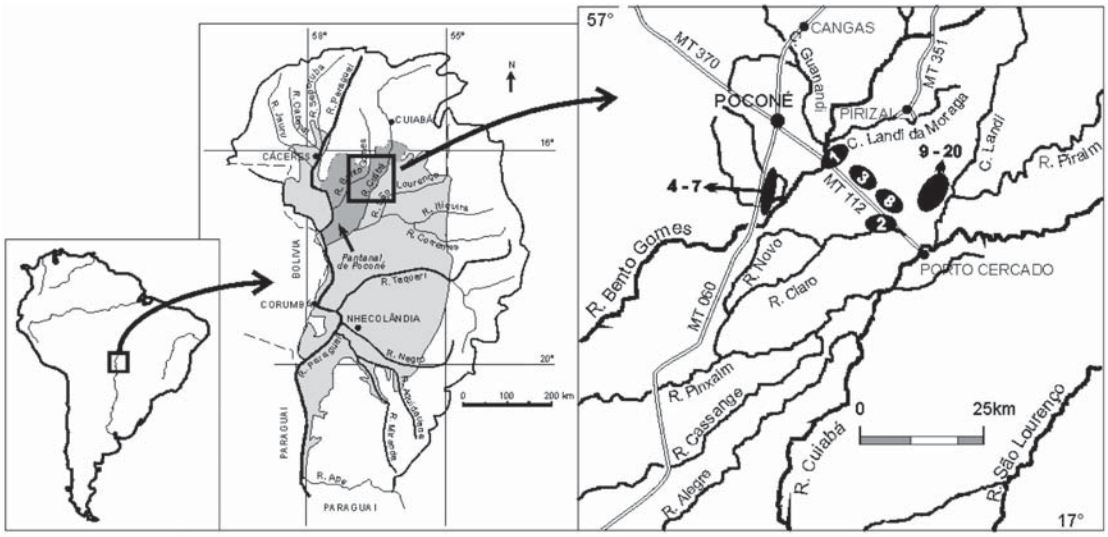

Fig. 1. Map of the study area. The numbers indicate the position of the studied *Vochysia divergens* plots.

Mean annual precipitation is ca. 1400 mm with maximum rainfall in January and minimum rainfall in July (Fig. 2). Mean annual temperature is 25.8 °C, with October being the hottest and July the coldest months (Almeida 1998).

Flooding follows the rainy season, as shown by the gauge of the Cuiabá River (Fig. 2). However, because of the flat landscape, the flood pattern inside the Pantanal is strongly influenced by local precipitation. The Pantanal of Poconé is in the upper Pantanal, where floods are rather shallow up to about 2 m depth. During the low water period, the Pantanal and many of the floodplain lakes are disconnected from the river channel. In addition to annual flood cycles, the Pantanal is subject to multi-years periods of high floods and pronounced droughts as shown by the hydrograph of the Paraguay River at Ladário at the outlet of the Pantanal (Fig. 3).

Soils are of fluvio-lacustric origin of Pleistocene age and mineralogically partly modified (Zeilhofer 1996). They are sandy, slightly acidic, with high aluminium content, and of low fertility (Radam 1982; Anon. 1997; Couto et al. 2002; Zeilhofer & Schessl 1999). Sediments deposited along the major rivers are of Holocene age.

Vegetation cover

According to Loureiro et al. (1982), the vegetation of the northeast of the Pantanal of Poconé belongs in its majority to the subformation *Savana Parque* without gallery forest. The heterogeneity of the Pantanal landscape results from a variety of small-scale geomorphological units (Sánchez 1978; Nunes da Cunha et al. in press, a, b), which in combination with the annual floods create a large diversity of habitats.

