ELSEVIER

Global and Planetary Change 33 (2002) 107–116

GLOBAL AND PLANETARY CHANGE

www.elsevier.com/locate/gloplacha

Carbon storage increases by major forest ecosystems in tropical South America since the Last Glacial Maximum and the early Holocene

Hermann Behling*

Center for Tropical Marine Ecology, University of Bremen, Fahrenheitstrasse 6, 28359 Bremen, Germany

Received 3 May 2000; received in revised form 17 April 2001; accepted 4 July 2001

Abstract

To study the carbon storage increase of major forest ecosystems in tropical South America, such as Amazon rain forest, Atlantic rain forest, semideciduous forest, and *Araucaria* forest, the Last Glacial Maximum (LGM) and the early Holocene vegetation cover were reconstructed by pollen records. Marked forest expansion points to a significant total carbon storage increase by tropical forests in South America since the LGM and the early Holocene. The Amazon rain forest expansion, about 39% in area, had 28.3×10^9 tC (+20%), the highest carbon storage increase since the LGM. The expansion of the other much smaller forest areas also had a significant carbon storage increase since the LGM, the Atlantic rain forest with 4.9×10^9 tC (+55%), the semideciduous forest of eastern Brazil with 6.3×10^9 tC (+46%), the *Araucaria* forest with 3.4×10^9 tC (+108%). The estimated carbon storage increase of the four forest biomes since the early Holocene is also remarkable. The extensive deforestation in the last century strongly affected the carbon storage by tropical forests.

Keywords: carbon storage increase; South America; Amazon rain forest; Atlantic rain forest; semideciduous forest; *Araucaria* forest; Last Glacial Maximum; early Holocene

1. Introduction

The estimation of past terrestrial carbon storage by the reconstruction of past vegetation cover is an important contribution to understand the global carbon cycle and the reduction of the greenhouse gas CO_2 by vegetation.

Based on palaeodata or on vegetation modeling, terrestrial carbon storage have been estimated for the Last Glacial Maximum (LGM) on a global scale (e.g. Adams et al., 1990; Prentice and Fung, 1990; Prentice et al., 1993; Van Campo et al., 1993; Crowley, 1995). In this context, the formation of tropical forest ecosystems since the last LGM plays an important role for the reduction of CO_2 by carbon storage.

This study focuses on the reconstruction of the major forest ecosystems in tropical South America: the Amazon rain forest, the Atlantic rain forest, the semideciduous forest in eastern Brazil, and the Brazil-

* Tel.: +49-421-220-8321; fax: +49-421-220-8330.
E-mail address: hbehling@zmt.uni-bremen.de (H. Behling).

PII: S0921-8181(02)00065-6

ian *Araucaria* forest, to understand the importance of tropical forests by the fixation of CO_2 since the LGM. The development of these ecosystems may have a strong potential in carbon storage. Further, it is important to estimate which consequence the deforestation of these tropical forests will have for the carbon storage.

Pollen analytical studies in sediment deposits from tropical South America are still rare, but increased over the last few years and allow to reconstruct past vegetation cover in more details. Two-time slices were studied and compared with the modern potential natural vegetation cover, the LGM (when area of forest cover was probably the lowest) and the early Holocene (when most forest cover still does not reached the modern potential forest area).

