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Late-glacial and Holocene vegetation history of the Magellanic rain forest in southwestern Patagonia, Chile

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Abstract A ^{14}C -dated high-resolution palaeoenvironmental record from a mire in southern Chile is used to reconstruct the Late-glacial and Holocene vegetation history of the Magellanic rain forest. The Late-glacial environment after around 15400–13500 cal B.P. was dominated by *Gunnera magellanica*, *Nothofagus* species (*dombeyi* type) and Gramineae (Poaceae) indicating an open parkland with cool and damp climatic conditions. At the end of the Late-glacial there was an increase in *G. magellanica* and a decline in *Nothofagus dombeyi* type. This ecological signal is interpreted as a result of a re-advance of the Gran Campo Nevado icefield, caused by either Younger Dryas cooling or a latitudinal shift of the southern Westerlies. After around 11250–10750 cal B.P. *Nothofagus* species, *Drimys winteri* and *Embothrium coccineum* expanded, indicating development of the Magellanic rain forest. At 4254±120 cal B.P. a tephra layer was deposited by the eruption of the Mt. Burney volcano leading to a long-term decline of the *Nothofagus* forest. A primary succession was then initiated, lasting for over 800 years before pre-eruption vegetation patterns redeveloped. In summary, our results indicate the extreme sensitivity of

the Magellanic rain forest to climatic or volcanic impacts and the slow recovery of a mature forest after environmental changes.

Keywords Magellanic rain forest · Primary succession · Volcanic impact · Younger Dryas · Southern Westerlies · Southern Chile

Introduction

On the western side of the Patagonian Andes, the temperate Magellanic rain forest extends from 47°30'S to the southern coast of Tierra del Fuego at 56°S (Veblen et al. 1996). This is the southernmost forest ecosystem on earth and possibly the only one which has been spared the impacts of human civilization until recently. This makes the Magellanic rain forest a unique inventory of a pristine ecosystem, which is an ideal investigation area to study the responses of natural impacts on the environment.

The dominant and sometimes monotypical tree species is *Nothofagus betuloides*, the evergreen southern beech. Annual precipitation of more than 5000 mm on the windward side of the southern Andes (Veblen et al. 1996) supports a vegetation mosaic of *Nothofagus* rain forests interspaced with peat forming mires.

On the western margin of the Magellanic rain forest, wetlands become dominant. This landscape is known as Magellanic moorland and consists of blanket mires and large cushion bogs of *Astelia pumila* and *Donatia fascicularis*. In the coastal zone of the western fjord region of Chile, *Nothofagus* trees are only present in wind protected and better drained locations. In the area of the Magellanic rain forest itself, blanket mires form enclaves of up to a few hectares in size within the *Nothofagus* forest.

In comparison to the Valdivian and northern Patagonian rain forests, the species diversity of the Magellanic rain forest is low (Gajardo 1995; Veblen et al. 1996). Under the canopy of *Nothofagus betuloides* there are other woody species such as *Drimys winteri*, *Maytenus magellanica* and *Desfontainia spinosa*. The forest edges

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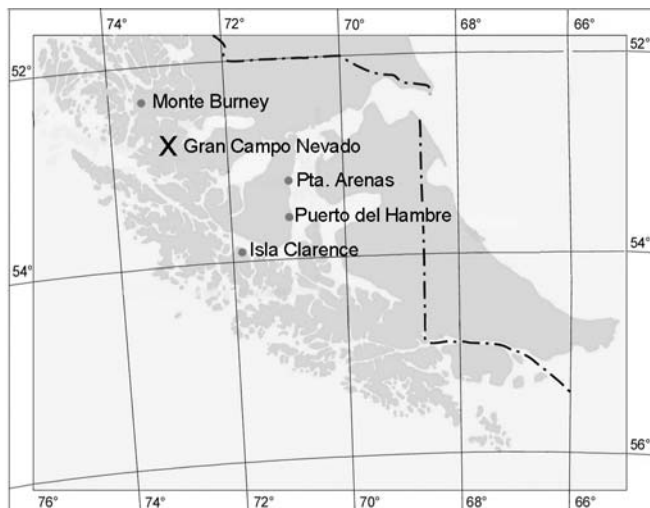