Major geomorphological units are *Campos* that are

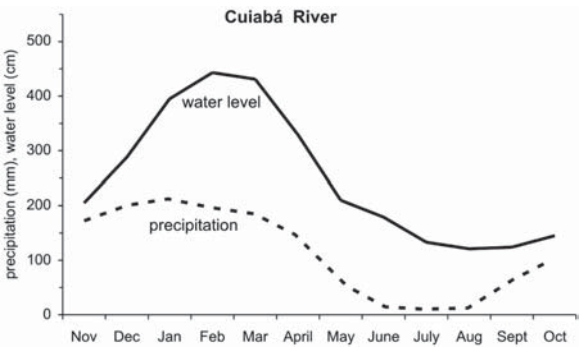

Fig. 2. Mean annual water level fluctuation of the Cuiabá River (1933-1993) and mean precipitation near Cuiabá, northern Pantanal (1971-1988). Rainfall data from INEMET, river level data from DNAEE.

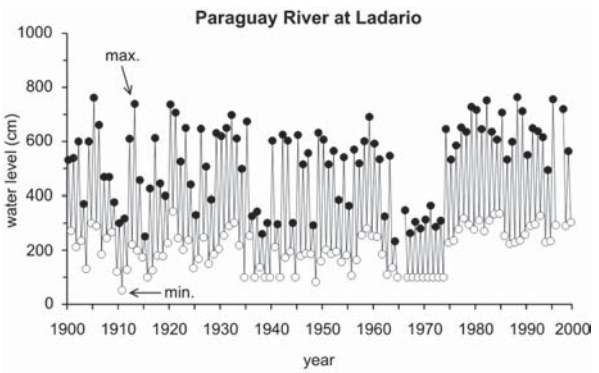

Fig. 3. Annual water level fluctuations of the Paraguay River at Ladário from 1900 to 2000 (full circles = annual maxima, empty circles = annual minima). Data from DNAEE.

seasonally flooded flat savanna areas called hyperseasonal by Eiten (1982), with three subtypes: *Campos limpos* and *campos sujos* are savannas without and with shrubs and trees, respectively, and *campos de murunduns* are savannas with termite mounds, covered with trees (termite savannas). *Cordilheiras* and *capões* are remnants of palaeo-levees covered with forest, reaching ca. 1 m above the mean flood level. Levees and terraces are depositions of recent sediments covered with forest, found along the Piraim, Cuiabá, and Bento Gomes River. Shallow seasonal channels in the *campos de murunduns* with a close connection to the groundwater table covered with forest are called *landis,* without forest *vazantes* (Ribeiro et al. 1999). Other specific habitats of the Pantanal are permanent lakes (*baías),* perennial river channels, permanent small drainage channels inside the flood-plain (*corixos*), and permanent swamps (*brejos)* covered by aquatic and semi-aquatic herbaceous plants. For detailed characterization and species lists see Nunes da Cunha (1990, 1998), Nunes da Cunha & Junk (1999, 2001) and Schessl (1999).

Material and Methods

Morphology

Vochysia is a tree 7-25 m tall, with a dense leafy crown. The stem is cylindrical with 30-50 cm diameter at breast height, shedding bark in irregular pieces. The leaves are simple, in whorls of three to four, coriaceous, glabrous, brilliant on the upper side and opaque on the underside, 7-13 cm long and 3 cm broad; petiols are 2-3 cm long. Inflorescence is racemose, terminal, subpyramidal, 20-28 cm long with pedicelled yellow flowers. Fruit capsules are oblong, trigonous, glabrous, with 4-5 seeds (Lorenzi 1998).

Phenology

Phenology of 15 selected *Vochysia* individuals was observed during the study period of 1998. The period of flowering was determined by the appearance of the first buds until the disappearance of the last flower and that of fruiting from the appearance of the first young fruit until the end of seed dispersal (Maia 1997). For quantification of phenological observations 30 litter samplers with a total surface area of 7.54 m^2 were distributed under *cambará* trees. Litter was collected monthly and separated according to leaves, flowers, fruits, and miscellaneous. For the determination of seed weight, seeds were collected separately.

