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Effects of beaver (*Castor canadensis*) on the nutrient dynamics of the Southern Beech forest of Tierra del Fuego (Argentina)

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Abstract. *Alterations induced by beaver (*Castor canadensis*) provide a striking example of how the animals influence forest ecosystems. Beavers modify stream morphology and hydrology by removing trees, building dams and retaining sediment and organic material in the stream channel. We studied the effect of beaver impoundments on nutrient dynamics of the native forest (*Nothofagus sp.*) of Isla Grande of Tierra del Fuego (Argentina), by comparing sediments and pond waters of beaver altered and unaltered sites (controls) over a 3 year period. Concentration of organic carbon, nitrogen, phosphorous, and inorganic nitrogen (nitrate --N and nitrite--N) were significantly greater in sediments of beaver sites. Also nitrites and nitrates were higher in beaver pond waters.*

Resumen. *Las alteraciones provocadas por las actividades del castor (*Castor canadensis*) resultan un ejemplo claro de cómo los animales influencian el ecosistema forestal. Los castores modifican la morfología e hidrología de las cursos de agua por la remoción de árboles, construcción de diques y retención de sedimento y materia orgánica en la cuenca. Nosotros estudiamos el efecto de los endicamientos producidos por el castor sobre la dinámica de nutrientes del bosque de* Nothofagus *de Tierra del Fuego (Argentina) comparando sedimentos y agua de estanques de sitios alterados por castor y no alterados (controles) durante un periodo de 3 años. Las concentraciones de carbono, nitrógeno orgánico e inorgánico (N--nitrato y N--nitrito) y fósforo fueron significativamente mayores en los sedimentos de sitios alterados. Tambien las concentraciones de nitratos y nitritos fueron significativamente más altas en aguas de estanques de castor.*

Introduction

Animals have an important influence on the flow of energy and materials in ecosystems (Botkin et al. 1981, Naiman 1988, Brown 1995). Beaver, *Castor canadensis,* is considered one of the most important natural agents of alteration as well as a keystone species (Paine 1966). Beaver alter stream ecosystems in several ways mainly by building dams and cutting trees. Hydrological changes, nutrient cycling, and decomposition processes are the. most evident reported effects of beaver activity on the native forests of the northern hemisphere (Naiman et al. 1988, Johnston and Naiman 1990, Smith et al. 1991). However, the influence of beaver on undisturbed austral ecosystems where they were introduced for pelt production is not well known.

In 1946, 25 mating pairs of *Castor canadensis* trapped in Canada were introduced on the Isla Grande of Tierra del Fuego, Argentina, in an effort to promote fur exploitation. The absence of most natural predators, laws regulating hunting and the abundance of forage and habitats, led to a rapid increase of the population. Density estimations in extensively colonized habitats showed 0.7 active colonies per km^2 (Lizarralde 1993). Beaver area of colonization comprises not only the whole Isla Grande, but also some Chilean islands of the Archipelago of Tierra del Fuego with a geographical range of about 70000 km^2. Previous data also indicated that demographic expansion of beaver caused environmental alterations A me riparian systems of the southern beech forest (Lizarralde et al. 1989).

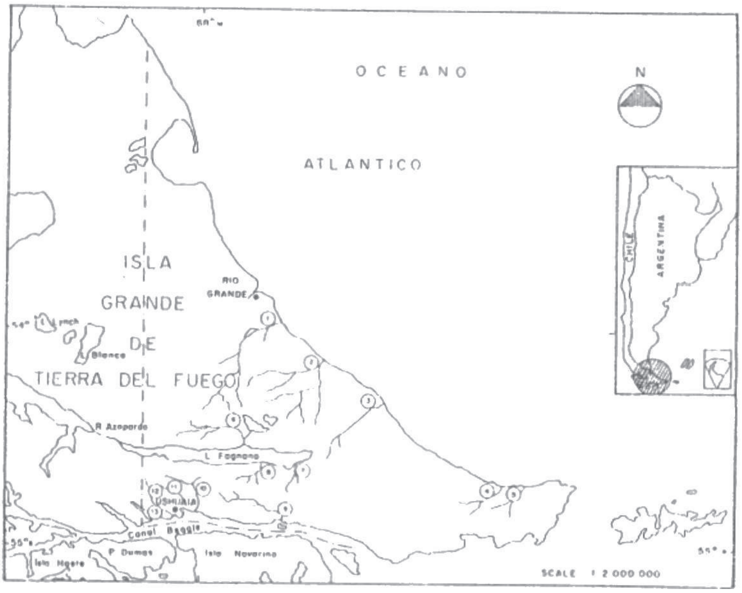

Figure 1. Location of sampling sites in the main basins of Isla Grande.