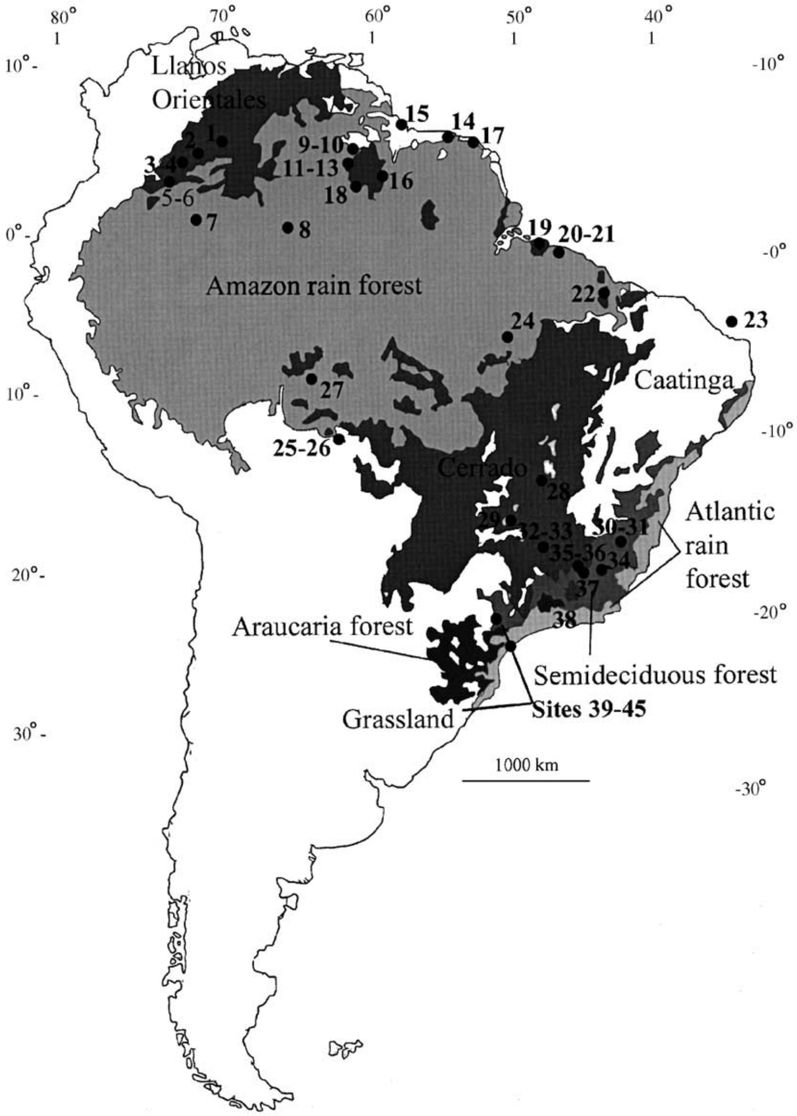

Fig. 1. The map shows major biomes of South America (adapted from Seibert, 1996) and the location of the sites of the used pollen records (Nos. 1–45). For the sites, Nos. 1–45, see Table 1.

Table 1
List of 45 studied pollen records

No.	Site	Coordinates	Elevation (m a.s.l.)	Age range (year BP)	Reference
1	Laguna Sardinas	4°58′ N, 69°28′ W	180	0–11,600	Behling and Hooghiemstra, 1998
2	Laguna Angel	4°28′ N, 70°34′ W	200	2000–10,030	Behling and Hooghiemstra, 1998
3	Laguna El Pinal	4°08′ N, 71°23′ W	180	0–18,000	Behling and Hooghiemstra, 1999
4	Laguna Carimagua	4°04′ N, 70°14′ W	180	0–8270	Behling and Hooghiemstra, 1999
5	Laguna de Agua Sucia	3°35′ N, 73°31′ W	300	0–5500	Wijmstra and Van der Hammen, 1966
6	Laguna Loma Linda	3°18′ N, 73°23′ W	310	0–8720	Behling and Hooghiemstra, 2000
7	Pantano de Monica	0°42′ S, 72°04′ W	160	0–11,150	Behling et al., 1999
8	Morro dos Seis Lagos	0°16′ S, 66°41′ W	300	0– > 42,000	Colinvaux et al., 1996
9	Quebrada Arapán	5°20′ N, 61°06′ W	900	0–ca. 3100	Rull, 1991
10	Valle de Urué	5°02′ N, 61°10′ W	940	0–ca. 1700	Rull, 1991
11	Laguna Divina Pastora	4°42′ N, 61°04′ W	800	0–ca. 5300	Rull, 1991
12	Laguna Santa Teresa	4°43′ N, 61°05′ W	880	0–ca. 5100	Rull, 1991
13	Santa Cruz de Mapaurí	4°56′ N, 61°06′ W	940	0–ca. 9800	Rinaldi et al., 1990
14	Ogle Bridge	6°50′ N, 58°10′ W	0	0–45,000	Van der Hammen, 1963
15	Alliance Borehole (T 28)	5°53′ N, 54°54′ W	0	–	Wijmstra, 1971
16	Lake Moriru	3°54′ N, 59°31′ W	110	0–(18,000?)	Wijmstra and Van der Hammen, 1966
17	GUY 2	5°44′ N, 53°51′ W	0	0–9000	Tissot and Marius, 1992
18	Lago do Galheiro	3°7′ N, 60°41′ W	70	0–1200	Absy, 1979
19	Lago Arari	0°39′ S, 49°70′ W	0	0–7500	Absy, 1985
20	Lagoa da Curuça A	0°46′ S, 47°51′ W	35	9500–11,700	Behling, 1996
21	Lagoa da Curuça B	0°46′ S, 47°51′ W	35	0–9500	Behling, 1996
22	Lago do Aquiri	3°10′ S, 44°59′ W	10	6700–7450	Behling and Costa, 1997
23	GeoB 3104-1	3°40′ S, 37°43′ W	−767	8500–>42,000	Behling et al., 2000
24	Carajas CSS2	6°20′ S, 50°25′ W	700–800	0–>50,000	Absy et al., 1991
25	Laguna Bella Vista	13°37′ S, 61°33′ W	200–250	0–>52,000	Mayle et al., 2000
26	Laguna Chaplin		200–250	0–38,000	Mayle et al., 2000
27	Katira Creek	9°S, 63°W	80	18,000–49,000?	Van der Hammen and Absy, 1994; Absy and Van der Hammen, 1976
28	Agua Emendadas	15°S, 47°35′ W	1040	0–26,000	Barberi, 1994; Salgado-Labouriau et al., 1998
29	Cromínia	17°15′ S, 49°25′ W	730	0–32,000	Ferraz-Vicentini and Salgado-Labouriau, 1996; Salgado-Labouriau et al., 1997
30	Lago do Pires	17°57′ S, 42°13′ W	390	0–9700	Behling, 1995b
31	Lagoa Nova	17°58′ S, 42°12′ W	390	ca. 100–10,020	Behling, in preparation
32	Lagoa Serra Negra	19°S, 46°57′ W	1170	0–>40,000	De Oliveira, 1992
33	Salitre	19°S, 46°46′ W	1050	0–50,000	Ledru, 1993; Ledru et al., 1994, 1996
34	Lagoa Silvana	19°31′ S, 42°25′ W	240–300	0–ca. 10,200	Rodriges-Filho et al., 2002
35	Lago dos Olhos	19°38′ S, 43°54′ W	730	0–19,000	De Oliveira, 1992
36	Lagoa Santa	19°38′ S, 43°54′ W	730	0–6200	Parizzi et al., 1998
37	Catas Altas	20°05′ S, 43°22′ W	755	ca. 18,000–>48,000	Behling and Lichte, 1997
38	Morro de Itapeva	22°47′ S, 45°32′ W	1850	0?–35,000	Behling, 1997a
39	Botucatú	22°48′ S, 48°23′ W	770	ca. 18,000–30,000	Behling et al., 1998
40	Serra Campos Gerais	24°40′ S, 50°13′ W	1200	0–12,500	Behling, 1997b
41	Volta Velha	26°04′ S, 48°38′ W	5	0–ca. 35,000	Behling and Negelle, 2001
42	Serra da Boa Vista	27°42′ S, 49°09′ W	1160	0–14,000	Behling, 1995a
43	Morro da Igreja	28°11′ S, 49°52′ W	1800	0–10,200	Behling, 1995a
44	Serra do Rio Rastro	28°23′ S, 49°33′ W	1420	1000–11,210	Behling, 1995a
45	Fazenda do Pinto	29°24′ S, 50°34′ W	900	0–6750	Behling et al., 2001