Seedling establishment

Seedling establishment was studied in five different environments: soil covered and not covered with organic litter layer inside the *cambarazal*, soil below the mother tree with little litter, soil in the open *campo* with high radiation rates at the border of the *cambarazal*, and a *cambarazal* previously burned. The areas were fenced for protection against disturbance by humans and cattle. In every area 16 plots of 1 m^2 were selected and the seedlings were labeled. From November 1998 to June 1999, every 15 days growth, mortality and the occurrence of new seedlings were recorded before, during and after the flood period.

Grazing effect

To study the impact of cattle grazing on plant species composition in *campo limpo,* in 1993 three plots of 20 m × 20 m were fenced with barbed wire to prevent the entry of animals. In 1999 the occurrence of woody species was recorded in the fenced plots.

Population structure

Areas ($n = 20$) of different physiognomy dominated by *Vochysia* (*cambarazais*) were selected in the Pirizal region for community analysis. In the centre of each of these areas a plot of 50 m × 5 m was established and divided in 10 subunits of 5 m × 5 m to characterize the vegetation. Tree species were determined, height was estimated and circumference at breast height of all individuals with more than 1 cm, corresponding to 0.3 cm DBH, was measured. This paper refers only to *Vochysia*. Length of the flood period was registered by visiting the plots at monthly intervals during the flood period that lasted in 1997/1998 from January to May. Plant samples were deposited in the herbarium (HC-UFMT) of the University of Mato Grosso in Cuiabá. The basal area of the species per unit area was calculated. A raw-data matrix of tree mean diameter data was established for cluster analysis using mean Euclidian distance coefficient and average linkage clustering (UPGMA).

Impact of fire

In 1999, a wild fire affected part of the study area. In 2000, the impact of the fire on the *Vochysia* stands was analysed in four plots of 15 m × 5 m in size, counting number and determining DBH of dead and living trees. The percentage of dead trees in adjacent plots not affected by fire was also determined.

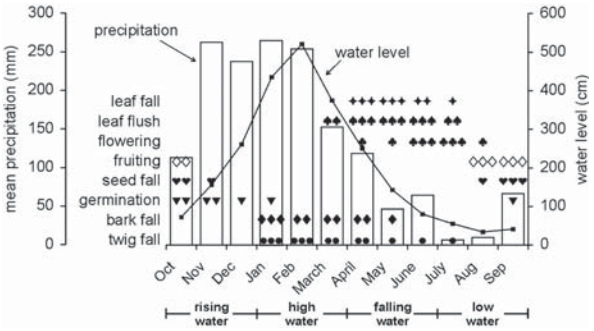

Fig. 4. Phenological aspects of *Vochysia divergens* in relation to water level and precipitation during the study period 1998 - 1999. Bark fall: The apical parts of the twigs shed the outer layer of the bark from January to May. Intensity of the respective event is indicated by the number of symbols: 3 = high, 2 = medium, 1 = low intensity.

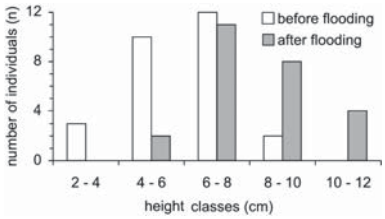

Fig. 5. Number of individuals and height classes of *Vochysia divergens* saplings before and after 5 months of flooding. Before flooding $n = 28$, after flooding $n = 26$.

Results

Phenology

The main leaf shedding period is April to June at the end of the aquatic phase (Fig. 4). At the same time the flush of new leaves occurs, so that the tree always bears leaves. Flowering begins with decreasing water level and continues until July. During that period the trees dominate the landscape of the Pantanal with their beautiful yellow flowers. Seed production reaches the maximum during the dry period and continues until the beginning of the rainy season in November (Fig. 4). Winged seeds have a mean weight of 0.053 g (0.015-0.070 g; $n = 50$). The weight without wings is 0.045 g (0.013 - 0.067 g; $n = 50$). Viability is maintained for about 6 mo.