Fig. 1 Survey map of southern South America with the Gran Campo Nevado study area (x) and further palaeoecological investigation sites (modified according to Schneider et al. 2003)

are formed by bushes such as *Embothrium coccineum*, *Berberis illicifolia* or *Fuchsia magellanica*. The conifer *Pilgerodendron uviferum* grows in waterlogged areas. A second *Nothofagus* species, *N. antarctica*, also tolerates these wet conditions close to mires. *N. antarctica* is a typical pioneer plant, also forming the timberline in Patagonia and Tierra del Fuego (Veblen et al. 1983).

The major part of the peat mass of the blanket mires in the zone of the Magellanic rain forest originates from Cyperaceae and Juncaceae species (Juncanae mires). The occurrence of *Astelia pumila* and *Donatia fascicularis* increases towards the west. Empetraceae and Ericaceae (Ericaceae type), represented by *Empetrum rubrum* and *Pernettya mucronata*, mark the transition between mire and forest. The edges of mires and young moraines are covered by the pioneer plant *Gunnera magellanica*.

Although there is a large number of mires and lakes suitable for palaeo-archives in coastal and Andean southern Chile, only a few palaeoenvironmental studies have been performed in the zone of the Magellanic rain forest and the Magellanic moorland (Auer 1958; Heusser 1995a, b, 1998; Heusser et al 2000; Markgraf 1993a, b). In the Magellanic rain forest Auer (1958) analyzed peat profiles from Isla Clarence (T39, T40; Fig. 1), Lago Laina (T41), Bahia Beubasin (T42), Bahia Sarmiento (T43), Fjord Martinez (T44) and Bahia Plüschow (T46). These records are up to now the only references for the areas of western Tierra del Fuego.

In our study we present the first investigation for reconstructing the Late-glacial and Holocene vegetation history of the Magellanic rain forest in superhumid Patagonia.

Material and methods

We examined a mire named Gran Campo-2 (GC-2, S 52°48'37'', W 72°55'46''; 70 m a.s.l.) on Península Muñoz Gamero, east of the Gran Campo Nevado ice field in southern Patagonia, Chile (Fig. 1). The mire vegetation is dominated by *Marsippospermum grandiflorum*, *Schoenus* spp. and *Astelia pumila* among other plants (Fesq-Martin 2003). The occurrence of plants typical of juncoid mires (vegetation dominated by Cyperaceae and Juncaceae), and cushion bogs with *Donatia fascicularis* and *Astelia pumila* indicates the transitional location of the investigation area between the evergreen Magellanic rain forest (to the east) and the Magellanic moorland (to the west).

The mire was surveyed and densely cored to map peat depths (Fesq-Martin 2003). From the deepest area a profile was recovered with a Russian corer. The resulting stratigraphy is given in Fig. 2. The 2.7 m long core consists of peat and a glacial lake sediment at the base. Between 42–50 cm depth a tephra layer was recognized, which originated from a major eruption of the Mt. Burney volcano (Hohner 2002; Kilian et al. 2003) dated to 4254±120 cal B.P. (McCulloch and Davies 2001). Seven samples taken from the GC-2 core have been dated with the AMS radiocarbon technique (Table 1). The ¹⁴C ages were calibrated using INTCAL98 (Stuiver et al. 1998). Results span a calibrated age range between 2800 and 15400 years B.P. (Table 1, Fig. 2).