This paper examines the dynamics of beaver impoundments in Tierra del Fuego to understand the role beaver play in a pristine ecosystem. We expect to find major effects on the nutrient cycles in active colony sites as well as in areas abandoned by beaver. The objective of the present study was to estimate the accumulation of principal organic elements (carbon, nitrogen, and phosphorus) and inorganic compounds (nitrate, nitrite, and ammonium) in beaver ponds (altered) and in unaltered riffles of the *Nothofagus* forest.

Materials and Methods

Study area

The study was conducted on the main drainage basins of Isla Grande (52°-56° S) at the southernmost tip of South America (Archipelago of Tierra del Fuego) (Figure 1). Most of the study area was described by Lizarralde (1993). Isla Grande has a glacial topography as a consequence of Quaternary glacial advances in the Holocene. The relief shows the main Andes Cordillera to the South and low lying Patagonian plains with smooth undulations to the North of the island. Insular conditions and the Antarctic influence result in a cold-temperate climate (Pisano 1981). Annual mean temperature is about 5° C. The mean temperatures in summer and winter are 10° C and 0° C respectively (Burgos 1985).

Roughly 31 % of the island is covered by a native subantarctic forest typical of the montane rainforest of the Andes. The forest is mostly made up of deciduous beech *Nothofagus pumilio* (lenga) and the evergreen beech *Nothofagus betuloides* (guindo). Shrubs such as *Pernettya mucronata* (chaura), *Berberis ilicifolia* (michay) and *Chiliotrichum diffusum* (mata negra), and graminoids *Gummera, Marsippospermum* and *Juncus* grow in riparian areas. *N. betuloides is* associated with hydromorphous soils and *N.pumilio is* restricted to well drained podsoles and acid forest soils and forms native stands alternating with *Sphagnum* bogs (Moore 1983).

Sampling procedure and chemical analysis

The contents of principal organic elements and inorganic compounds of 50 sediments (n=32 and n=18 from beaver and control sites respectively) and 60 pond-riffle water samples (n=39 and n=21 from beaver and control sites respectively) were examined over a 3 year period. Sediment and pond water from beaver altered sites were seasonally sampled from stream sections. Additional unaltered control sites, from riffles or watercourses with no history of beaver, were also sampled (Figure 1). Each site (altered and unaltered) was chosen according to habitat type, stored organic material, seasonal hydrologic regime, dominant vegetation and no evidence of human disturbance.

Sediment and water samples were collected from each of the sites during the ice free period (October to May) of 1991, 1992 and 1993. Sediment cores of about 1,000 - 2,000 g were taken in the ponds behind dams (altered sites) or riparian zones of unaltered sites from 10 to 20 cm depth and stored at -20° C in plastic bags. Then they were melted, weighed and homogenized. Concentrations of total organic carbon (C), organic nitrogen (N), organic phosphorus (P), nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+) and phosphate (PO_4) were determined.

Organic carbon was extracted using the modified Walkley Black method (Etchevehere 1976). Organic nitrogen was determined on air dried soil by Kjeldahl method (Brener and Mulvaney 1982). To estimate total P, the sample was extracted with hydrochloric acid (HCI and $HClO_4$) then analyzed with the colorimetric method. Nitrite--N, nitrate--N and ammonium--N, were analyzed by the Keeney and Nelson (1982) methods, after 2M KCL extraction. Ammonium was distilled with MgO from the extract. Nitrite and nitrate were extracted by distillation, reduction in cadmium column and the modified Griess Ilosvay colorimetric method. Inorganic phosphates were estimated by colorimetry and organic phosphates were calculated by difference.

Water samples (500 cm^3) from beaver ponds and unaltered riffles were collected at 10 cm depth in plastic bottles and stored at 4°C until standard analysis. Carbonate and bicarbonate (volumetry and titrated with 0.05N H_2SO_4), chloride by volumetry and titrated with $Hg(NO_3)_2$, sulfate (determined by $BaC1_2$ Tween 80 solution), calcium and magnesium (determined by 0.01N EDTA), sodium and potassium (flame photometry). Nitrate (cadmium reduction and modified Griess-ilosvay methods) and nitrite (colorimetric method) were determined with HACH NutriVer 3 Kit. Sediment and water pH was determined with a Beckman pH meter.

Non-parametric Kruskal Wallys one way analysis of variance (ANOVA) was used to test for significant differences ($P<0.01$ and $P<0.05$) between altered and control sites (Sokal and Rohlf 1981, BMDP microcomputer software, BMDP Statistical Software Ltd. Ireland Version 7.0).