Seedling establishment

Seed germination starts with the first light rains in September/October. In November 1998, at the end of the dry season, 179 seedlings were registered in the total area of 80 m^2. The largest number of seedlings was observed in the area without a litter layer followed by the area in the *campo* at the border of the *cambarazal*. When the water reached the experimental plots in the beginning of January, the seedlings had a mean height of 6-8 cm. The development of 28 saplings was observed during the flood period. Plants slightly increased in size (Fig. 5). Mortality reached ca. 7% after 150 d of flooding. About half of the time the saplings were totally flooded, but did not shed leaves under water.

Grazing effect

Two of the fenced *campo limpo* plots that were inundated during about 3-4 mo per year, showed strong growth of woody species (Table 1, Fig. 6). *Vochysia* was found in these plots. In the third plot, which was subjected to flooding for about 5-6 mo, only one woody plant specimen established.

Diameter class structure

The cluster analysis based on mean stem diameters (cophenetic relation = 0.95) shows (Fig. 7) three well-defined groups: (1) plots 8 and 7 with a high mean stem diameter value of 27 cm, high basal areas and few individuals; (2) plots 9, 11, 1 and 3 with stem diameter values of 9-15 cm; (3) large group with low mean stem diameter values of 6.6-12 cm, low basal areas and many

Table 1. Species composition and growth of woody species in three plots of 400 m^2 each in the *campos limpos* of the Ipiranga Farm after 7 yr of protection against cattle grazing.

	n	Mean height (m).	Total basal area (cm^2)	Height min. (m)	Height max. (m)
Plot 1					
Vochysia divergens	12	2.50	4.016	1.50	2.50
Eugenia florida	2	0.98	0.589	0.80	1.15
Combretum laxum	3	0.43	0.730	0.40	0.57
Byrsonima orbigniana	6	1.80	5.637	1.60	2.00
Plot 2					
Licania parvifolia	21	1.80	11.740	0.50	2.50
Byrsonima orbigniana	1		0.675		1.80
Combretum laxum	9	0.50	0.150	0.33	0.37
Coccoloba spec.	2	0.55	0.020	0.49	0.49
Vochysia divergens	1		0.115		1.33
Plot 3					
Combretum laxum	1		0.020		1.41

Fig. 6. Fenced plot in a man-made *campo limpo* after 7 yr of protection against grazing. Several tree species have successfully established, including *Vochysia divergens* (cambará).

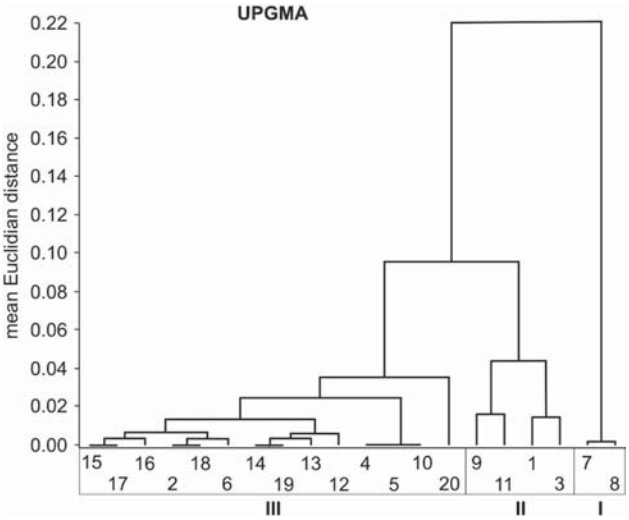

Fig. 7. Dendrogram of multivariate analysis showing the different groups of 20 plots of *Vochysia divergens* communities based on stem diameter (Cophenetic relation 0.95%).

individuals (Fig. 8). Group one represents *cambarazais* with several old and large specimens with diameters of up to 63, respectively 51 cm. The second group contains many medium sized species with diameters of 21 to 41 cm. The third group corresponds to early stages of community development, including monotypical and mixed stands. Specimens with diameters larger than 18 cm are rare or absent (Fig. 8).