Samples for pollen analysis were collected continuously each 2 cm of the core, thus each sample covers 2 cm of sediment. The samples were processed using standard techniques (for example Faegri and Iversen 1989). Exotic spores (*Lycopodium*) were added to allow calculation of pollen concentration. Frequencies (%) of trees, shrubs and herbs typically added up to terrestrial pollen sums of 400–900 grains. Pollen of aquatic plants and spores were calculated separately and related to the sum of terrestrial pollen. Identification of pollen and spores is based on reference material (Fesq-Martin 2003) and published keys (Heusser 1971; Markgraf and D'Antoni 1978). Juncaceae and Cyperaceae are summarized as Juncanae type. *Pernettya mucronata* (Ericaceae) and *Empetrum rubrum* (Empetraceae) are combined as Ericaceae type in the text. Plant nomenclature was made with reference to Moore (1983). Charcoal particles larger than 30 µm were counted.

Results

In our palynological analysis we distinguished 26 types of pollen and spores. We classified *Nothofagus* pollen grains as *N. dombeyi* type; differentiation to species level failed. Percentage pollen diagrams and pollen concentration, which were drawn up using EXCEL, are presented in Fig. 3. Based on changes in the frequencies of the pollen types we divided the diagram into three major pollen assemblage zones (PAZ) and eight subzones (Table 2):

PAZ 1 (270–192 cm): Late-glacial (15400–13500 to 11250–10750 cal B.P.), *Gunnera* Biozone I

This zone is dominated by non-arboreal pollen types including *Gunnera magellanica* as well as Gramineae (Poaceae), Compositae (Asteraceae), Ericaceae type and the arboreal pollen of the *Nothofagus dombeyi* type. Mire plants are only recorded in traces, but freshwater aquatics such as *Myriophyllum quitense* and records of testate amoebae (Testaceae) indicate a lake environment. Three radiocarbon dates (Table 1) give a chronology of this profile section, which consists of fine lake sediments.