Results and Discussion

Standing stocks of principal elements differed greatly between unaltered and beaver-altered sites. Mean organic carbon (C), organic nitrogen (N), organic phosphorus (P) and inorganic nitrogen (NO_2^---N and NO_3^---N) were significantly greater in beaver sites (Table 1). Pond water had significantly greater concentration of nitrite, nitrate and potassium than control water (Table 2). In contrast, bicarbonate. concentration was higher in riffles. All other water variables were not significantly different between altered and unaltered sites. Values of pH showed no differences between beaver and control study sites (Table 1 and 2).

These effects induced by beaver could be considered as major factors influencing the processes of nutrient transformation in southern beech forest. Theoretically, these effects would result from modifications in soil aeration and the subsequent alteration in the aerobic.-anaerobic conditions of stream channel modified by beaver. However, the real interaction between aerobiosis and anaerobiosis conditions can not be answered at present. All of these beaver events are of primary importance to microbiological processes such as nitrogen mineralization (Patrick 1982), organic carbon decomposition (Kilham and Alexander 1984) and phosphorus availability (Fabre 1988). Beaver impoundments appear to cause less alteration of ecosystem level processes in wetlands than in uplands because wetland soil and vegetation were already render saturated conditions before impoundment (Naiman et al. 1986).

1n particular, modifications of the aquatic and terrestrial biotic composition were observed in the southern beech forest. Clear cutting by beaver in riparian forest dominated by deciduous (*Nothofagus pumilio*) or evergreen (*Nothofagus betuloides*) species promoted the formation of grasslands with high productivity probably due to increased light, organic material, mud humidity (Lizarralde et al. 1989). Submerged vegetation and algae (*Diatoma, Cyanophyta, and Clorophyta*), *indicators of* a high nitrogen content, were also identified in beaver sites (Lizarralde 1993). It was also noted that these environments are suitable for introduced sahmonid fish species (*Salmo truttafario*, *Salvenfnus fontinalis,* and *Onchorrychus mybis*) and that. they contained invertebrate

Table 1. Mean concentration of principal organic elements and inorganic compounds in sediments of beaver-altered and control sites.

	Beaver sites (n=32)		Control sites (n=18)		
	Mean	SD	Mean	SD	P
pH	5.37	0.50	5.32	0.32	0.40
C (%)	14.50	11.92	2.18	2.46	0.0001
N (%)	0.73	0.57	0.26	0.21	0.0006
P (ppm)	179.91	136.59	96.66	60.28	0.02
NO_3-N (ppm)	35.07	64.68	3.03	2.97	0.0004
NO_2-N (ppm)	10.03	14.04	0.40	0.30	0.0001
PO_4 (ppm)	926.66	641.00	560.0	344.95	0.18
NH_4 (ppm)	51.52	70.19	-	-	-

Table 2. Mean concentration (mg/L) of principal organic elements and inorganic compounds in pond water (beaver) and riffle (control) sites.

	Beaver sites (n=39)		Control sites (n=21)		
	Mean	SD	Mean	SD	P
pH	7.34	1.36	7.91	1.14	0.41
Carbonate	1.53	3.01	3.21	4.37	0.09
Chloride	12.99	11.27	7.49	2.48	0.43
Sulfate	5.62	7.66	3.96	3.09	0.83
Nitrite	0.11	0.20	0.01	0.02	0.009
Nitrate	2.18	2.9	0.26	0.24	0.004
Calcium	8.08	6.14	9.07	5.21	0.36
Magnesium	1.46	1.59	1.70	1.59	0.64
Sodium	6.36	6.07	3.64	5.81	0.11
Potassium	0.54	0.44	0.27	0.28	0.009

communities typical of slow water habitats. In addition, they became the nesting places of a number of migratory birds (Lizarralde et al. unpublished observations).

Basically, our results indicate that beaver-altered sites had higher levels of organic and inorganic nitrogen (NO_2^---N, NO_3^- --N) suggesting that seasonal hydrologic changes could be affecting nitrification and denitrification and also resulted in accumulated organic carbon and phosphorus in the stream channel. In consequence, by changing the hydrology regime, beaver alter the character of stream channels when compared with unmodified watercourses. Our data also suggest that beaver ponds may be considered as sources of essential nutrients (P and N) and carbon. Unfortunately no specific information documenting the turnover times for carbon and essential nutrients in southern beech forest has been reported and specific studies will be necessary. In general, slow decomposition processes in cold boreal regions also result in long-term storage of carbon, phosphorus, and nitrogen (Pastor 1986, Francis et al. 1985, Pinay and Naiman 1991). For instance, a standing stock of carbon in a riffle has been reported to be replaced every 24 years as compared with 161 years for the beaver ponds (Naiman et al. 1986).

These and other aspects of the environmental processes induced by beaver on the native beech forest of Tierra del Fuego remain to be studied. The southern population of *Castor canadensis* is an example of an introduced species that rapidly exploited the environment in a new habitat and future research is required.

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