Site locations (Nos. 1–45) are shown in Fig. 1.

2. Methods

Four major neotropical forest ecosystems, the Amazon rain forest, the Atlantic rain forest, the semideciduous forest from eastern Brazil, and the *Araucaria* forest, have been selected to estimate past carbon storage changes (Fig. 1). Available data on the potential natural distribution (pre-Columbian settlement) of these ecosystems have been used for the modern forest area.

Based on 45 pollen records for the four neotropical forest ecosystems, vegetational shifts have been reconstructed and changes in forest area have been estimated for the LGM (about 18,000 ^{14}C year BP) and the early Holocene (about 7000 ^{14}C year BP) (Table 1 and Fig. 1). For a complete list of available pollen records and their location, see also Behling (1998) and Behling and Hooghiemstra (2001).

Pollen records allow to identify past changes of different biomes. For example, the record from Catas Altas near Belo Horizonte (Behling and Lichte, 1997) documents that the modern semideciduous forest biome was replaced by grassland during the LGM, indicating that subtropical grassland has been extended at least 750 km from the south to the north. Pollen records from Laguna Loma Linda in Colombia (Behling and Hooghiemstra, 2001) and from Lago do Pires in southeastern Brazil (Behling, 1995b) show that the modern rain forest biome was replaced by savanna vegetation during the early Holocene. At both sites, forest expanded since mid-Holocene times and the modern forest/savanna boundary is about 100 km distant to the location.

The network of data points is still small in view of the huge areas under consideration, but available pollen records allow an approximate estimation of past forest cover increase or reduction. For regions with no or little data, available data points have been used to interpolate for the entire forest regions.

Mean carbon storage values for different ecosystems were calculated by several authors, e.g. Olson et al. (1983). There are different values and some uncertainties with a relatively high error range of the mean carbon storage values for the different biomes. For the total carbon storage (vegetation, soil, and litter) calculation, the values were taken from summarised list of Adams et al. (1990). The used values are shown in Table 1.

There is a relatively wide range of data on the total carbon storage for tropical rain forest in the literature. Values range between about 170 and 430 tC/ha (e.g. Adams et al., 1990). It has to be considered that the Amazon rain forest includes different vegetation types, e.g. terra firme forest, varzéa forest, semideciduous forest, Amazon caatinga, and others. In addition, changes in the area of inundated forests (varzéa) occurred in the past (Behling and Costa, 2000). For this study, the Amazon rain forest has been used as a whole and was not differentiated in vegetation types. An intermediate value of 300 tC/ha has been used. Future studies may refine the area of different Amazon rain forest types. There are no data available for the total carbon storage of the *Araucaria* forest, but the value for the warm temperate forest of 330 tC/ha will be close.

3. Results

3.1. Modern potential natural and past forest areas

The results of Late Quaternary vegetational shifts and estimated modern and past forest areas for different neotropical ecosystems are shown in Tables 2 and 3, respectively. The following sections describe the results for the four forest ecosystems in more details.