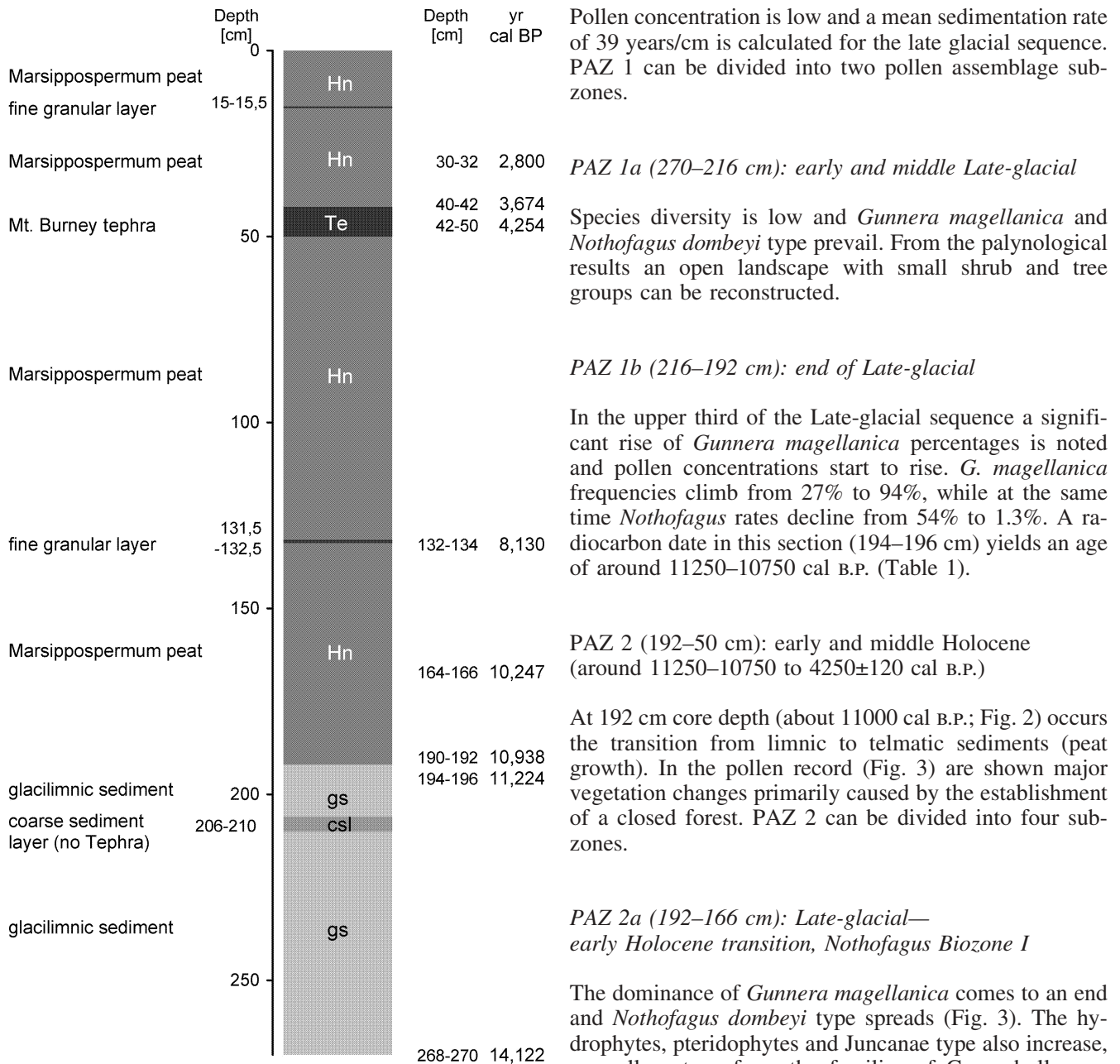


Fig. 2 Stratigraphic log of the GC-2 core (S 52°48'37", W 72°55'46"; 70 m a.s.l.). Hn: Marsippospermum peat, Te: Mt. Burney Tephra, gs: glacilimnic sediment, csl: coarse sediment layer

Table 1 AMS ^{14}C dates and calibrated ages of selected samples from the GC-2 core with the maximum-minimum 2σ ranges

Core	Depth (cm)	^{14}C age	Calibrated age, B.P.	Maximum	Minimum
				2σ B.P.	2σ B.P.
GC2	30–32	2,618±32	2,800	2,828	2,786
GC2	40–42	3,382±44	3,674	3,855	3,524
GC2	132–134	7,288±67	8,130	8,332	7,997
GC2	164–166	9,024±80	10,247	10,450	9,944
GC2	190–192	9,659±83	10,938	11,250	10,753
GC2	194–196	9,740±42	11,224	11,276	11,166
GC2	268–270	12,017±203	14,122	15,431	13,528