Impact of fire

One year after the wild fire of 1999 in some *cambará* stands mortality was very high (Fig. 9) and varied between 57% and 86% of larger trees (mean mortality of all trees 75%). Small size classes are not represented in this inventory, because they were burned completely. Fire affected trees of all large size classes. In neighbouring old stands not affected by the fire, dead trees comprised < 5%, in young stands < 2%, therefore the number of individuals that were already dead before the fire affected the stands can be neglected.

Discussion

Allen & Valls (1987) explain the spread of invasive plants into pastures of the Pantanal as due to inadequate pasture management, mainly overgrazing in the early 1970s. This will not hold for *Vochysia divergens* as shown by the exclosure experiments on the Ipiranga Farm. After 7 yr, two of three plots of 400 m^2 protected against grazing cattle contained woody species including *Vochysia* (Table 1), whereas the surrounding pasture was free of them (Fig. 6). Animal density was about one cattle per 2 ha pasture. Since the rancher did not apply other weed control methods, this points to efficient control of the woody vegetation by grazing animals in this case.

Why *Vochysia* has been spreading recently may be answered by the analysis of the environmental requirements of the species and major changes in environmental conditions during this period. *Vochysia* occurs from Paraguay to Mexico, colonizing tropical and subtropical humid riparian forests (Thiele 1997), i.a. in Goiás, Mato Grosso (Brazil) and Bolivia (Stafleu 1948). Nunes da Cunha collected *Vochysia* along the Teles Pires River

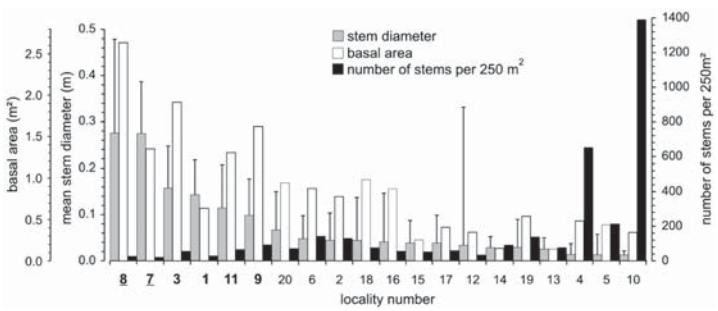

Fig. 8. Mean stem diameter + standard deviation, basal area and number of stems per plot of 20 stands of *Vochysia divergens*. The numbers 8 and 7 correspond to old *Vochysia divergens* stands, the numbers 3, 1, 11 and 9 to stands of intermediate age and the remaining plots to young stands separated by the multivariate analysis on stem diameter (Fig. 7).

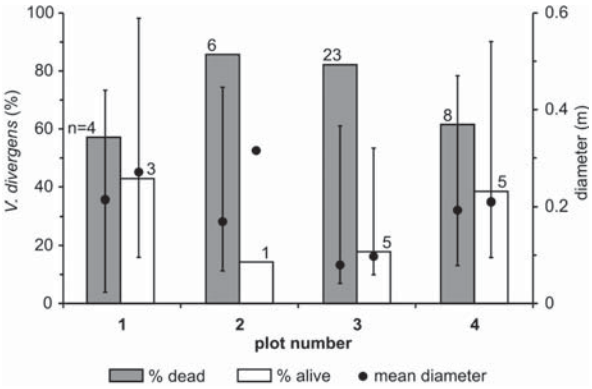

Fig. 9. Total number and percentage of dead and living trees of *Vochysia divergens*, and mean, maximum and minimum DBH of the stems in four plots one year after a wild fire.