3.1.1. Amazon rain forest

The Amazon rain forest is the largest forest ecosystem in South America (Fig. 1). It extends between

Table 2
Total carbon storage on vegetation, soil, and litter for different ecosystems

Ecosystem	tC/ha
Amazon rain forest (tropical equatorial forest)	300
Atlantic rain forest (tropical equatorial forest)	430
Semideciduous forest—eastern Brazil (tropical evergreen seasonal)	260
Llanos Orientales/Orinoco Llanos (savanna)	89
Cerrado (tropical woodland)	135
Caatinga (tropical semidesert shrub)	24
Araucaria forest (temperate forest)	330
South Brazilian campos (temperate grasslands)	140

Table 3
Summarised Late Quaternary vegetational shifts

Modern	←	Past (LGM and early Holocene)
Amazon rain forest	←	Savanna
		Llanos type (north) and cerrado (south)
Atlantic rain forest	←	Semideciduous forest (west)
		Caatinga (north)
		Grassland (south)
Araucaria forest	←	Grassland
Semideciduous forest	←	Cerrado (west)
		Grassland (south)

2600 and 3500 km from the Andes to the Atlantic Ocean. The maximal extension from north to south is between 1300 and 2000 km. According to Harcourt and Sayler (1996), the Amazon rain forest covers an area of about 5,600,000 km^2.

If and how far the Amazon rain forest was replaced by savanna during glacial times is much under debate (e.g. Colinvaux, 1993; Bush, 1994; Van der Hammen and Absy, 1994; Hooghiemstra, 1997). Pollen records from the Amazon region are rare and document mostly Holocene time periods. The lack of data still allows much speculation on the Amazon rain forest history.

However, new pollen studies from the savanna regions north and south of the Amazon rain forest and transition zones to savanna allow to estimate the past Amazon rain forest area. An overview of the Late Quaternary history of the South American savanna regions, both north and south of the equator, based on 32 pollen records is published in Behling and Hooghiemstra (2001). During the full glacial period, savannas expanded due to markedly drier conditions. This is suggested from, e.g. the Laguna El Pinal record (Behling and Hooghiemstra, 1999), the Laguna Bella Vista and Chaplin record (Mayle et al., 2000), and the Carajas record (Absy et al., 1991). The Amazon rain forest area must have been reduced in the northern and southern regions. Whether these drier conditions led to 'forest refugia' cannot be answered from the available data. The early Holocene (until about 6000–5000 ^{14}C year BP) was drier in most of the South American savannas than during late glacial and late Holocene periods (e.g. the site Laguna Loma Linda, Behling and Hooghiemstra, 2000 and the site Carajas, Absy et al., 1991). The distribution of savanna vegetation during the early Holocene was much larger than during late Holocene periods.

Based on pollen data, the Amazon rain forest on the northern hemisphere, compared to the modern potential natural distribution, was probably about 200 km further south during the LGM and 100 km further south during the early Holocene. In the southern hemisphere, the shift was somewhat larger, probably about 300 km further north for the LGM and 100 km further north for the early Holocene.

The estimated reduced forest area on both hemispheres for the LGM, compared to the modern area, is in total about 1,570,000 km^2 (north 2600 × 200 km—replaced by the savanna of the Llanos type, and south 3500 × 300 km—replaced by the savanna of the cerrado type). The estimated reduced area for the early Holocene, compared to the modern area, is about 610,000 km^2 (2600 × 100 and 3500 × 100 km, respectively). There was probably no or only little reduction in the western region (Andean border) and the eastern Atlantic coastal region (Behling, 1996) due to the higher precipitation rates in these regions.

3.1.2. Atlantic rain forest

The natural extension of the Atlantic rain forest is a 100–200-km-broad and 3200-km-long coastal strip from Natal in northeastern Brazil to Porto Alegre in southern Brazil (Fig. 1). The estimated potential natural Atlantic forest area including the semideciduous forest, which is found under drier conditions further inland, is 1,090,000 km^2 (Fundação S.O.S. Mata Atlântica, 1992). From this area is the Atlantic rain forest, about 320,000 km^2.

Pollen analytical results from southern Brazil (Behling and Negelle, 2001) indicate that the southern tropical Atlantic rain forest region was moved at least 500 km further north and mostly replaced by grassland during the LGM. Data from southeastern Brazil (Behling, 1997a) show that the Atlantic rain forest belt was much smaller than today due to the drier conditions and probably several times fragmented. The marine core GeoB 3104-1 near Fortaleza indicates also dry conditions for northeastern Brazil for the LGM (Behling et al., 2000). In southeastern Brazil, the Atlantic rain forest must have been partly replaced by semideciduous forest and in northeastern Brazil mostly by semideciduous forest and partly by caatinga (tropical semidesert shrub) vegetation. How far the continental shelf was covered with Atlantic rain forest or coastal restinga vegetation during glacial low sea-level stands is unclear. During the early Holocene was the Atlantic rain forest zone in southeastern Brazil, as, e.g. the pollen record from Lago do Pires suggests (Behling, 1995b), markedly smaller than the present day. The Atlantic rain forest area was probably, in northeastern Brazil, also smaller during the early Holocene than today.

The Atlantic rain forest area is estimated by 150,000 km^2 (1500×100 km) for the LGM. It has to be considered that this reconstruction is based on some uncertainties such as the possible rain forest fragmentation, the unknown vegetation cover of the continental shelf, and only a few available pollen records. The estimated area for the early Holocene is about 250,000 km^2 (3200×80 km).