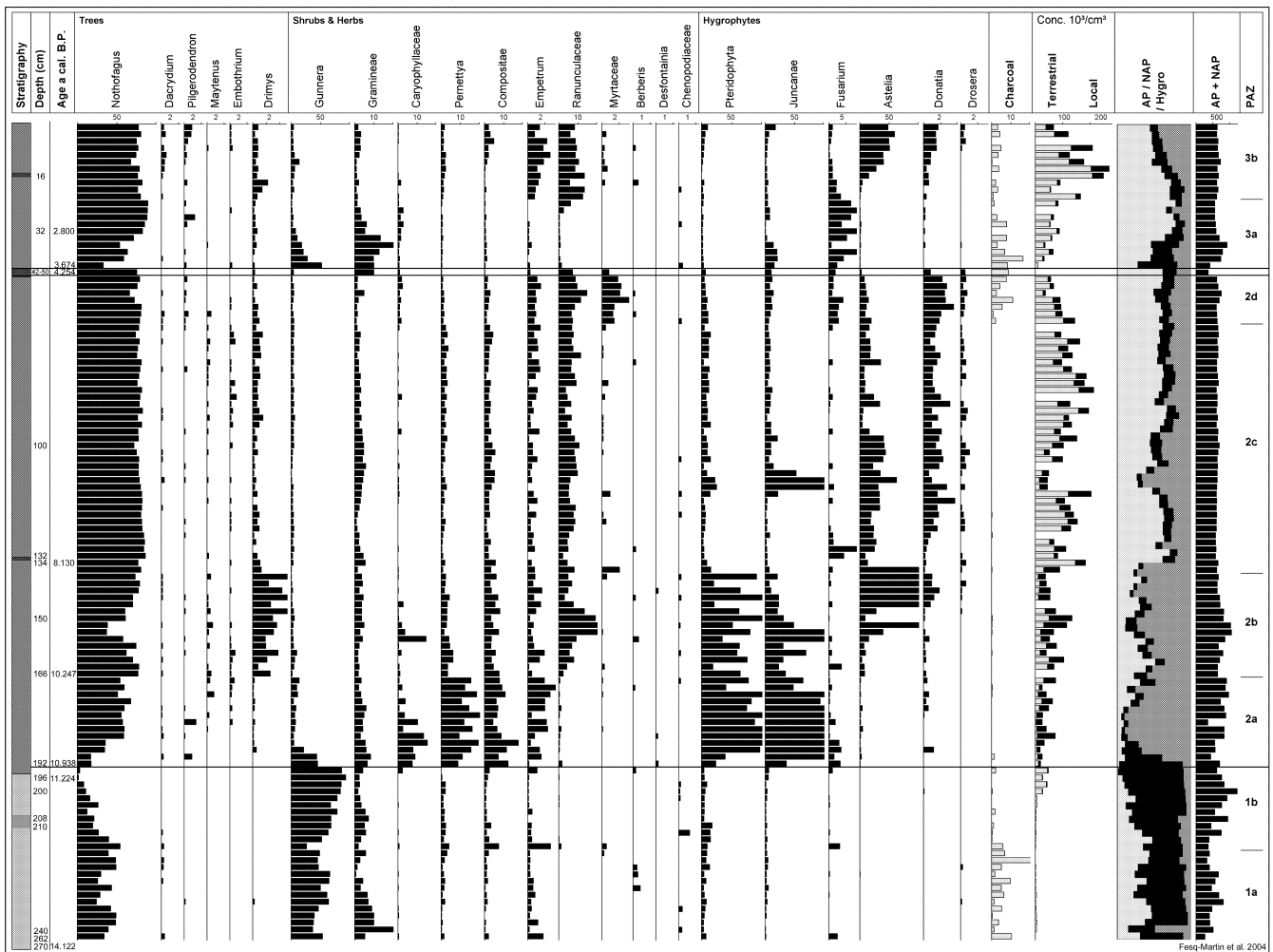


Fig. 3 GC-2 pollen diagram. 26 types of pollen and spores and their frequencies (horizontal bars), calculated in relation to the sums of all terrestrial pollen grains. Not shown are *Fuchsia mag-*

ellanica, *Ribes magellanicum* and *Myriophyllum quitense*, because of low frequencies and concentrations. Stratigraphic details see Fig. 2

Table 2 Pollen assemblage zones (PAZ) and subzones referring to the GC-2 pollen diagram (Fig. 3)

Pollen Assemblage zones	Characteristic pollen types	Depth (cm)
GC-2-PAZ-1a	<i>Gunnera</i> — <i>Nothofagus</i> —Gramineae	270–216
GC-2-PAZ-1b	<i>Gunnera</i> —Gramineae	216–192
GC-2-PAZ-2a	<i>Nothofagus</i> —Ericaceae—Compositae—Caryophyllaceae— Juncanae—Pteridophyta	192–166
GC-2-PAZ-2b	<i>Nothofagus</i> — <i>Drimys</i> —Ranunculaceae— <i>Astelia</i>	166–136
GC-2-PAZ-2c	<i>Nothofagus</i> —Ranunculaceae— <i>Astelia</i> — <i>Donatia</i>	136–64
GC-2-PAZ-2d	<i>Nothofagus</i> —Ranunculaceae—Myrtaceae— <i>Donatia</i>	64–50
Mt. Burney tephra		42–50
GC-2-PAZ-3a	<i>Nothofagus</i> — <i>Gunnera</i> —Gramineae	42–22
GC-2-PAZ-3b	<i>Nothofagus</i> —Ranunculaceae— <i>Empetrum</i> — <i>Astelia</i> — <i>Donatia</i>	22–0