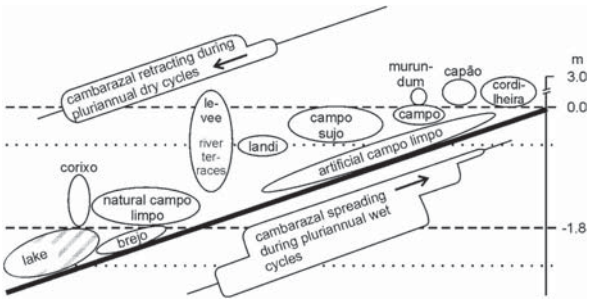

Fig. 10. Distribution and abundance of *Vochysia divergens* in different landscape units of the Pantanal of Poconé along the flood gradient and its shift during multi-years wet and dry periods. Mean annual water level fluctuations ===== during multi-years wet cycles and :::::: dry cycles. The diameter of the figures around the distribution of the *cambarazais* indicates their relative abundance.

near the Pará border. It also occurs in the Araguaia National Park (Ratter 1987). *Vochysia* colonizes the gallery forests of the rivers from central Amazonia to Paraguay and spreads from the São Lourenço and Cuiabá Rivers into the Pantanal (Anon. 1982).

Seedling establishment

Vochysia is a flood-tolerant species with relatively small and numerous seeds. In dry years, seed production is low. Observations in the dry summer of 1999 indicate increased abscission rates and very high predation by parrots and insect larvae. Seeds are spread at the beginning of the rainy season by wind and water. Distribution by water currents results in a patchy accumulation of seeds and high seedling density. The highest rate of seedling establishment was found on bare soil, pointing to the ability of the plant to colonize disturbed areas, for example recently-exposed sedimentation areas along rivers. Instead of seed banks, *Vochysia* forms sapling banks in the understorey which grow very slowly in the shade, but replace dead trees as soon as light conditions on the forest floor indicate gaps in the canopy. This leads to the maintenance of *Vochysia* dominated communities (*cambarazais*), despite the fact that the species has many characteristics of a pioneer species or a species of early successional stages.

The observations of seedling establishment show a strong resistance of seedlings and saplings to long-term flooding. The capacity to maintain leaves intact below the water surface for several months can be considered a competitive advantage, because it enables the sapling to photosynthesize and grow slowly even below the water surface, or at least immediately after emergence of the leaves. Similar adaptations have been reported from flood-adapted trees of the Amazon floodplain (Waldhoff et al. 1998).

Occurrence

Vochysia occurs naturally, within the study area, mainly in communities subjected to periodical flooding or waterlogging of the soils, e.g. (1) the *campos de murunduns*, where the areas between the termite mounds are colonized, (2) the flooded forests of the *landis,* (3) the flooded riverine forests and (4) the *campos sujos*. In these areas *Vochysia* can form nearly monospecific stands covering 5 - 7% of the total area of the Pantanal of Poconé, as shown by 1994 satellite images (Faßnacht 1995). All the plots we investigated were flooded in 1997/1998 for 4-5 months and to a depth of 0.4-0.8 m. In non-flooded habitats and communities, *Vochysia* is rare or absent. Invasion also occurs only into periodically flooded or waterlogged pastures and not into upland pastures (Fig. 10). This points to the hydrological regime as driving factor for the expansion of *Vochysia*. The hydrological regime in the individual sites is very complex, because it is affected during high water by the connected rivers but also by local rains that inundate depressions even in periods of relatively low river levels. Changes in soil structure and soil nutrient content can be excluded as reason for the spread of *Vochysia* because soil analyses (not shown in this paper) show similarity in grain size distribution, mineral type, and nutrient status of the top soil layer of the investigated plots.