3.1.3. Semideciduous forest (eastern Brazil)

The tropical semideciduous forest of the east Brazilian region occurs in large areas mainly in southeastern Brazil and further north in the form of a small belt between the Atlantic rain forest and cerrado vegetation (Fig. 1). The modern potential natural semideciduous forest covered an area of about 770,000 km^2 (Fundação S.O.S. Mata Atlântica, 1992).

During the LGM, huge areas of semideciduous forest were in southern southeast Brazil replaced by subtropical grassland (e.g. the sites Botucatú and Catas Altas, Behling et al., 1998; Behling and Lichte, 1997) (see also Section 3.1.4) and further north by cerrado vegetation. During the early Holocene, large areas of present-day potential natural semideciduous forest were covered by cerrado (e.g. the site Lago do Pires, Behling, 1995b).

The estimated areas of semideciduous forest are about 250,000 km^2 for the LGM and 500,000 km^2 for the early Holocene.

3.1.4. Araucaria forest (Brazil)

The subtropical *Araucaria* forest occurs on the south Brazilian highland between latitudes 24° and 30°S primarily at elevations between 1000 and 1400 m and, in southeastern Brazil, in small isolated "Islands" between 18° and 24°S and in elevations between 1400 and 1800 m (Fig. 1). The original distribution of the Brazilian *Araucaria* forest was studied by Hueck (1953, 1966) and is estimated at about 200,000 km^2.

Pollen analytical studies from southern Brazil (three sites in Santa Catarina and one site in Paraná State, Behling, 1995a, 1997b, 1998), show that huge areas of grassland (campos) were still found on the south Brazilian highlands during late glacial and early to mid-Holocene times. Initial expansion of *Araucaria* forests started from gallery forests along the rivers about 3000 ^{14}C year BP. A pronounced expansion of *Araucaria* forests on the highlands, replacing the grassland (campos) vegetation, is found in Santa Catarina since the last 1000 years, and in Paraná (Serra Campos Gerais) since the last 1500 years.

Pollen records from southeastern Brazil document that the southern modern *Araucaria* forest belt had not moved during glacial times to southeastern Brazil. Results from the Botucatú region, about 230 km west of the city São Paulo, indicate an almost treeless glacial landscape (Behling et al., 1998). Pollen data from Catas Altas, about 80 km east of Belo Horizonte, show that the last glacial landscape was here, covered with large areas of subtropical grasslands and small areas of *Araucaria* forests along the rivers, where today tropical semideciduous forests exist (Behling and Lichte, 1997). The record indicates that subtropical grassland vegetation, which is found today in patches on the highlands in southern Brazil, expanded from southern Brazil over more than 750 km to southeastern Brazil from latitudes of about 28°/27°S to at least 20°S. The

Table 4
Estimated areas for major South American forest ecosystems in km^2

Ecosystem/period	Modern	Early Holocene	LGM
Amazon rain forest	5,600,000	4,990,000 (610,000; 12%)	4,030,000 (1,570,000; 39%)
Atlantic rain forest	320,000	260,000 (60,000; 23%)	150,000 (170,000; 113%)
Semideciduous forest (eastern Brazil)	770,000	500,000 (270,000; 54%)	250,000 (520,000; 208%)
Araucaria forest	200,000	20,000 (180,000; 900%)	20,000 (180,000; 900%)

The increase of forest area since the LGM and the early Holocene, compared to the modern area, in km^2 and in %, is shown in brackets.

existing *Araucaria* forest, mostly in the form of small gallery forests in lower elevated regions in southeastern Brazil during the LGM, was replaced by tropical forests. *Araucaria* forest species moved into the upper mountain regions, e.g. in Campos do Jordão (Behling, 1997a).

The area of the *Araucaria* forest was markedly reduced and replaced by grassland. Pollen percentages of *Araucaria angustifolia* itself were in the range of about 1% during glacial and early Holocene periods (e.g. the sites Morro da Igreja and Serra Campos Gerais Behling, 1995a, 1997b). During the late Holocene, before serve logging of *Araucaria* trees, pollen percentages were about 10%. It is suggested that the *Araucaria* forest area was not larger than 10% of the modern potential natural area, that means about 20,000 km^2, during full glacial and early Holocene times.

3.2. Estimated carbon storage increase

Based on the total carbon storage values for different vegetation types (Table 1) and the reconstructed forest areas for the LGM and the early Holocene (Table 3), past carbon storages were calculated. The results are shown in Table 4. The estimated increase of the total carbon storage since the LGM and the early Holocene period is shown in Table 5. For the calculation, the carbon storage of the former vegetation was included. For example, parts of the modern Amazon rain forest area in the north were mostly covered by savanna of the Llanos type and in the south mostly by the cerrado type. The carbon storage of these replaced savanna areas was included in the carbon storage of the area under consideration.

The Amazon rain forest area increased since the LGM to about 39% and since the early Holocene to about 11%, compared to the present-day potential natural forest area. The resulting carbon storage increase is 28.3×10^9 tC (20%) since the LGM and 11.3×10^9 tC (7%) since the early Holocene (Table 6).

The Atlantic rain forest area increased since the LGM by 113% and since the early Holocene by 23% compared to the modern potential natural forest area. The carbon storage increase is 4.9×10^9 tC (55%) since the LGM and 1.1×10^9 tC (13%) since the early Holocene.