The structure of the *Nothofagus* forest must have been relatively open to allow the existence of a shrub and herb layer. The establishment of the Magellanic rain forest is indicated by the first occurrences of *Drimys winteri*, *Embothrium coccineum* and *Maytenus magellanica*. These three species are typical floral components of the Magellanic rain forest (Moore 1983; Veblen et al. 1983; Donoso 1993). Two ^{14}C dates at 190 cm and

166 cm confirm the development of the Magellanic rain forest in our area between around 11250–10750 cal B.P. and 10450–9940 cal B.P. (Table 1).

The pollen curve of the Juncanae type and the values of pteridophyte spores reach their Holocene maximum. This shows the development of a minerotrophic juncoid mire. The components of the cushion bog vegetation

communities including *Astelia pumila* and *Donatia fascicularis* are only represented by very low values.

PAZ 2b (166–136 cm): *Drimys* Biozone

During this interval pollen concentration increases and the high frequencies of *Drimys winteri* are most noteworthy. The high *D. winteri* values lasted for over 2000 years as indicated by two radiocarbon dates (Table 1) at 166 cm and 132 cm (around 10450–9940 and 8330–8000 cal B.P.). The *Nothofagus* values show a small decline, pointing towards the existence of a *Drimys winteri*-enriched Magellanic rain forest.

We can also detect an increase of taxa in the Ranunculaceae family and a reduction of Ericaceae type and Compositae percentages, which indicates the existence of a herb layer. The reduction of the shrub layer was probably caused by the expansion of *Drimys winteri*.

At this point *Astelia pumila* is expanding strongly and *Donatia fascicularis* levels rise. This represents the expansion of cushion bog communities in the surroundings of the site. Also *Drosera uniflora*, a typical bog plant, is registered for the first time. There is a parallel decline of juncoid mire communities as indicated by the decreasing values of Juncanae and Pteridophyta types.

PAZ 2c (136–64 cm): *Nothofagus* Biozone II

Nothofagus dombeyi type pollen dominates this zone, with the highest pollen concentration in our record. Low proportions of *Podocarpaceae*, *Maytenus magellanica*, *Embothrium coccineum* and *Drimys winteri* were found too. We reconstruct a fully developed rain forest ecosystem probably represented by *Nothofagus betuloides*, a highly competitive species (Donoso 1993; Pisano 1978).

Ranunculaceae pollen is still present with substantial percentages and Myrtaceae pollen becomes more frequent. The moorland types *Donatia fascicularis* and *Drosera uniflora* indicate the continuous presence of nutrient-poor mires. The *Astelia pumila* pollen curve demonstrates a distinct decline from its pre-8000 cal B.P. plateau, but remains continuously present. Apart of one single peak of the Juncanae type, this assemblage subzone is characterized by uniformity.

The origin of a fine granular layer at 131.5–132.5 cm (Fig. 2) at the beginning of PAZ 2c is unclear, but probably caused by a tephra (volcanic ash) deposition of limited dimensions. An impact on the vegetation dynamics is not recognized.

PAZ 2d (64–50 cm): *Nothofagus* Biozone III

This subzone shows the same characteristics as subzone 2c except for an increase in Myrtaceae pollen and charcoal particles. The values of *Donatia fascicularis* also increase slightly.

PAZ 3 (50–0 cm): Post-Mt. Burney phase (4254±120–0 cal B.P.)

The Mt. Burney tephra (Fig. 2) is a layer of 8 cm thickness (50–42 cm) resulting from an eruption at 4254±120 cal B.P. (Hohner 2002; Kilian et al. 2003). PAZ 3 can be divided into 2 subzones.