Diameter class and age structure

The analysis of stem diameter by multivariate analysis in the different *Vochysia* plots shows three different mean diameter classes corresponding to different age classes. According to Ishima (1998), *Vochysia* shows, in the southern Pantanal, a mean diameter increment of about 0.7 cm.yr^{-1}. For the first five years growth is quicker, but large trees have small increment rates. Growth is more retarded by drought stress than by

flooding. If this increment rate is also assumed for the Pantanal of Poconé, a mean tree diameter of 27.5 and 27.3 cm in the plots of diameter class one corresponds to a mean age of ca. 39 yr. In this class maximum age is ca. 90 and 73 yr respectively, and there are many individuals > 45 yr. In these plots there are few young specimens. A mean diameter of 9.9-15.7 cm in the plots of diameter class two corresponds to a mean age of 14.1-22.4 yr. All plots of this class contain several individuals with an estimated age of > 35 yr. Young specimens are frequent. The third diameter class comprises plots with a mean diameter of 1.3-6.7 cm, corresponding to a mean age of ca. 3-9.6 yr. In this class, the overwhelming majority of the trees have a DBH < 18 cm, corresponding to an age < 25 yr. Only in some plots are there a few specimens older than 25 yr, as for instance plot 12 with one specimen of 54 cm diameter, corresponding to ca. 77 yr. This points to a catastrophic event that affected *Vochysia* stands ca. 25 yr ago.

Impact of fire

During 1962-1972 Paraguay River shows a multi-years period of low floods (Fig. 3). In this period, vegetation of the Pantanal suffered severe drought stress. Many swamps and shallow lakes dried out completely during the dry season and fire spread over large areas of the Pantanal. Fire-resistant trees of the *cerrado* vegetation were scarcely affected (Coutinho 1982) but the flood-adapted and fire-intolerant *Vochysia* was strongly reduced because the bark is easily damaged. In *Vochysia* stands one year after the wild fire in the study area, 75% of all *cambará* trees in the four investigated plots were killed (Fig. 9). Dead trees provide additional fuel for repeated wild fires that, during multi-years dry periods, can eliminate entire *cambarazais* excepting a few individuals, as shown in plot 12 where a single tree of 54 cm diameter occurred in the middle of young trees with a diameter less than 18 cm (Fig. 8). Only in areas not or little affected by the fires, have entire stands survived as represented by the plots of diameter class one and to a smaller extent by the plots of diameter class two.

In the following multi-annual period of high floods and high rainfall, starting in 1974 and continuing until present, flood-tolerant species were favoured and *Vochysia* spread into all periodically-flooded areas, being limited only by long-term and high flooding as happens in the natural *campos limpos*. The communities described by the third diameter class are early successional stages in a very dynamic successional development. The observed invasion of *campos limpos* by *Vochysia* represents the occupation of its natural habitats under favourable hydrologic and climatic conditions (Fig. 10). Cattle grazing eliminates seedlings and saplings growing in small numbers in open areas as shown by the fenced plots (Fig. 6), but it does not effectively control spread of the plants along the edges of existing stands where seedling density is very high. However, long-term survival is possible only in areas not affected by fire. In these areas community development continues and reaches advanced seral stages with many old and a few young specimens of *Vochysia*.

With respect to the overall dynamics of the plant community development in the Pantanal, the periodical spread and retreat of native plant species such as *Vochysia* points to the great importance of changes over several years in the flood regime as driving factor as indicated by the flood pulse concept (Junk et al. 1989). This statement is of specific importance for populations of long-living plants, which need more time than populations of annual plants to reestablish after strong setbacks by multi-years extreme droughts and floods.

Acknowledgements. The paper is part of the Brazilian-German bilateral cooperation in science and technology in the framework of the SHIFT Program (Studies on Human Impact on Forests and Floodplains in the Tropics). We gratefully acknowledge the help of the Brazilian Research Council (CNPq), the German Ministry of Science and Technology (BMBF), the Federal University of Mato Grosso (UFMT), Cuiabá, Brazil, and the Max-Planck-Institute of Limnology, Plön, Germany. We thank Mrs. Ruthmarie Mitsch, Columbus, Ohio, for correction of the English.

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Received 31 January 2002;
Accepted 2 December 2003.
Co-ordinating Editor: J.B. Wilson.