The semideciduous forest area of eastern Brazil increased since the LGM by 208% and since the early Holocene by 54%. The carbon storage increase is 6.3×10^9 tC (46%) since the LGM and 3.4×10^9 tC (20.3%) since the early Holocene.

The *Araucaria* forest area of Brazil increased since the LGM and the early Holocene by 900%, compared to present-day potential natural forest area. The resulted carbon storage increase is 3.4×10^9 tC (108%) since the LGM and the early Holocene.

Table 5
Estimated total carbon storage for major South American forest ecosystems in $\times 10^9$ tC

Ecosystem/period	Modern	Early Holocene	LGM
Amazon rain forest	168	156.7	139.7
Atlantic rain forest	13.8	12.2	8.9
Semideciduous forest (eastern Brazil)	20	16.7	13.7
Araucaria forest	6.6	3.2	3.2

Basis for the area under consideration is the modern potential natural forest area.

Table 6
Estimated increase of total carbon storage in $\times 10^9$ tC for major South American forest ecosystems since the LGM and the early Holocene period

Ecosystem/period	Early Holocene	LGM
Amazon rain forest	11.3 (7%)	28.3 (20%)
Atlantic rain forest	1.6 (13%)	4.9 (55%)
Semideciduous forest (eastern Brazil)	3.4 (20%)	6.3 (46%)
Araucaria forest	3.4 (108%)	3.4 (108%)

The increase of total carbon storage since the LGM and the early Holocene is shown in brackets.

4. Discussion and conclusion

The major forest ecosystems of South America, the Amazon rain forest, the Atlantic rain forest, the semideciduous forest of eastern Brazil, and *Araucaria* forest of southern Brazil play an important role in the carbon storage since the LGM. The increase in carbon storage due to forest expansion ranges between about 20% and 100% (Table 5). The results show that also during the Holocene, the carbon storage increase in the tropics was high. The four forest ecosystems under consideration can be seen as a major sink for atmospheric CO_2.

The Amazon rain forest expansion has the highest carbon storage increase since the LGM. The calculated moderate increase can still be higher, if future pollen analytical results document that the Amazon rain forest area was smaller as reconstructed here. The total carbon storage increase by the Amazon rain forest since the early Holocene is remarkable. The much smaller area of the Atlantic rain forest (17.5 times smaller), the semideciduous forest of eastern Brazil (7.3 times), and the Brazilian *Araucaria* forest (28 times) compared to the Amazon rain forest have a relatively significant higher carbon storage increase in percent than the Amazon rain forest (Table 5). Especially, the *Araucaria* forest, which had a marked expansion during the late Holocene, has a very high total carbon storage increase. Here, a grassland biome changed to a forest biome.

The reconstructed maps for the LGM by Adams et al. (1990) and Adams and Post (1999), which were used for the carbon storage estimation, show a marked stronger South American forest reduction especially by the Amazon rain forest than in this study. Modeling experiments of global vegetation patterns show, for tropical South America, a moderate reduction of the Amazon rain forest for the LGM (Prentice et al., 1993). For southeastern Brazil is modeled a marked extension of evergreen/warm-mixed forests, a reduction of the Atlantic rain forest and tropical seasonal forests at the LGM (Prentice et al., 1993). The marked extension of evergreen/warm-mixed forests at the LGM is not supported by pollen records from sites in southeastern Brazil (e.g. Behling and Lichte, 1997; Behling et al., 1998). The new results presented in this paper may precisely estimate the total carbon storage for the four major forest ecosystems of tropical South America.

The intense deforestation and land use during the last century in South America (Harcourt and Sayler, 1996) strongly affected the carbon storage by tropical forests. From the potential natural area remains 90% of the Brazilian Amazon rain forest, only 9% of the Atlantic rain forest and east Brazilian semideciduous forest, and 19% of the *Araucaria* forest. The marked clearance of these tropical forests during the last century released CO_2 to the atmosphere. Ongoing and future deforestation of the Amazon rain forest will contribute to a marked increase of atmospheric CO_2.

On the other hand, the results indicate a high potential of carbon fixation by these tropical forest biomes by reforestation. It is suggested that the reforestation of the former *Araucaria* forest area may contribute to an important reduction of the greenhouse gas CO_2 by terrestrial carbon storage.

This study can be seen as an exercise to reconstruct the history of biomes in more details for a better terrestrial carbon storage estimation using palaeodata. Future studies with more available pollen records, detailed reconstruction of ecosystem areas, and better carbon storage values for different biomes may allow precision of the carbon storage estimation.

Acknowledgements

Jonathan Adams, J. Guiot, and one unknown reviewer are thanked for providing constructive comments on the manuscript. The "Deutsche Forschungsgemeinschaft (DFG)" is acknowledged for the scholarship while writing this paper.

References

Absy, M.L., 1979. A palynological study of Holocene sediments in the Amazon basin. PhD thesis, University of Amsterdam, 86 pp.

Absy, M.L., 1985. Palynology of Amazonia: the history of the forests as revealed by the palynological record. In: Prance, G.T., Lovejoy, T.E. (Eds.), Key Environments of Amazonia. Pergamon, Oxford, pp. 72–82.