PAZ 3a (42–22 cm): *Gunnera* Biozone II

The first peat sample (40–42 cm) directly above the Mt. Burney tephra was radiocarbon dated to around 3850–3520 cal B.P. (Table 1, Fig. 2). This indicates a hiatus in peat growth of over 500 years after the Mt. Burney eruption. The frequency of *Gunnera magellanica* pollen rises from 4% below the tephra layer to a maximum of 52.5% at the restart of peat growth (Fig. 3). The *G. magellanica* maximum is accompanied by a higher frequency of Gramineae pollen. The percentage of *Nothofagus dombeyi* type pollen drops from 79.4% just before the Mt. Burney eruption to a post-volcanic level of 33.3%. Likewise *Drosera uniflora* and pollen from the families of Ranunculaceae and Myrtaceae nearly disappear. Cushion bog vegetation represented by *Astelia pumila* and *Donatia fascicularis* decreases to its lowest Holocene level. On the other hand, the values of Juncanae type show an increase after the volcanic disturbance.

Nothofagus dombeyi type pollen increases gradually, showing percentages of over 89% at the end of the PAZ 3a subzone. Neither Ranunculaceae nor Myrtaceae pollen reach levels comparable to those in assemblage zones PAZ 2c and 2d. The end of the *Gunnera magellanica* peak (30–32 cm) is radiocarbon dated to around 2830–2790 cal B.P. This defines a time span of more than 800 years for increased *G. magellanica* frequencies.

PAZ 3b (22–0 cm): *Nothofagus* Biozone IV

In the uppermost 20 cm of the GC-2 profile the pollen percentages of Ranunculaceae, Ericaceae type, Compositae, Myrtaceae and the species *Drimys winteri*, *Astelia pumila*, *Donatia fascicularis* and *Drosera uniflora* rise again. *A. pumila* almost reaches values comparable to those of its early maximum in PAZ 2b. The cushion bog vegetation appeared relatively late in the Holocene and shows the longest interval for post-volcanic regeneration.

After a time span of over 1400 years the processes of primary succession were completed, and not only the Magellanic rain forest but also the mire ecosystem then reached conditions comparable to those in the mid-Holocene prior to the devastating Mt. Burney eruption.

The origin of a fine granular layer (15–15.5 cm) is unclear, possibly caused by a weak tephra deposition from the Mt. Burney volcano. As a potential consequence a minor increase of *Gunnera magellanica* (14%, 10–12 cm) is observed, but in comparison with the vegetation

dynamics of PAZ 3a this fluctuation does not appear significant.

Discussion

The Magellanic rain forest (47°30'–56°S) is the southernmost forest ecosystem in the world. During the Late-glacial period (PAZ 1a) the vegetation was rich in *Gunnera magellanica*, *Nothofagus* spp. (perhaps *Nothofagus antarctica*) and Gramineae, indicating an open landscape with small groups of shrubs and trees. The early presence of the *Nothofagus* genus points to nearby glacial refugia (Markgraf 1993b; Markgraf et al. 1996; Villagran et al. 1995). It is not clear which *Nothofagus* species is involved, but probably *N. antarctica* and *N. betuloides* colonized the deglaciated land first. This is supported by modern analogues in recently de-glaciated areas of southern Chile (Donoso 1993). All this indicates a cool but relatively moist climate.

The strong presence of *Gunnera magellanica* in the Late-glacial vegetation marks a substantial difference to the reconstructed vegetation of the areas further east of the southern Andes. On Peninsula Brunswick (Heusser et al. 2000; McCulloch and Davies 2001) and in southern Tierra del Fuego (Markgraf et al. 1996) a vegetation rich in Ericaceae and Gramineae predominated in the Late-glacial, indicating a dryer climate in these areas compared to the western Chilean Archipelago. This suggests that in the early and middle Late-glacial a west-east precipitation gradient was already established. The relatively high charcoal percentages in the PAZ 1a probably originate from fires to the east where vegetation suggests aridity (Markgraf et al. 1996). This would further underline the existence of a precipitation gradient from west to east.

At the end of the Late-glacial (PAZ 1b), before around 11280–11170 cal B.P., we record an expansion of *Gunnera magellanica* and a decline in *Nothofagus dombeyi* type. This change in pollen spectra points to an increased openness of the landscape, and we relate this to a readvance of the Gran Campo Nevado ice field. The trigger for this glacier fluctuation could have been either a cooling synchronous with the end of the Younger Dryas (Heusser 1995a; Heusser et al. 2000; Stebich 1999), or an increase in precipitation caused by a shift of the southern Westerlies (Heusser 1989; Markgraf 1989; McCulloch and Davies 2001). In view of the second possibility, no clear proof for a climatic signal comparable to the north Atlantic Younger Dryas can be deduced from our palynological data.

In the early Holocene (PAZ 2a) the establishment of the Magellanic rain forest (*Nothofagus* Biozone I) is indicated by the first occurrences of *Drimys winteri*, *Embothrium coccineum* and *Maytenus magellanica*. These three species are typical floral components of the Magellanic rain forest (Moore 1983; Veblen et al. 1983; Donoso 1993). Two ¹⁴C dates at 190 cm and 166 cm confirm the development of the Magellanic rain forest in our area between around 11250–10750 cal B.P. and about

10450–9940 cal B.P. This compares well with the dates obtained in Puerto del Hambre (Fig. 1) (McCulloch and Davies 2001; Heusser 1995a) and in southern Tierra del Fuego (Markgraf et al. 1996).

The high *Drimys winteri* values in PAZ 2b, lasting for over 2000 years, can be interpreted as a signal for synecological dynamics in forest succession. The *Nothofagus* values show a small decline, pointing towards the existence of a *D. winteri*-enriched Magellanic rain forest (*Drimys* Biozone). High *D. winteri* values are also recorded in the pollen diagram T 41 from Isla Clarence (Fig. 3) by Auer (1958), which shows a rise of the *D. winteri* curve parallel to the *Gunnera magellanica* decline in the early Holocene.

The rising charcoal curve in PAZ 2d probably reflects fires occurring in forests or steppe environments to the east of the Andes. Fires in the evergreen Magellanic rain forest are very unlikely and the occasionally occurring easterly winds in the Gran Campo Nevado area (Schneider et al. 2003) are the most likely source of the charcoal particles registered in our archive.

The rain forest assemblage of *Nothofagus* Biozones II–III shows a remarkable stability until 4254±120 cal B.P., when the deposition of a tephra layer from Mt. Burney caused long lasting environmental change.

We interpret these significant vegetation changes in PAZ 3a as a result of the tephra deposition in the area, which together with associated precipitation of volcanic volatiles must have led to a partial or complete destruction of the *Nothofagus* forest, creating habitats for pioneer plants like *Gunnera magellanica* and Gramineae species. The rise of *G. magellanica* is interpreted as an indicator for processes of primary succession after the tephra deposition, representing recovery of the ecosystem. The dynamics are comparable with the rise of *G. magellanica* in the latest Late-glacial period (PAZ 1b). The particular role of *G. magellanica* in processes of primary succession can be attributed to its independence of soil related nitrogen. Several species of the genus *Gunnera* are known to have a symbiotic relationship with *Nostoc* Cyanobacteria (Schmidt 1991). In our study it was possible to document these *Gunnera-Nostoc* symbioses (Fesq-Martin 2003), which are able to fix atmospheric nitrogen, even in *G. magellanica* plants from the Gran Campo Nevada area.

After a time span of over 1400 years the processes of primary succession were completed and not only the Magellanic rain forest but also the mire ecosystem again reached conditions comparable to those in the mid Holocene prior to the devastating Mt. Burney eruption.

The cushion bog vegetation appeared relatively late in the Holocene and shows the longest interval for post-volcanic regeneration (PAZ 3b). Therefore we consider these floral elements of the Magellanic moorlands to be especially sensitive indicators of environmental changes.

Regeneration of the Magellanic rain forest to the earlier mid Holocene conditions took until around 2830–2790 cal B.P., underlining the long phase of succession of this ecosystem in this extremely damp, cool and windy region.

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