Absy, M.L., Van der Hammen, T., 1976. Some palaeoecological data from Rondônia, southern part of the Amazon basin. Acta Amazonica 6, 293–299.

Absy, M.L., Cleef, A.M., Fournier, M., Martin, L., Servant, M., Sifeddine, A., Ferreira da Silva, M., Soubies, F., Suguio, K., Turcq, B., Van der Hammen, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60,000 derniéres anneés. Premiére comparaison avec d'autres régions tropicales. Comptes Rendus de l'Academie des Sciences de Paris 312 (II), 673–678.

Adams, J.M., Post, W.M., 1999. A preliminary estimate of changing calcrete carbon storage on land since the Last Glacial Maximum. Global and Planetary Change 20, 243–256.

Adams, J.M., Faure, H., Faure-Denard, L., McGlade, J.M., Woodward, F.I., 1990. Increases in terrestrial carbon storage form the Last Glacial Maximum to the present. Nature 348, 711–714.

Barberi M., 1994. Paleovegetacao e paleoclima no Quaternário tardio da vereda de Águas Emendadas, DF. Mestrado, University of Brasilia, 93, 110 pp.

Behling, H., 1995a. Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil). Vegetation History and Archaeobotany 4, 127–152.

Behling, H., 1995b. A high resolution Holocene pollen record from Lago do Pires, SE Brazil: vegetation, climate and fire history. Journal of Paleolimnology 14, 253–268.

Behling, H., 1996. First report on new evidence for the occurrence of *Podocarpus* and possible human presence at the mouth of the Amazon during the Late Glacial. Vegetation History and Archaeobotany 5, 241–246.
Behling, H., 1997a. Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro de Itapeva, SE Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 129, 407–422.
Behling, H., 1997b. Late Quaternary vegetation, climate and fire history in the *Araucaria* forest and campos region from Serra Campos Gerais (Paraná), S Brazil. Review of Palaeobotany and Palynology 97, 109–121.
Behling, H., 1998. Late Quaternary vegetational and climatic changes in Brazil. Review of Palaeobotany and Palynology 99, 143–156.
Behling, H., in preparation. Late Quaternary vegetation, climate and fire history from Lagoa Nova in the southeastern Brazilian lowland.
Behling, H., Costa, M.L., 1997. Studies on Holocene tropical vegetation, mangrove and coast environments in the state of Maranhão, NE Brazil. Quaternary of South America and Antarctic Peninsula 10, 93–118.
Behling, H., Costa, M.L., 2000. Holocene environmental changes from the Rio Curuá record in the Caxiuanã region, eastern Amazon Basin. Quaternary Research 53, 369–377.
Behling, H., Hooghiemstra, H., 1998. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. Palaeogeography, Palaeoclimatology, Palaeoecology 139, 251–267.
Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. Journal of Paleolimnology 21, 461–476.
Behling, H., Hooghiemstra, H., 2000. Holocene Amazon rain forest—savanna dynamics and climatic implications: high resolution pollen record Laguna Loma Linda in eastern Colombia. Journal of Quaternary Sciences 15, 687–695.
Behling, H., Hooghiemstra, H., 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons. In: Markgraf, V. (Ed.), Interhemispheric Climate Linkages. Academic Press, London, pp. 307–321.
Behling, H., Lichte, M., 1997. Evidence of dry and cold climatic conditions at glacial times in tropical Southeastern Brazil. Quaternary Research 48 (3), 348–358.
Behling, H., Negelle, R.R.B., 2001. Late Quaternary tropical rain forest and climate dynamics from the Atlantic lowland in southern Brazil. Quaternary Research 56, 383–389.
Behling, H., Lichte, M., Miklos, A.W., 1998. Evidence of a forest free landscape under dry and cold climatic conditions during the last glacial maximum in the Botucatú region (São Paulo State), Southeast Brazil. Quaternary of South America and Antarctic Peninsula 11, 99–110.
Behling, H., Berrio, J.C., Hooghiemstra, H., 1999. Late Quaternary pollen records from the middle Caquetá river basin in central Colombian Amazon. Palaeogeography, Palaeoclimatology, Palaeoecology 145, 193–213.
Behling, H., Arz, H.W., Pätzold, J., Wefer, G., 2001. Late Quaternary vegetational and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104-1. Quaternary Science Reviews 19, 981–994.
Behling, H., Bauermann, S.G., Neves, P.C., 2001. Holocene environmental changes from the São Francisco de Paula region, southern Brazil. Journal of South American Earth Sciences 14, 631–639.
Bush, M.B., 1994. Amazonian speciation: a necessarily complex model. Journal of Biogeography 21, 5–17.
Colinvaux, P.A., 1993. Pleistocene biogeography and diversity in tropical forests of South America. In: Goldblatt, P. (Ed.), Biological Relationships Between Africa and South America. Yale Univ. Press, New Haven, London, pp. 473–499.
Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. Science 274, 85–87.
Crowley, T.J., 1995. Ice age terrestrial carbon changes revisited. Global Biogeochemical Cycle 9, 377–389.
De Oliveira, P.E., 1992. A palynological record of late Quaternary vegetational and climatic change in southeastern Brazil. PhD thesis, The Ohio State University, Columbus, 238 pp.
Ferraz-Vicentini, K.R., Salgado-Labouriau, M.L., 1996. Palynological analysis of a palm swamp in central Brazil. Journal of South American Earth Sciences 9, 207–219.
Fundação S.O.S. Mata Atlântica, 1992. Mata Atlântica. Fundação S.O.S. Mata Atlântica, São Paulo.
Harcourt, C.S., Sayler, J.A. (Eds.), 1996. The conservation atlas of tropical forests. The Americas. Simon and Schuster, New York.
Hooghiemstra, H., 1997. Tropical rain forest versus savanna: two sides of a precious medal? A comment. NWO/Huygenslezing 1997. Netherlands Organization for Scientific Research, The Hague, pp. 31–43.
Hueck, K., 1953. Distribuição e habitat natural do Pinheiro do Paraná (*Araucaria angustifolia*). Bolm. Fac. Filos. Ciênc. Univ. São Paulo, Bot. 10, 1–24.
Hueck, K., 1966. Die Wälder Südamerikas. Fischer, Stuttgart, 422 pp.
Ledru, M.P., 1993. Late Quaternary environmental and climatic changes in central Brazil. Quaternary Research 39, 90–98.
Ledru, M.P., Behling, H., Fournier, M., Martin, L., Servant, M., 1994. Localisation de la forêt d'Araucaria du Brésil au cours de l'Holocène. Implications paléoclimatiques. Comptes Rendus de l'Academie des Sciences de Paris 317, 517–521.
Ledru, M.P., Soares Braga, P.I., Soubiés, F., Fournier, M., Martin, L., Suguio, K., Turcq, B., 1996. The last 50,000 years in the neotropics (southern Brazil): evolution of vegetation and climate. Palaeogeography, Palaeoclimatology, Palaeoecology 123, 239–257.
Mayle, F., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science 290, 2291–2294.
Olson, J.S., Watts, J.A., Allinson, L.J., 1983. Carbon in live vegetation in major world ecosystems. Environmental Sciences Division Publication No. 1997. Oak Ridge National Laboratory, Tennessee.
Parizzi, M.G., Salgado-Labouriau, M.L., Kohler, H.C., 1998. Genesis and environmental history of Lagoa Santa, southeastern Brazil. Holocene 8, 311–321.

Prentice, I.C., Fung, I.Y., 1990. The sensitivity of terrestrial carbon storage to climate change. Nature 346, 48–50.
Prentice, I.C., Sykes, M.T., Lautenschlager, M., Harrison, S.P., Denissenko, O., Bartlein, P.J., 1993. Modelling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. Global Ecology and Biogeography Letters 3, 67–76.
Rinaldi, M., Rull, V., Schubert, C., 1990. Analisis paleoecologico de una turbera en la Gran Sabana (Santa Cruz de Mapauri), Venezuela: resultados preliminares. Acta Cientifica Venezolana 41, 66–68.
Rodriges-Filho, S., Behling, H., Irion, G., Müller, G., 2002. Evidence for lake formation as a response to an inferred Holocene climatic transition in Brazil. Quaternary Research 57, 1–7.
Rull, V., 1991. Contribución a la paleoecologia de Pantepui la Gran Sabana (Guayana Venezolana): clima, biogeografía, y ecología. Scientia Guaianae 2, 1–133.
Salgado-Labouriau, M.L., Casseti, V., Ferraz-Vicentini, K.R., Martin, L., Soubiès, F., Suguio, K., Turcq, B., 1997. Late Quaternary vegetational and climatic changes in cerrado and palm swamp from central Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 128, 215–226.
Salgado-Labouriau, M.L., Barberi, M., Ferraz-Vicentini, K.R., Parizzi, M.G., 1998. A dry climatic event during the late Quaternary of tropical Brazil. Review of Palaeobotany and Palynology 99, 115–129.
Seibert, P., 1996. Farbatlas Südamerika: Landschaft und Vegetation Ulmer, Stuttgart, 288 pp.
Tissot, C., Marius, C., 1992. Holocene evolution of the mangrove ecosystem in French Guiana: a palynological study. In: Singh, K.P., Singh, J.S. (Eds.), Tropical Ecosystems: Ecology and Management. Wiley, New Delhi, pp. 333–347.
Van Campo, E., Guiot, J., Peng, C., 1993. A data-based re-appraisal of the terrestrial carbon budget at the Last Glacial Maximum. Global and Planetary Change 8, 189–201.
Van der Hammen, T., 1963. A palynological study on the Quaternary of British Guyana. Leidse Geologische Mededelingen 29, 126–168.
Van der Hammen, T., Absy, M.L., 1994. Amazonia during the last glacial. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 247–261.
Wijmstra, T.A., 1971. The palynology of the Guiana coastal basin. PhD dissertation, University of Amsterdam, 63 pp.
Wijmstra, T.A., Van der Hammen, T., 1966. Palynological data on the history of tropical savannas in northern South America. Leidse Geologische Mededelingen 38, 71–90.